

3



chapter three

Animal Architecture



New Designs for Living

Zoologists today recognize 32 phyla of multicellular animals, each phylum characterized by a distinctive body plan and array of biological properties that set it apart from all other phyla. Nearly all are the survivors of perhaps 100 phyla that were generated 600 million years ago during the Cambrian explosion, the most important evolutionary event in the history of animal life. Within the space of a few million years virtually all of the major body plans that we see today, together with many other novel plans that we know only from the fossil record, were established. Entering a world sparse in species and mostly free of competition, these new life forms began widespread experimentation, producing new themes in animal architecture. Nothing since then has equaled the Cambrian explosion. Later bursts of speciation that followed major extinction events produced only variations on established themes.

Once forged, a major body plan becomes a limiting determinant of body form for descendants of that ancestral line. Molluscs beget only molluscs and birds beget only birds, nothing else. Despite the appearance of structural and functional adaptations for distinctive ways of life, the evolution of new forms always develops within the architectural constraints of the phylum's ancestral pattern. This is why we shall never see molluscs that fly or birds confined within a protective shell.

Cnidarian polyps have radial symmetry and cell-tissue grade of organization, (*Dendronephthya* sp.).

The English satirist Samuel Butler proclaimed that the human body was merely “a pair of pincers set over a bellows and a stewpan and the whole thing fixed upon stilts.” While human attitudes toward the human body are distinctly ambivalent, most people less cynical than Butler would agree that the body is a triumph of intricate, living architecture. Less obvious, perhaps, is that humans and most other animals share an intrinsic material design and fundamental functional plan despite vast differences in structural complexity. This essential uniformity of biological organization derives from the common ancestry of animals and from their basic cellular construction. In this chapter, we will consider the limited number of body plans that underlie the diversity of animal form and examine some of the common architectural themes that animals share.

The Hierarchical Organization of Animal Complexity

Among the different metazoan groups, we can recognize five major grades of organization (table 3.1). Each grade is more complex than the preceding one and builds upon it in a hierarchical manner.

The unicellular protozoan groups are the simplest animal-like organisms. They are nonetheless complete organisms that perform all basic functions of life as seen in more complex animals. Within confines of their cell, they show remarkable organization and division of labor, possessing distinct supportive structures, locomotor devices, fibrils, and simple sensory structures. The diversity observed among unicellular organisms is achieved by varying the architectural patterns of subcellular structures, organelles, and the cell as a whole (see Chapter 5).

Metazoa, or multicellular animals, evolved greater structural complexity by combining cells into larger units. A metazoan cell is a specialized part of the whole organism and, unlike a protozoan cell, it is not capable of independent existence. Cells of a multicellular organism are specialized for performing the various tasks accomplished by subcellular elements in unicellular forms. The simplest metazoans show the **cellular** grade of organization in which cells demonstrate division of labor but are not strongly associated to perform a specific collective function (table 3.1). In the more complex **tissue** grade, similar cells are grouped together and perform their common functions as a highly coordinated unit. In animals of the tissue-organ grade of organization, tissues are assembled into still larger functional units called **organs**. Usually one type of tissue carries the burden of an organ’s chief function, as muscle tissue does in the heart; other tissues—epithelial, connective, and nervous—perform supportive roles. The chief functional cells of an organ are called its **parenchyma** (pa-ren´ka-ma; Gr. *para*, beside, + *enchyma*, infusion). The supportive tissues are its **stroma** (Gr. bedding). For instance, in the vertebrate pancreas the secreting cells are the parenchyma; the capsule and connective tissue framework represent the stroma.

Most metazoa (nemertean and all more structurally complex phyla) have an additional level of complexity in which different organs operate together as **organ systems**. Eleven different kinds of organ systems are observed in metazoans: skeletal, muscular, integumentary, digestive, respiratory, circulatory, excretory, nervous, endocrine, immune, and reproductive. The great evolutionary diversity of these organ systems is covered in Chapters 5–20.

Complexity and Body Size

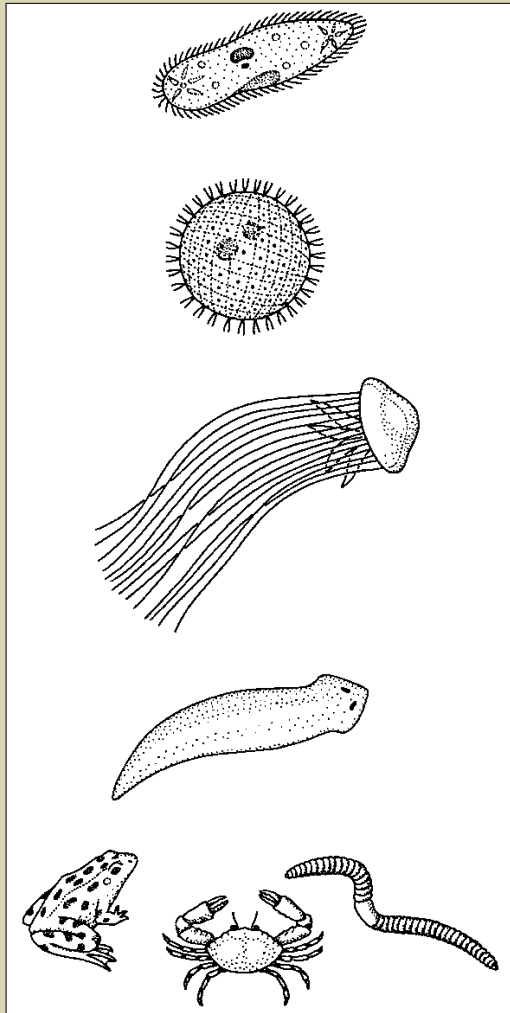
The opening essay (p. 51) suggests that size is a major consideration in the design of animals. The most complex grades of metazoan organization permit and to some extent even promote evolution of large body size (figure 3.1). Large size confers several important physical and ecological consequences for an organism. As animals become larger, the body surface increases much more slowly than body volume because surface area increases as the square of body length (length^2), whereas volume (and therefore mass) increases as the cube of body length (length^3). In other words, a large animal will have less surface area relative to its volume than will a small animal of the same shape. The surface area of a large animal may be inadequate for respiration and nutrition by cells located deep within the body. There are two possible solutions to this problem. One solution is to fold or invaginate the body surface to increase surface area or, as exploited by flatworms, flatten the body into a ribbon or disc so that no internal space is far from the surface. This solution allows the body to become large without internal complexity. However, most large animals adopted a second solution; they developed internal transport systems to shuttle nutrients, gases, and waste products between the cells and the external environment.

Larger size buffers an animal against environmental fluctuations; it provides greater protection against predation and enhances offensive tactics, and it permits a more efficient use of metabolic energy. A large mammal uses more oxygen than a small mammal, but the cost of maintaining its body temperature is less per gram of weight for a large mammal than for a small one. Large animals also can move at less energy cost than can small animals. A large mammal uses more oxygen in running than a small mammal, but energy cost of moving 1 g of its body over a given distance is much less for a large mammal than for a small one (figure 3.2). For all of these reasons, ecological opportunities of larger animals are very different from those of small ones. In subsequent chapters we will describe the extensive adaptive radiations observed in taxa of large animals, covered in Chapters 8–20.

Extracellular Components of the Metazoan Body

In addition to the hierarchically arranged cellular structures discussed, metazoan animals contain two important noncellular components: body fluids and extracellular structural ele-

table 3.1 Levels of Organization in Organismal Complexity



1. *Protoplasmic level of organization.* Protoplasmic organization is found in unicellular organisms. All life functions are confined within the boundaries of a single cell, the fundamental unit of life. Within a cell, living substance is differentiated into organelles capable of carrying on specialized functions.
2. *Cellular level of organization.* Cellular organization is an aggregation of cells that are functionally differentiated. A division of labor is evident, so that some cells are concerned with, for example, reproduction, others with nutrition. Such cells have little tendency to become organized into tissues (a tissue is a group of similar cells organized to perform a common function). Some protozoan colonial forms that have distinct somatic and reproductive cells might be placed at the cellular level of organization. Many authorities also place sponges at this level.
3. *Cell-tissue level of organization.* A step beyond the preceding is the aggregation of similar cells into definite patterns or layers, thus becoming a **tissue**. Some authorities assign sponges to this level, although jellyfishes and their relatives (Cnidaria) more clearly demonstrate the tissue plan. Both groups are still largely of the cellular grade of organization because most of the cells are scattered and not organized into tissues. An excellent example of a tissue in cnidarians is the nerve net, in which the nerve cells and their processes form a definite tissue structure, with the function of coordination.
4. *Tissue-organ level of organization.* Aggregation of tissues into organs is a further step in complexity. Organs are usually made up of more than one kind of tissue and have a more specialized function than tissues. This is the organizational level of the flatworms (Platyhelminthes), in which there are a number of well-defined organs such as eyespots, digestive tract, and reproductive organs. In fact, the reproductive organs are well organized into a reproductive system.
5. *Organ-system level of organization.* When organs work together to perform some function we have the most complex level of organization—the organ system. Systems are associated with basic body functions—circulation, respiration, digestion, and others. The simplest animals that show this type of organization are nemertean worms, which have a complete digestive system distinct from the circulatory system. Most animal phyla demonstrate this type of organization.

ments. In all eumetazoans, body fluids are subdivided into two fluid “compartments:” those that occupy **intracellular space**, within the body’s cells, and those that occupy **extracellular space**, outside the cells. In animals with closed vascular systems (such as segmented worms and vertebrates), extracellular fluids are subdivided further into **blood plasma** (the fluid portion of the blood outside the cells; blood cells are really part of the intracellular compartment) and **interstitial fluid**. Interstitial fluid, also called tissue fluid, occupies the space surrounding cells. Many invertebrates have open blood systems, however, with no true separation of blood plasma from interstitial fluid.

If we were to remove all specialized cells and body fluids from the interior of the body, we would be left with the third

The term intercellular, meaning “between cells,” should not be confused with the term intracellular, meaning “within cells.”

element of the animal body: extracellular structural elements. This is the supportive material of the organism, including loose connective tissue (especially well developed in vertebrates but present in all metazoa), cartilage (molluscs and chordates), bone (vertebrates), and cuticle (arthropods, nematodes, annelids, and others). These elements provide mechanical stability and protection. In some instances, they act also as a

figure 3.1

Graph showing evolution of length increase in the largest organisms present at different periods of life on earth. Note that both scales are logarithmic.

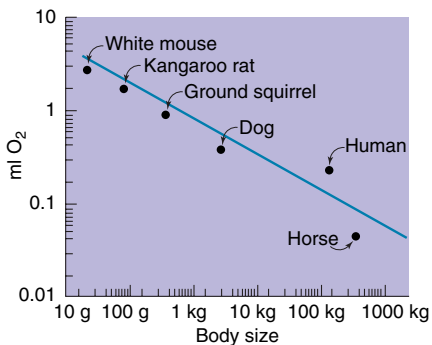
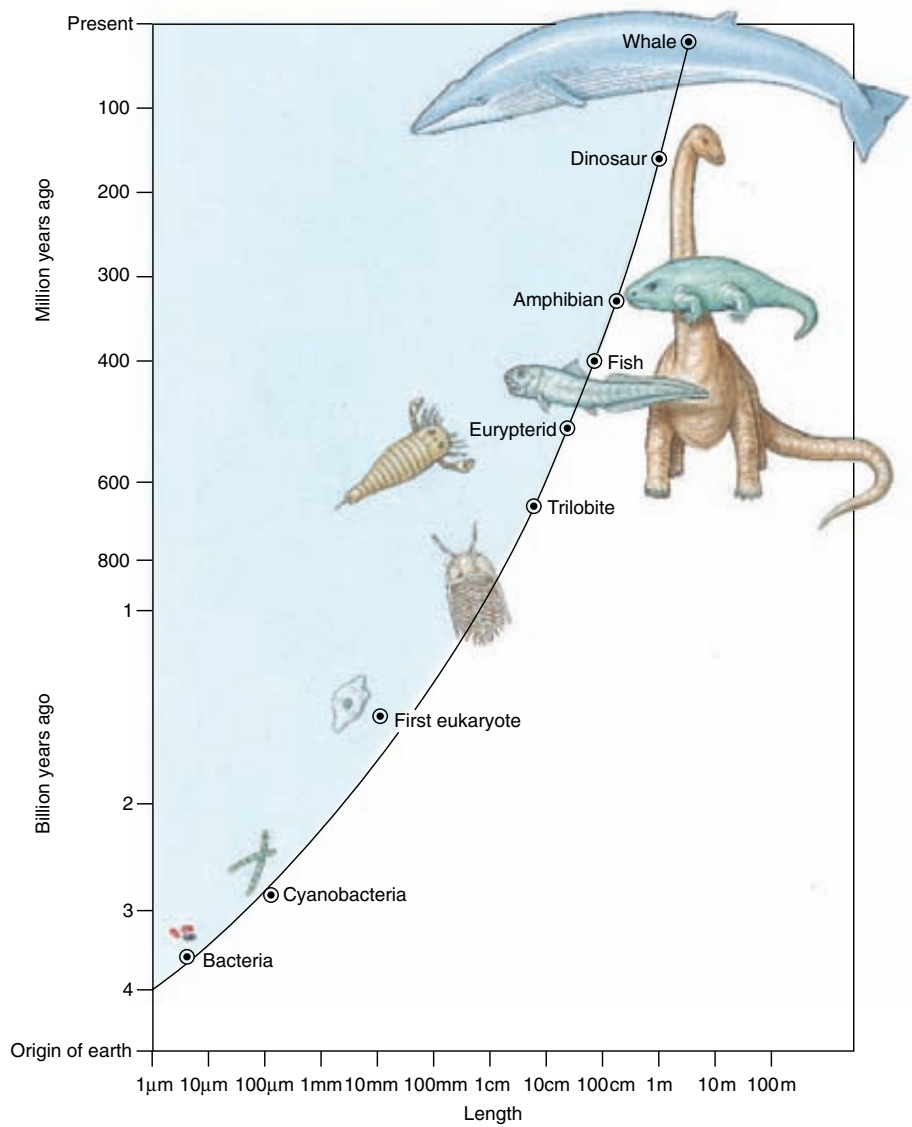


figure 3.2

Net cost of running for mammals of various sizes. Each point represents the cost (measured in rate of oxygen consumption) of moving 1 g of body over 1 km. The cost decreases with increasing body size.

depot of materials for exchange and serve as a medium for extracellular reactions. We will describe the diversity of extracellular skeletal elements characteristic of the different groups of animals in Chapters 10–20.

Types of Tissues

A tissue is a group of similar cells, together with associated cell products, specialized for performance of a common function. The study of tissues is called **histology** (Gr. *bistos*, tissue, + *logos*, discourse). All cells in metazoan animals take part in the formation of tissues. Sometimes cells of a tissue may be of several kinds, and some tissues have a great many intercellular materials.

During embryonic development, the germ layers become differentiated into four kinds of tissues. These are epithelial,

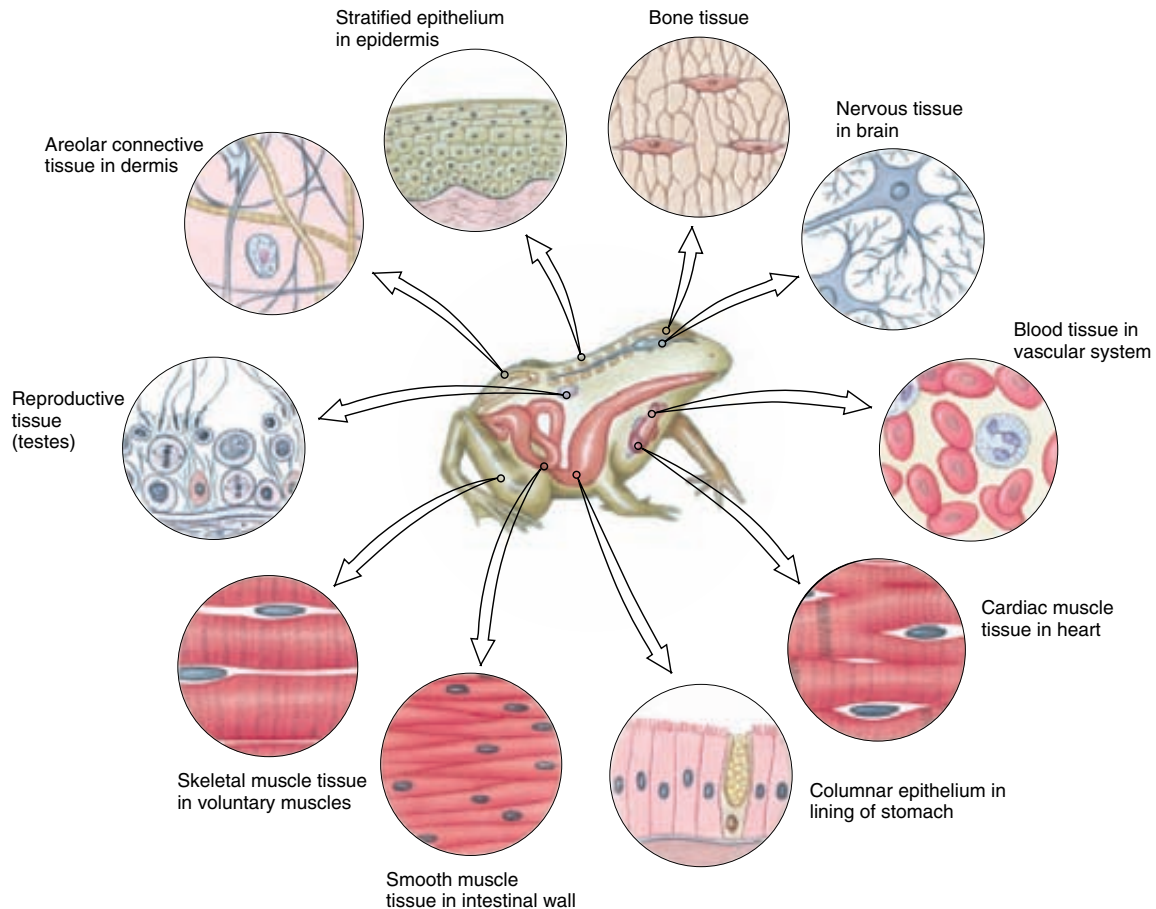


figure 3.3

Types of tissues in a vertebrate, showing examples of where different tissues are located in a frog.

connective (including vascular), muscular, and nervous tissues (figure 3.3). This is a surprisingly short list of only four basic tissue types that are able to meet the diverse requirements of animal life.

Epithelial Tissue

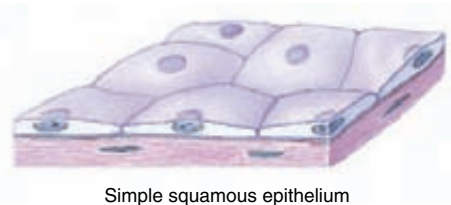
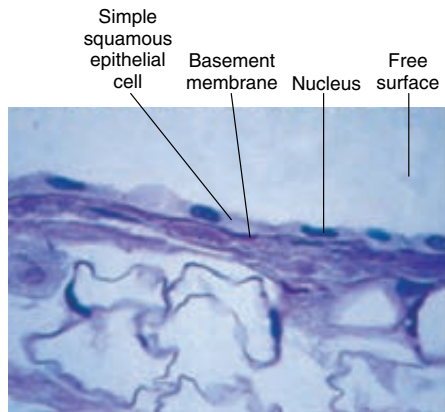
An **epithelium** (pl., epithelia) is a sheet of cells that covers an external or internal surface. Outside the body, epithelium forms a protective covering. Inside, an epithelium lines all organs of the body cavity, as well as ducts and passageways through which various materials and secretions move. On many surfaces epithelial cells are often modified into glands that produce lubricating mucus or specialized products such as hormones or enzymes.

Epithelia are classified by cell form and number of cell layers. Simple epithelia (figure 3.4) are found in all metazoan animals, while stratified epithelia (figure 3.5) are mostly restricted to the vertebrates. All types of epithelia are sup-

ported by an underlying basement membrane, which is a condensation of the ground substance of connective tissue. Blood vessels never enter epithelial tissues, so they are dependent on diffusion of oxygen and nutrients from underlying tissues.

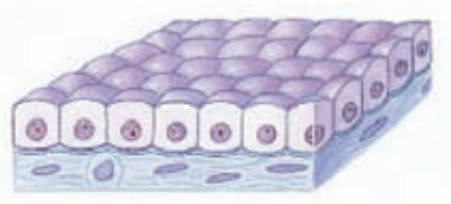
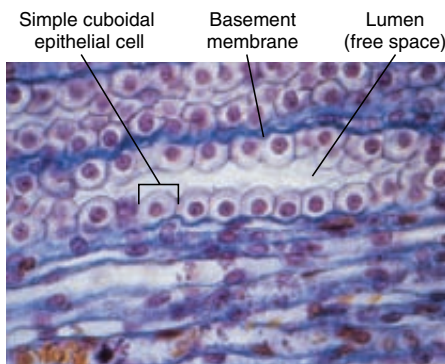
Connective Tissue

Connective tissues are a diverse group of tissues that serve various binding and supportive functions. They are so widespread in the body that removal of other tissues would still leave the complete form of the body clearly apparent. Connective tissue is made up of relatively few **cells**, a great many extracellular **fibers**, and a fluid, known as **ground substance** (also called **matrix**), in which the fibers are embedded. We recognize several different types of connective tissue. Two kinds of **connective tissue proper** occur in vertebrates. **Loose connective tissue** is composed of fibers and both fixed and wandering cells suspended in a syrupy ground substance. **Dense connective tissue**, such as tendons and ligaments, is composed



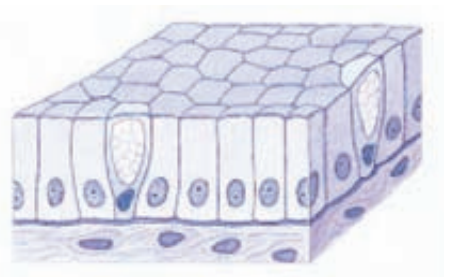
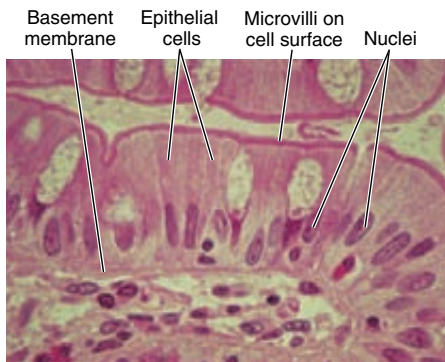
Simple squamous epithelium

Simple squamous epithelium, composed of flattened cells that form a continuous delicate lining of blood capillaries, lungs, and other surfaces where it permits the passive diffusion of gases and tissue fluids into and out of cavities.



Simple cuboidal epithelium

Simple cuboidal epithelium is composed of short, boxlike cells. Cuboidal epithelium usually lines small ducts and tubules, such as those of the kidney and salivary glands, and may have active secretory or absorptive functions.



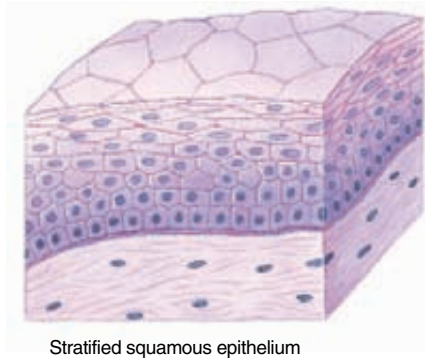
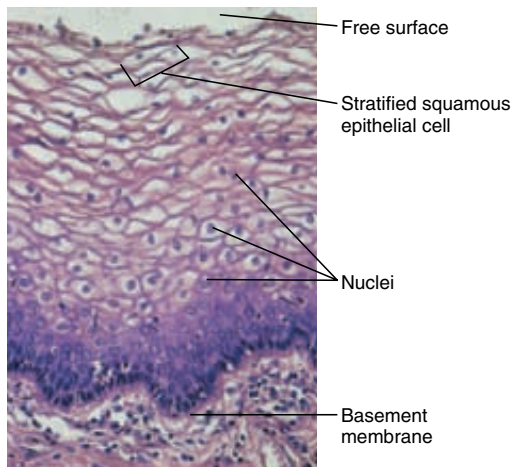
Simple columnar epithelium

Simple columnar epithelium resembles cuboidal epithelium but the cells are taller and usually have elongate nuclei. This type of epithelium is found on highly absorptive surfaces such as the intestinal tract of most animals. The cells often bear minute, fingerlike projections called microvilli that greatly increase the absorptive surface. In some organs, such as the female reproductive tract, the cells are ciliated.

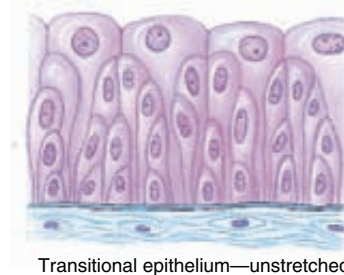
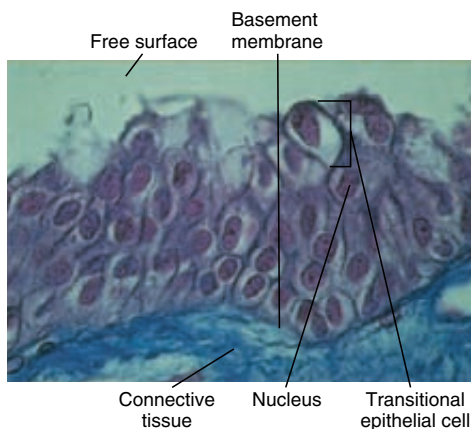
figure 3.4
Types of simple epithelium

largely of densely packed fibers (figure 3.6). Much of the fibrous tissue of connective tissue is composed of **collagen** (Gr. *kolla*, glue, + *genos*, descent), a protein material of great tensile strength. Collagen is the most abundant protein in the animal kingdom, found in animal bodies wherever both flexibility and resistance to stretching are required. The connective tissue of invertebrates, as in vertebrates, consists of cells, fibers, and ground substance, but usually it is not as elaborately developed.

Other types of connective tissue include **blood**, **lymph**, and **tissue fluid** (collectively considered vascular tissue), composed of distinctive cells in a watery ground substance, the plasma. Vascular tissue lacks fibers under normal conditions. **Cartilage** is a semirigid form of connective tissue with closely packed fibers embedded in a gel-like ground substance (matrix). **Bone** is a calcified connective tissue containing calcium salts organized around collagen fibers.



Stratified squamous epithelium consists of two to many layers of cells adapted to withstand mild mechanical abrasion. The basal layer of cells undergoes continuous mitotic divisions, producing cells that are pushed toward the surface where they are sloughed off and replaced by new cells beneath them. This type of epithelium lines the oral cavity, esophagus, and anal canal of many vertebrates, and vagina of mammals.



Transitional epithelium is a type of stratified epithelium specialized to accommodate great stretching. This type of epithelium is found in the urinary tract and bladder of vertebrates. In the relaxed state it appears to be four or five cell layers thick, but when stretched out it appears to have only two or three layers of extremely flattened cells.

figure 3.5
Types of stratified epithelium

Muscular Tissue

Muscle is the most common tissue of most animals. It originates (with few exceptions) from mesoderm, and its unit is the cell or **muscle fiber**, specialized for contraction. When viewed with a light microscope, **striated muscle** appears transversely striped (striated), with alternating dark and light bands (figure 3.7). In vertebrates we recognize two types of striated muscle: **skeletal** and **cardiac muscle**. A third kind of muscle is smooth (or visceral) muscle, which lacks the characteristic alternating bands of the striated type (figure 3.7). Unspecialized cytoplasm of muscles is called **sarcoplasm**, and contractile elements within the fiber are **myofibrils**.

Nervous Tissue

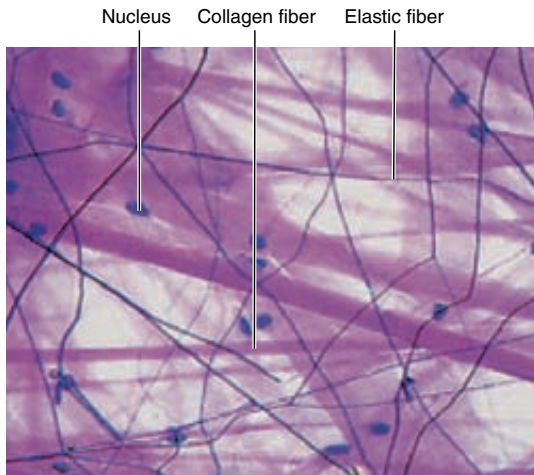
Nervous tissue is specialized for reception of stimuli and conduction of impulses from one region to another. Two basic types of cells in nervous tissue are **neurons** (Gr. nerve), the

basic functional unit of the nervous system, and **neuroglia** (nu-rog´le-a; Gr. nerve, + *glia*, glue), a variety of nonnervous cells that insulate neuron membranes and serve various supportive functions. Figure 3.8 shows the functional anatomy of a typical nerve cell.

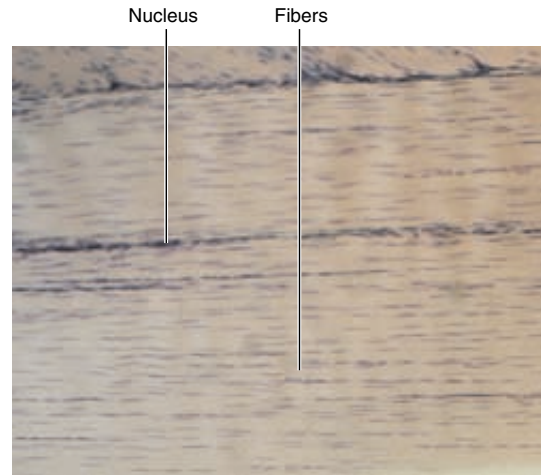
Animal Body Plans

As pointed out in the prologue to this chapter, the diversity of animal body form is constrained by ancestral history, habitat, and way of life. Although a worm that adopts a parasitic life in the intestine of a vertebrate will look and function very differently from a free-living member of the same group, both share distinguishing hallmarks of the phylum.

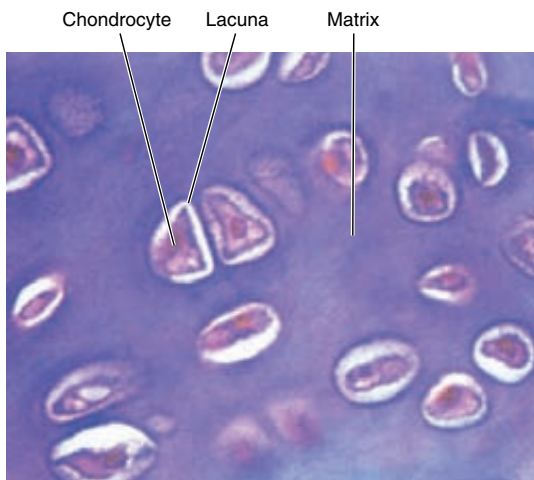
Major evolutionary innovations in the forms of animals include multicellularity, bilateral symmetry, “tube-within-a-tube” plan, and eucoelomate (true coelom) body plan. These advancements with their principal alternatives can be arranged in a branching pattern, as shown in figure 3.9.



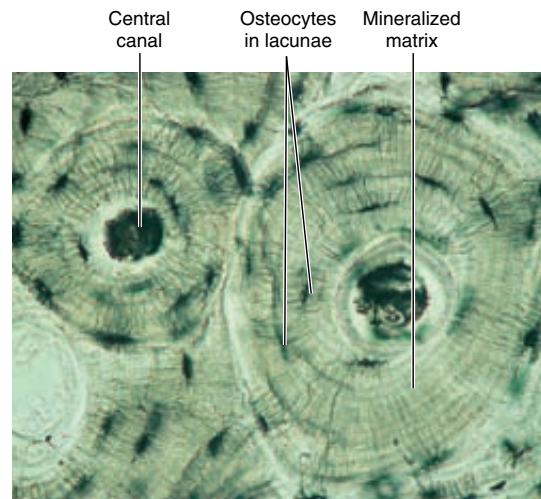
Loose connective tissue, also called areolar connective tissue, is the “packing material” of the body that anchors blood vessels, nerves, and body organs. It contains fibroblasts that synthesize the fibers and ground substance of connective tissue and wandering macrophages that phagocytize pathogens or damaged cells. The different fiber types include strong collagen fibers (thick and violet in micrograph) and elastic fibers (black and branching in micrograph) formed of the protein elastin. Adipose (fat) tissue is considered a type of loose connective tissue.



Dense connective tissue forms tendon, ligaments, and fasciae (fa' sha), the latter arranged as sheets or bands of tissue surrounding skeletal muscle. In tendon (shown here) the collagenous fibers are extremely long and tightly packed together.

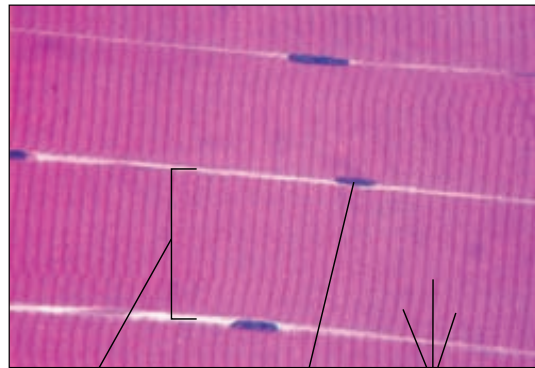


Cartilage is a vertebrate connective tissue composed of a firm gel ground substance (matrix) containing cells (chondrocytes) living in small pockets called lacunae, and collagen or elastic fibers (depending on the type of cartilage). In hyaline cartilage shown here, both collagen fibers and ground substance are stained uniformly purple, and cannot be distinguished one from the other. Because cartilage lacks a blood supply, all nutrients and waste materials must diffuse through the ground substance from surrounding tissues.



Bone, strongest of vertebrate connective tissues, contains mineralized collagen fibers. Small pockets (lacunae) within the matrix contain bone cells, called osteocytes. The osteocytes communicate with blood vessels that penetrate into bone by means of a tiny network of channels called canaliculi. Unlike cartilage, bone undergoes extensive remodeling during an animal's life, and can repair itself following even extensive damage.

figure 3.6
Types of connective tissue

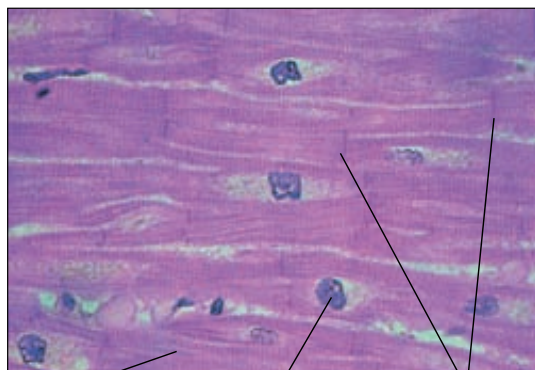


Skeletal muscle fiber Nucleus Striations

figure 3.7

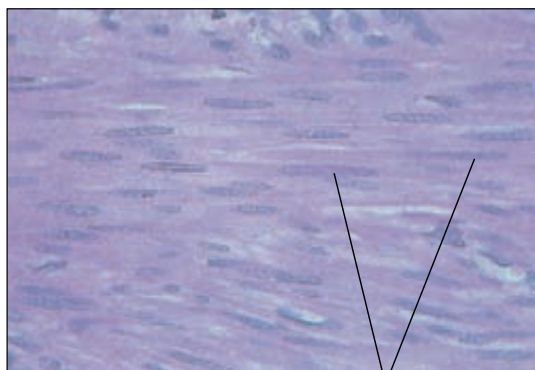
Types of muscle tissue

Skeletal muscle is a type of striated muscle found in both invertebrates and vertebrates. It is composed of extremely long, cylindrical fibers, which are multinucleate cells that may reach from one end of the muscle to the other. Viewed through the light microscope, the cells appear to have a series of stripes, called striations, running across them. Skeletal muscle is called voluntary muscle (in vertebrates) because it contracts when stimulated by nerves under conscious cerebral control.



Note striations Nucleus of cardiac muscle cell Intercalated discs (special junctions between cells)

Cardiac muscle is another type of striated muscle found only in the vertebrate heart. The cells are much shorter than those of skeletal muscle and have only one nucleus per cell (uninucleate). Cardiac muscle tissue is a branching network of fibers with individual cells interconnected by junctional complexes called intercalated discs. Cardiac muscle is called involuntary muscle because it does not require nerve activity to stimulate contraction. Instead, heart rate is controlled by specialized pacemaker cells located in the heart itself. However, autonomic nerves from the brain may alter pacemaker activity.



Nuclei of smooth muscle cells

Smooth muscle is nonstriated muscle found in both invertebrates and vertebrates. Smooth muscle cells are long, tapering strands, each containing a single nucleus. Smooth muscle is the most common type of muscle in invertebrates in which it serves as body wall musculature and lines ducts and sphincters. In vertebrates, smooth muscle cells are organized into sheets of muscle circling the walls of the alimentary canal, blood vessels, respiratory passages, and urinary and genital ducts. Smooth muscle is typically slow acting and can maintain prolonged contractions with very little energy expenditure. Its contractions are involuntary and unconscious. The principal functions of smooth muscles are to push the material in a tube, such as the intestine, along its way by active contractions or to regulate the diameter of a tube, such as a blood vessel, by sustained contraction.

Animal Symmetry

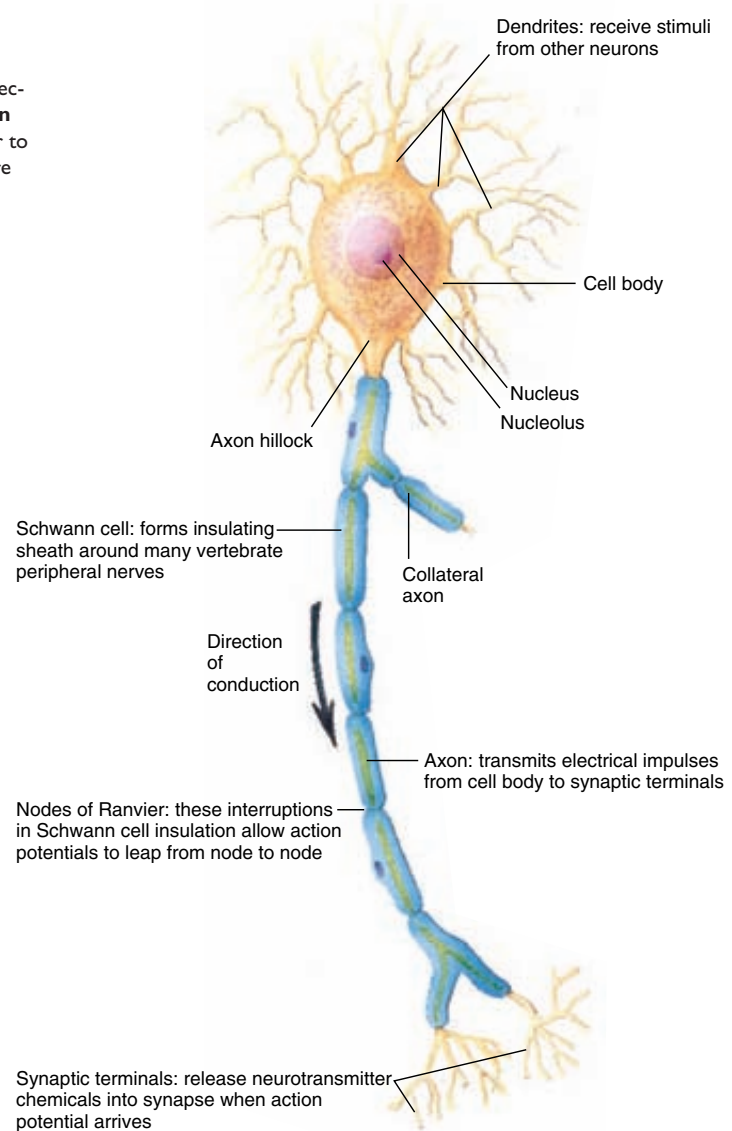
Symmetry refers to balanced proportions, or correspondence in size and shape of parts on opposite sides of a median plane. **Spherical symmetry** means that any plane passing through the center divides the body into equivalent, or mirrored, halves (figure 3.10). This type of symmetry is found chiefly among

some protozoan groups and is rare in metazoans. Spherical forms are best suited for floating and rolling.

Radial symmetry (figure 3.10) applies to forms that can be divided into similar halves by more than two planes passing through the longitudinal axis. These are the tubular, vase, or bowl shapes in which one end of the longitudinal axis is usually the mouth. Examples are the hydras, jellyfishes, sea

figure 3.8

Functional anatomy of a neuron. From the nucleated body, or soma, extend one or more **dendrites** (Gr. *dendron*, tree), which receive electrical impulses from receptors or other nerve cells, and a single **axon** that carries impulses away from the cell body to other nerve cells or to an effector organ. The axon is often called a **nerve fiber**. Nerves are separated from other nerves or from effector organs by specialized junctions called synapses.



urchins, and some sponges. A variant form is biradial symmetry, in which, because of some part that is single or paired rather than radial, only one or two planes passing through the longitudinal axis produce mirrored halves. Sea walnuts (phylum Ctenophora), which are more or less globular in form but have a pair of tentacles, are an example. Radial and biradial animals are usually sessile, freely floating, or weakly swimming. The two phyla that are primarily radial, Cnidaria and Ctenophora, are called the **Radiata**. Echinoderms (sea stars and their kin) are primarily bilateral animals (their larvae are bilateral) that have become secondarily radial as adults.

Bilateral symmetry applies to animals that can be divided along a sagittal plane into two mirrored portions, right and left halves (figure 3.10). The appearance of bilateral symmetry in animal evolution was a major innovation because

bilateral animals are much better fitted for directional (forward) movement than are radially symmetrical animals. Bilateral animals are collectively called **Bilateria**. Bilateral symmetry is strongly associated with cephalization, discussed on page 65.

Some convenient terms used for locating regions of animal bodies (Figure 3.11) are **anterior**, used to designate the head end; **posterior**, the opposite or tail end; **dorsal**, the back side; and **ventral**, the front or belly side. **Medial** refers to the midline of the body; **lateral** refers to the sides. **Distal** parts are farther from the middle of the body; **proximal** parts are nearer. A **frontal plane** (also sometimes called coronal plane) divides a bilateral body into dorsal and ventral halves by running through the anteroposterior axis and the right-left axis at right angles to the **sagittal plane**, the plane dividing an animal into right and left halves. A **transverse plane** (also called

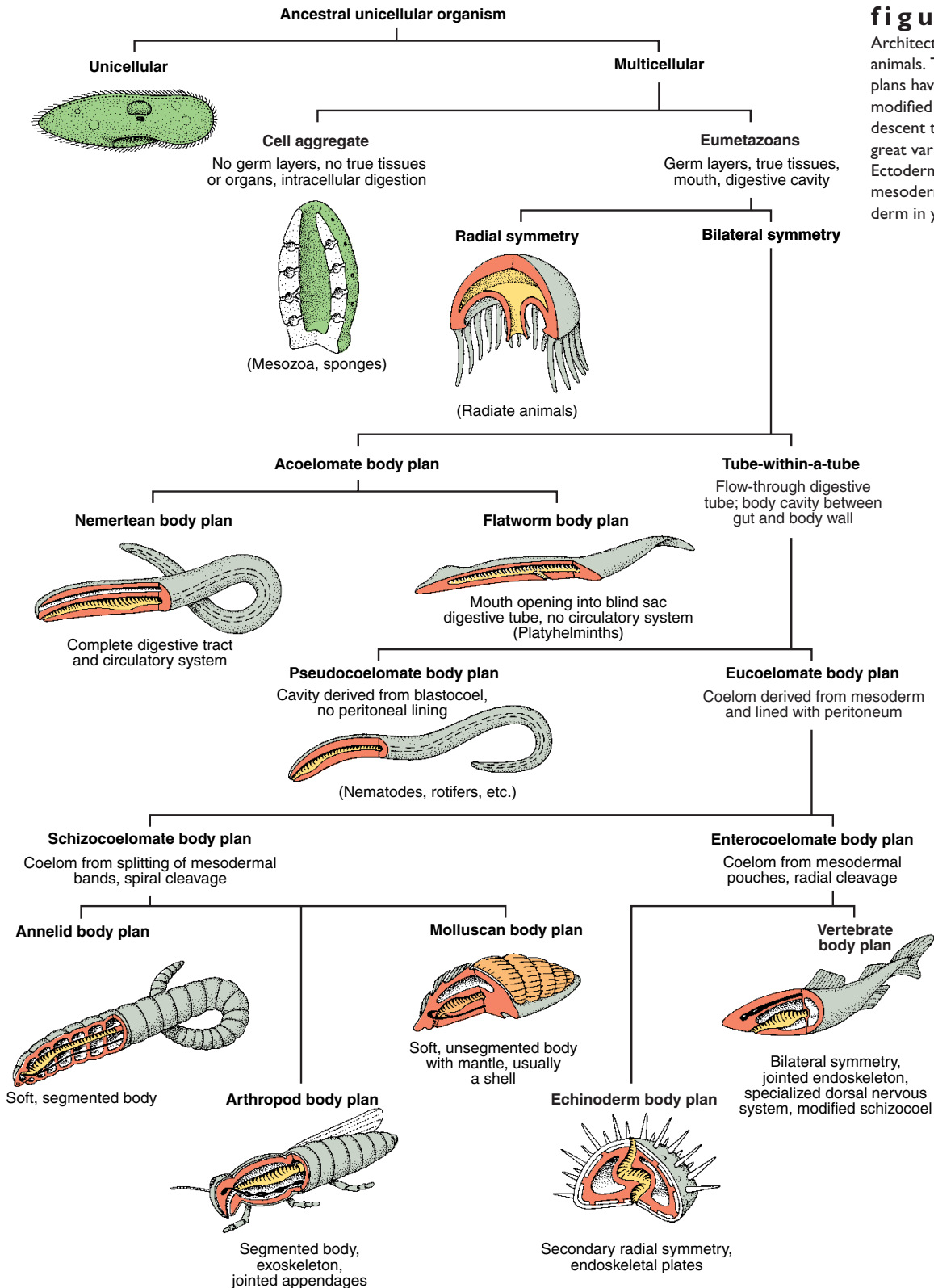


figure 3.9

Architectural patterns of animals. These basic body plans have been variously modified during evolutionary descent to fit animals to a great variety of habitats. Ectoderm is shown in gray, mesoderm in red, and endoderm in yellow.

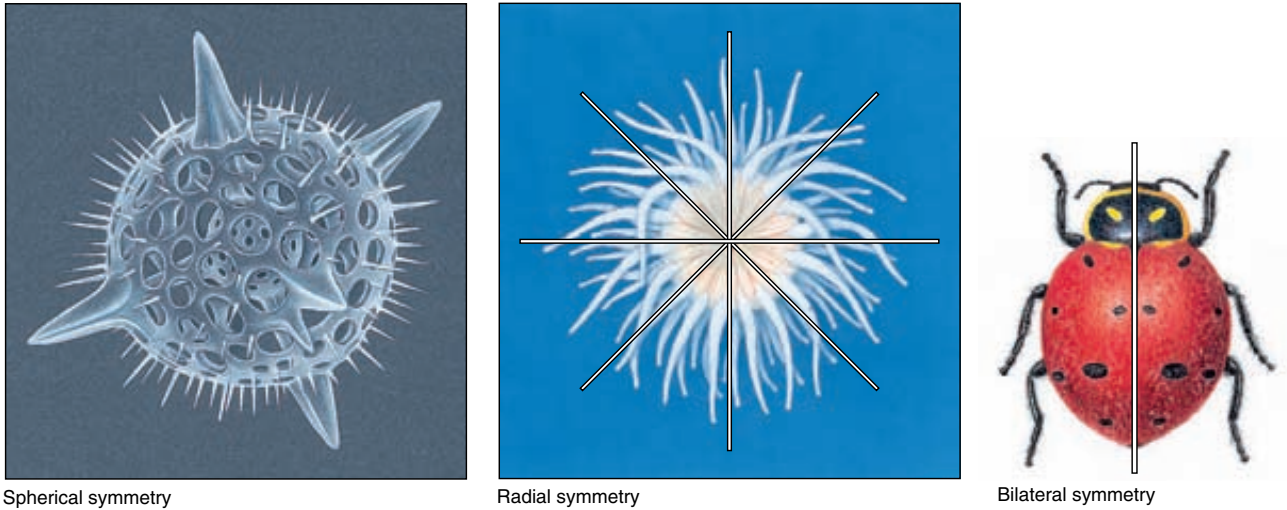


figure 3.10

The planes of symmetry as illustrated by spherically, radially, and bilaterally symmetrical animals.

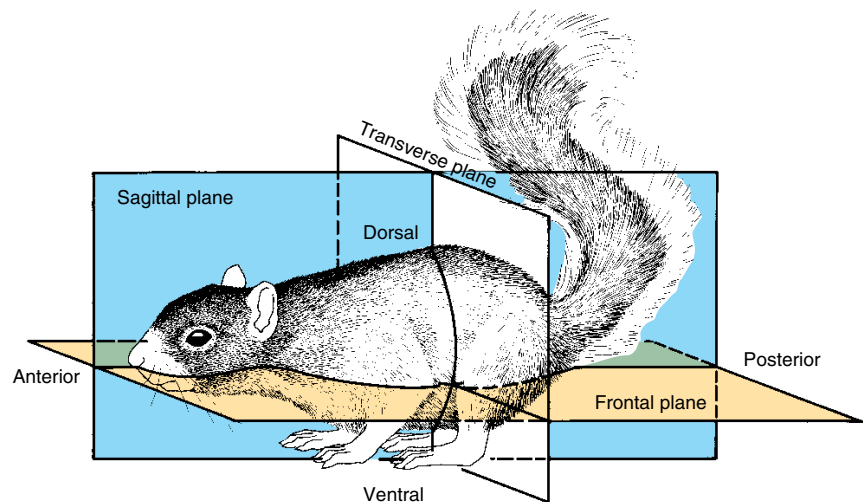


figure 3.11

Descriptive terms used to identify positions on the body of a bilaterally symmetrical animal.

a cross section) would cut through a dorsoventral and a right-left axis at right angles to both the sagittal and frontal planes and would result in anterior and posterior portions.

Developmental Patterns in Bilateral Animals

The expression of an animal's body plan is based on an inherited pattern of development. In sexual multicellular organisms, the extremely complex process of embryonic development of an animal from egg to fully differentiated adult is highly predictable and virtually flawless. When developmental alterations do appear during speciation events, changes tend to be confined to end stages of development. The organization of eggs

and early cleavage stages remain stubbornly resistant to change because any deviation introduced at an early stage would be ruinous to the entire course of development. Nevertheless, several times in the history of life just such radical transformations did occur to herald the appearance of completely new designs for living, such as new classes, phyla, or even major divisions within the animal kingdom.

Patterns of Cleavage

One of the most fundamental aspects of animal development indicating evolutionary relationships is symmetry of cleavage. Cleavage is the initial process of development following fertilization of the egg by a sperm: dividing a fertil-

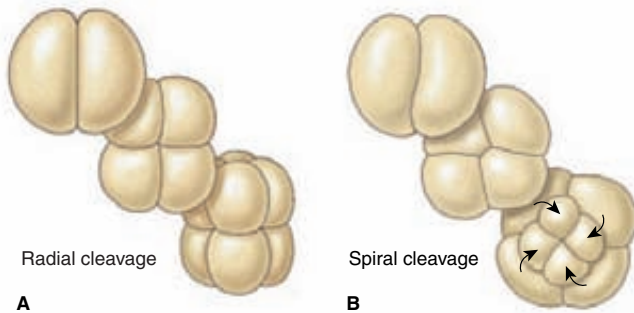


figure 3.12

Radial and spiral cleavage patterns shown at two-, four-, and eight-cell stages. **A**, Radial cleavage, typical of echinoderms, chordates, and hemichordates. **B**, Spiral cleavage, typical of molluscs, annelids, and other protostomes. Arrows indicate clockwise movements of small cells (micromeres) following division of large cells (macromeres).

ized egg, now called a **zygote**, into a large number of cells, called **blastomeres**.

Zygotes of many animals cleave by one of two patterns: radial or spiral (figure 3.12). In **radial cleavage**, the cleavage planes are symmetrical to the polar axis and produce tiers, or layers, of cells on top of each other. Radial cleavage is also said to be **regulative** because each blastomere of the early embryo, if separated from the others, can adjust or “regulate” its development into a complete and well-proportioned (though possibly smaller) embryo (Figure 3.13).

Spiral cleavage, found in several phyla, differs from radial in several ways. Rather than an egg dividing parallel or

perpendicular to the animal-vegetal axis, it cleaves oblique to this axis and typically produces a quartet of cells that come to lie not on top of each other but in the furrows between the cells (see figure 3.12). In addition, spirally cleaving eggs tend to pack their cells tightly together much like a cluster of soap bubbles, rather than just lightly contacting each other as do those in many radially cleaving embryos. Spirally cleaving embryos also differ from radial embryos in having a **mosaic** form of development, in which the organ-forming determinants in the egg cytoplasm become strictly localized in the egg, even before the first cleavage division. The result is that if the early blastomeres are separated, each will continue to develop for a time as though it were still part of the whole. Each forms a defective, partial embryo (figure 3.13). A curious feature of most spirally cleaving embryos is that at about the 29-cell stage a blastomere called the 4d cell is formed that will give rise to all mesoderm of the embryo.

The importance of these two cleavage patterns extends well beyond the differences we have described. They signal a fundamental dichotomy, an early evolutionary divergence of bilateral metazoan animals into two separate lineages. Spiral cleavage is found in annelids, molluscs, and several other invertebrate phyla; all are included in the **Protostomia** (“mouth first”) division of the animal kingdom (see the illustration inside the front cover of this book). The name Protostomia refers to the formation of the mouth from the first embryological opening, the blastopore. Radial cleavage is characteristic of the **Deuterostomia** (“mouth second”) division of the animal kingdom, a grouping that includes echinoderms (sea stars and their kin), chordates, and hemichordates. In Deuterostomia, the blastopore usually becomes the anus, while the mouth forms secondarily. Other distinguishing developmental hallmarks of these two divisions are summarized in figure 3.14.

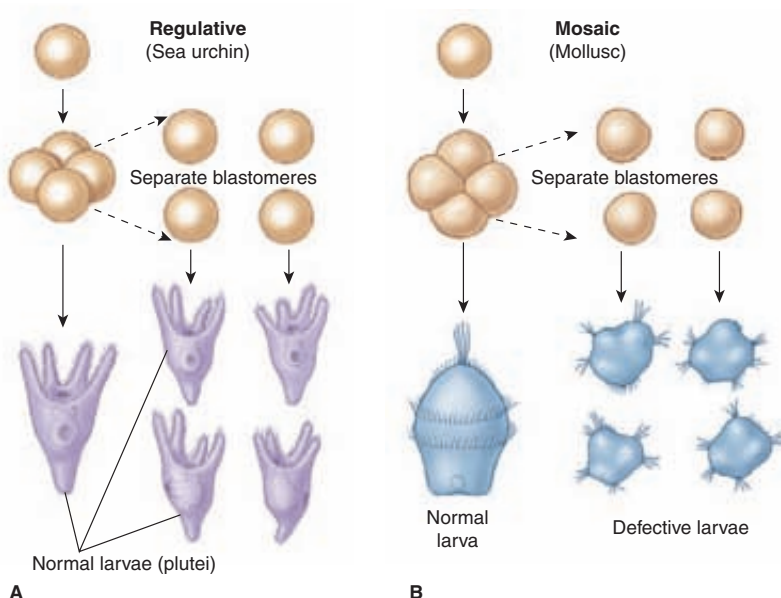


figure 3.13

Regulative and mosaic development. **A**, Regulative development. If the early blastomeres of a sea urchin embryo are separated, each will develop into a complete larva. **B**, Mosaic development. When the blastomeres of a mollusc embryo are separated, each gives rise to a partial, defective larva.

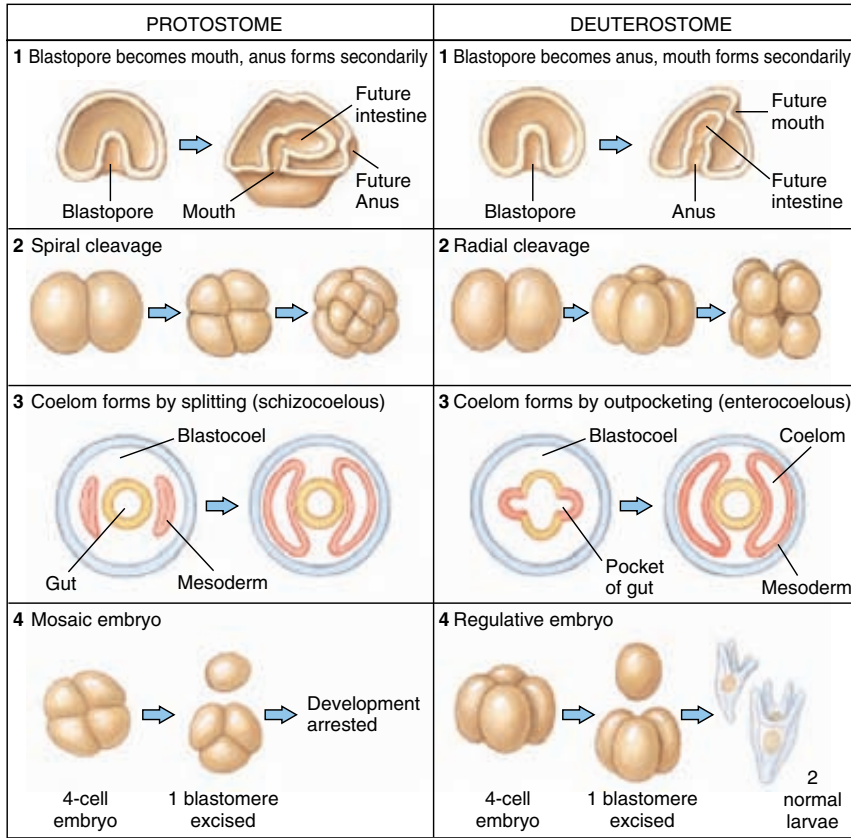


figure 3.14

Developmental tendencies of protostomes and deuterostomes. These tendencies are much modified in some groups, for example, the vertebrates. Cleavage in mammals is rotational rather than radial; in reptiles, birds, and many fishes the cleavage is discoidal. Vertebrates have also evolved a derived form of coelom formation that is basically schizocoelous.

Body Cavities

Another major developmental event affecting the body plan of bilateral animals was evolution of a **coelom**, a fluid-filled cavity between the outer body wall and the gut (see figure 3.9). A coelom also provides a tube-within-a-tube arrangement that allows much greater body flexibility than is possible in animals lacking an internal body cavity. A coelom also provides space for visceral organs and permits greater size and complexity by exposing more cells to surface exchange. A fluid-filled coelom additionally serves as a hydrostatic skeleton in some forms, especially many worms, aiding in such activities as movement and burrowing.

As shown in figure 3.9, the presence of a coelom is a key factor in the evolution of bilateral metazoan body planes.

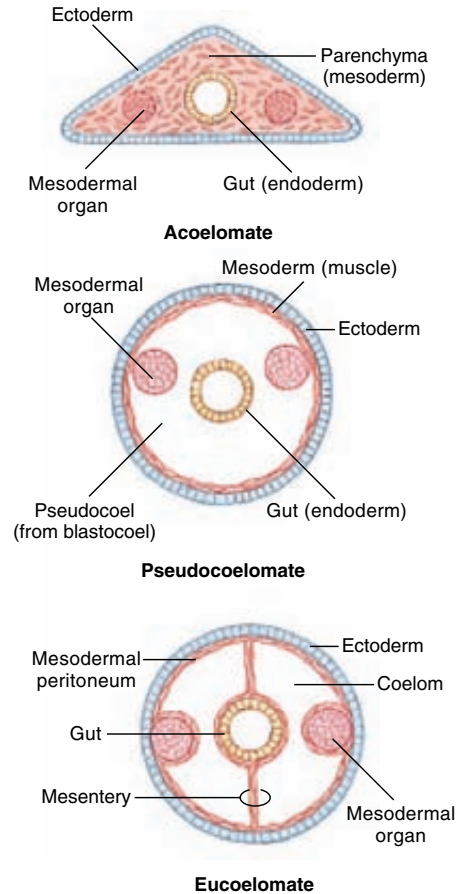


figure 3.15

Acoelomate, pseudocoelomate, and eucoelomate body plans.

Acoelomate Bilateria

Many bilateral animals do not have a true coelom. In fact, flatworms and a few others have *no body cavity* surrounding the gut (figure 3.15, *top*); they are “acoelomate” (Gr. *a*, without, + *koiloma*, cavity). The region between the ectodermal epidermis and the endodermal digestive tract is completely filled with mesoderm in the form of a spongy mass of space-filling cells called parenchyma.

Pseudocoelomate Bilateria

Nematodes and several other phyla have a body cavity surrounding the gut called a **pseudocoel** and its possessors have a tube-within-a-tube arrangement as do animals with a true

coelom. However, unlike a true coelom, a pseudocoel is derived from the embryonic blastocoel and is in fact a persistent blastocoel. It lacks a **peritoneum**, a thin cellular membrane derived from mesoderm that, in animals with a true coelom, lines the body cavity.

Eucoelomate Bilateria

The remaining bilateral animals possess a **true coelom** lined with mesodermal peritoneum (figure 3.15, *bottom*). A true coelom arises within the mesoderm itself and may be formed by one of two methods, **schizocoelous** or **enterocoelous** (figure 3.16), or by modifying these methods. The two terms are descriptive, for *schizo* comes from the Greek *schizein*, meaning to split; *entero* is derived from the Greek *enteron*, meaning gut; and *coelous* comes from the Greek *koiolos*, meaning hollow or cavity. In schizocoelous formation the coelom arises, as the word implies, from splitting of mesodermal bands that originate from cells in the blastopore region. (Mesoderm is one of three primary germ layers that appear very early in the development of all bilateral animals, lying between the innermost endoderm and outermost ectoderm.) In enterocoelous formation, the coelom comes from pouches of the archenteron, or primitive gut.

Once development is complete, the results of schizocoelous and enterocoelous formations are indistinguishable. Both give rise to a true coelom lined with a mesodermal peritoneum (Gr. *peritonaïos*, stretched around) and having mesenteries in which the visceral organs are suspended.

Metamerism (Segmentation)

Metamerism is a serial repetition of similar body segments along the longitudinal axis of the body. Each segment is called a metamere, or **somite**. In forms such as earthworms and other annelids, in which metamerism is most clearly represented, the segmental arrangement includes both external and internal structures of several systems. There is repetition of muscles, blood vessels, nerves, and the setae of locomotion. Some other organs, such as those of sex, may be repeated in

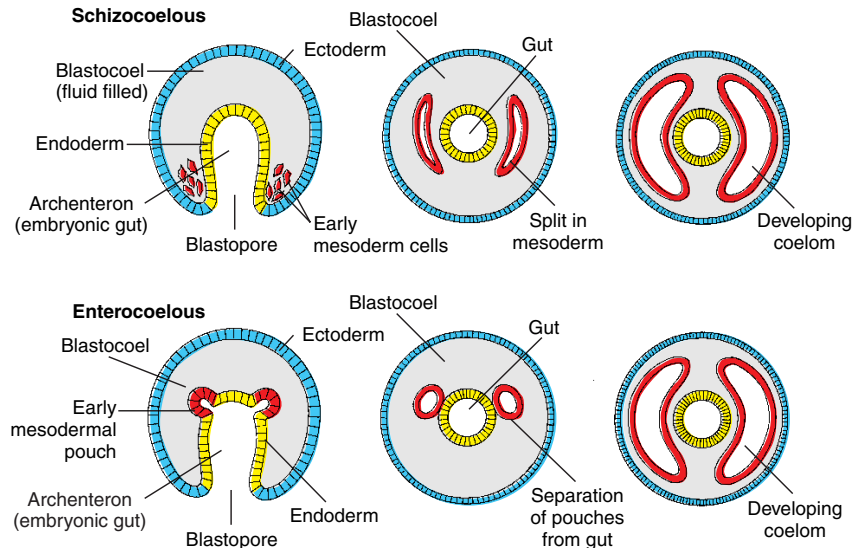


figure 3.16

Types of mesoderm and coelomic formation. In schizocoelous formation, the mesoderm originates from the wall of the archenteron near the blastopore and proliferates into a band of tissue which splits to form the coelom. In enterocoelous formation, most mesoderm originates as a series of pouches from the archenteron; these pinch off and enlarge to form the coelom. In both formations the coeloms expand to obliterate the blastocoel.

only a few somites. Evolutionary changes have obscured much of the segmentation in many animals including humans.

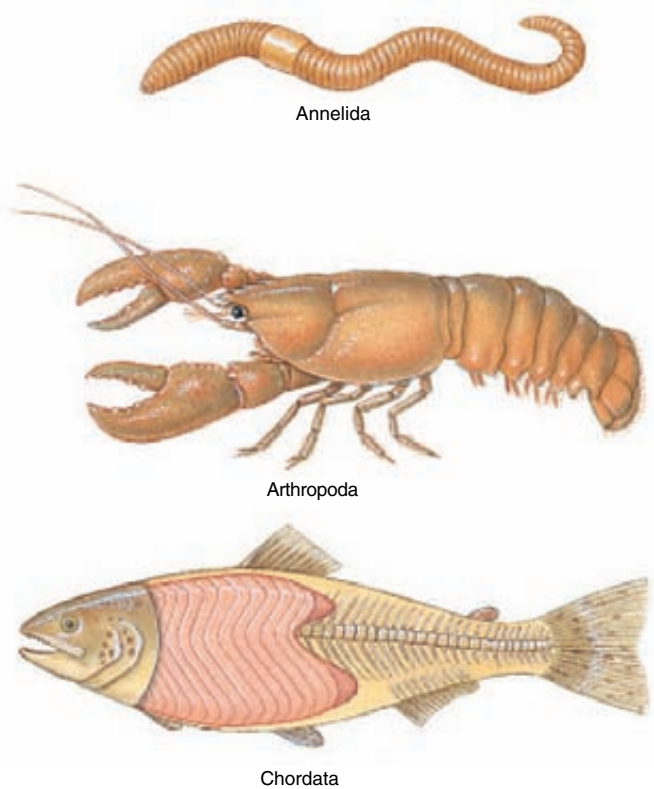
True metamerism is found in only three phyla: Annelida, Arthropoda, and Chordata (figure 3.17), although superficial segmentation of the ectoderm and the body wall may be found among many diverse groups of animals.

Cephalization

Differentiation of a head end is called **cephalization** and is found only in bilaterally symmetrical animals. Concentration of nervous tissue and sense organs in a head bestows obvious advantages to an animal moving through its environment head first. This is the most efficient positioning of instruments for sensing the environment and responding to it. Usually the mouth of an animal is located on the head as well, since so much of an animal's activity is concerned with procuring food. Cephalization is always accompanied by differentiation along an anteroposterior axis (**polarity**). Polarity usually involves gradients of activities between limits, such as between the anterior and the posterior ends.

figure 3.17

Segmented phyla. These three phyla illustrate an important principle in nature—metamerism, or repetition of structural units. Metamerism is homologous in annelids and arthropods, but chordates have derived their segmentation independently. Segmentation brings more varied specialization because segments, especially in arthropods, have become modified for different functions.

**summary**

From the relatively simple organisms that mark the beginnings of life on earth, animal evolution has progressed through a history of ever more intricately organized forms. Adaptive modifications for different niche requirements within a phyletic line of ancestry, however, have been constrained by the ancestral pattern of body architecture.

Cells became integrated into tissues, tissues into organs, and organs into systems. Whereas a unicellular organism carries out all life functions within the confines of a single cell, a complex multicellular animal is an organization of subordinate units that are united at successive levels. One correlate of increased body complexity is an increase in body size, which offers certain advantages,

such as more effective predation, reduced energy cost of locomotion, and improved homeostasis.

A metazoan body consists of cells, most of which are functionally specialized; body fluids, divided into intracellular and extracellular fluid compartments; and extracellular structural elements, which are fibrous or formless elements that serve various structural functions in the extracellular space. Cells of metazoans develop into various tissues made up of similar cells performing common functions. Basic tissue types are nervous, connective, epithelial, and muscular. Tissues are organized into larger functional units called organs, and organs are associated to form systems.

Every organism has an inherited body plan that may be described in terms of broadly inclusive characteristics, such as symmetry, presence or absence of body cavities, partitioning of body fluids, presence or absence of segmentation, degree of cephalization, and type of nervous system.

Based on several developmental characteristics, bilateral metazoans are divided into two major groups. The Protostomia are characterized by spiral cleavage, mosaic development, and the mouth forming at or near the embryonic blastopore. The Deuterostomia are characterized by radial cleavage, regulative development, and the mouth forming secondarily to the anus and not from the blastopore.

review questions

1. Name the five levels of organization in animal complexity and explain how each successive level is more complex than the one preceding it.
2. Can you suggest why, during the evolutionary history of animals, there has been a tendency for maximum body size to increase? Do you think it inevitable that complexity should increase along with body size? Why or why not?
3. What are the meanings of the terms “parenchyma” and “stroma” as they relate to body organs?

- Body fluids of eumetazoan animals are separated into fluid “compartments.” Name these compartments and explain how compartmentalization may differ in animals with open and closed circulatory systems.
- What are the four major types of tissues in the body of a metazoan?
- How would you distinguish between simple and stratified epithelium? What characteristic of stratified epithelium might explain why it, rather than simple epithelium is found lining the oral cavity, esophagus, and vagina?
- What are the three elements present in all connective tissue? Give some examples of the different types of connective tissue.
- What are three different kinds of muscle found among animals? Explain how each is specialized for particular functions.
- Describe the principal structural and functional features of a neuron.
- Match the animal group with its body plan:

___ Unicellular	a. Nematode
___ Cell aggregate	b. Vertebrate
___ Blind sac, acoelomate	c. Protozoan
___ Tube-within-a-tube, pseudocoelomate	d. Flatworm
___ Tube-within-a-tube, eucoelomate	e. Sponge
	f. Arthropod
	g. Nemertean
- Distinguish among spherical, radial, biradial, and bilateral symmetry.
- Use the following terms to identify regions on your body and on the body of a frog: anterior, posterior, dorsal, ventral, lateral, distal, proximal.
- How would frontal, sagittal, and transverse planes divide your body?
- What is the difference between radial and spiral cleavage?
- What are the distinguishing developmental hallmarks of the two major groups of bilateral metazoans, the Protostomia and the Deuterostomia?
- What is meant by metamerism? Name three phyla showing metamerism.

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See also general references on p. 406.

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