CHAPTER 1

Characteristics of Metazoan Development

Gary J. Brusca, Richard C. Brusca, and Scott F. Gilbert

As opposed to the protozoa, which are usually viewed as being unicellular, the metazoa are multicellular. This distinction is sometimes blurred, however, because there are a number of protozoa that form rather complex colonies with some division of labor among different cell types. The metazoa possess certain qualities that must be considered in concert with the basic idea of multicellularity. The cells of metazoa are organized into functional units, generally as tissues and organs, with specific roles that support the life of the whole animal. These cell types are interdependent and their activities are coordinated into predictable patterns and relationships. Structurally, the cells of metazoan animals are organized as layers, which develop through a series of events early in an organism's embryogeny. These embryonic tissues, or germ layers, are the framework upon which the metazoan body is constructed. *Thus, the cells of metazoa are specialized, interdependent, coordinated in function, and develop through layering during embryogeny.* This combination of features is absent from protozoa.

Eggs and Embryos

The attributes that distinguish the metazoa are the result of metazoan embryonic development. To put it another way, adult phenotypes result from specific sequences of developmental stages—evolutionary patterns reveal themselves, in part, through species' ontogenesis. Indeed, embryogenesis is the key feature distinguishing metazoa from protozoa. Bearing this in mind, it is not surprising to discover that both animal unity and diversity are as evident in patterns of development as they are in the architecture of adults. The patterns of development discussed in this chapter reflect this unity and diversity, and serve as a basis for understanding the embryogeny of specific phyla in later chapters.

Eggs

Biological processes are generally cyclical. The production of one generation after another through reproduction exemplifies this generality, as the term *life cycle* implies. At what point one begins describing such cycles is a matter of convenience. For our purposes in this chapter we choose to begin with the **egg**, or **ovum**—a remarkable cell capable of developing into a new individual. Once the egg is fertilized, all the different cell types of an adult metazoan are derived during embryogenesis from this single totipotent cell. A fertilized egg contains not only the information necessary to direct development, but also some quantity of nutrient material, called **yolk**, that sustains the early stages of life.

Animals that simply deposit their fertilized eggs, either freely or in capsules, are said to be **oviparous**. A great number of invertebrates as well as some vertebrates (amphibians, fishes, reptiles, and birds) are oviparous. Animals that brood their embryos internally and nourish them directly, such as placental mammals, are described as **viviparous**. **Ovoviviparous** animals brood their embryos internally but rely on the yolk within the eggs to nourish their developing young. Most internally-brooding invertebrates are ovoviviparous.

Eggs tend to be polarized along what is called their **animal-vegetal axis**. This polarity may be apparent in the egg itself, or it may be recognizable only as development proceeds. The vegetal pole is commonly associated with the formation of nutritive organs (e.g., the digestive system), whereas the animal pole tends to produce other regions of the embryo. These and many other manifestations of the egg's polarity will be explored more completely throughout this chapter.

Metazoan ova are categorized primarily by the amount and location of yolk within the cell (Figure 1.1), two factors that greatly influence certain aspects of development.

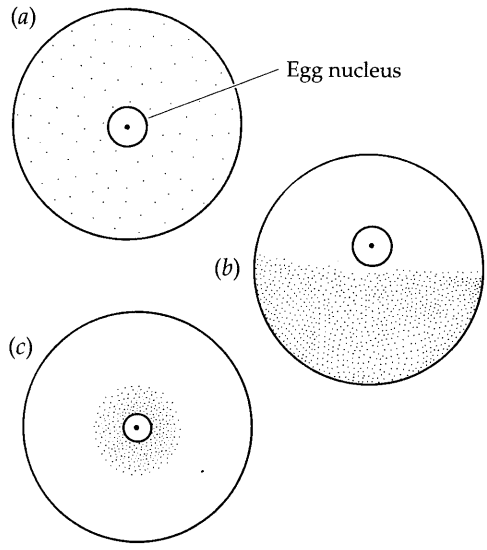


Figure 1.1 Types of ova. The stippling denotes the distribution and relative concentration of yolk within the cytoplasm. *(a)* An isolecithal ovum has a small amount of yolk distributed evenly. *(b)* The yolk in a telolecithal ovum is concentrated toward the vegetal pole. The amount of yolk in such eggs varies greatly. *(c)* A centrolecithal ovum has yolk concentrated at the center of the cell. (From Brusca and Brusca 1990.)

Isolecithal eggs contain a relatively small amount of yolk that is more-or-less evenly distributed throughout the cell. Ova in which the yolk is concentrated at one end (the vegetal pole) are termed **telolecithal eggs**; those in which the yolk is concentrated in the center are called **centrolecithal eggs**. The actual amount of yolk in telolecithal and centrolecithal eggs is highly variable. Yolk production (**vitellogenesis**) is typically the longest phase of egg production, and its duration varies by an order of magnitude among species. Rates of yolk production depend on the specific vitellogenic mechanism used. In general, so-called *r*-selected (opportunistic) species have evolved vitellogenic pathways for the rapid conversion of food into egg production, whereas so-called *K*-selected (specialized) species utilize slower pathways.

Cleavage

The stimulus that initiates development in an egg is usually provided at **fertilization** by the entry into the egg of a sperm cell and the subsequent fusion of the male and female nuclei to produce a fertilized egg, or **zygote**. The initial process of cell division of a zygote is called **cleavage**, and the resulting cells are called **blastomeres**. Certain aspects of the patterns of early cleavage are determined by the amount and placement of yolk, whereas other features are apparently inherent in the genetic programming of the particular organism. Isolecithal and weakly to moderately telolecithal ova generally undergo **holoblastic cleavage**. That is, the cleavage planes pass completely through the cell, producing blastomeres that are separated from one another by thin cell membranes (Figure 1.2*a*). Whenever very large amounts of yolk are present (e.g., as in strongly telolecithal eggs), the cleavage planes do not pass readily through the dense yolk, so the blastomeres are not fully separated by cell membranes. This pattern of early cell division is called **meroblastic cleavage** (Figure 1.2*b*). The pattern of cleavage in centrolecithal eggs is dependent on the amount of yolk and varies from holoblastic to various modifications of meroblastic (for examples, see the descriptions of arthropod development in Chapter 13).

ORIENTATION OF CLEAVAGE PLANES. A number of terms are used to describe the relationship of the planes of cleavage to the animal-vegetal axis of the egg and the relationships of the resulting blastomeres to each other (Figure 1.3). Cell divisions during cleavage are often referred to as either **equal** or **unequal**, the terms indicating the comparative sizes of groups of blastomeres. The term **subequal** is used when blastomeres are only slightly different in size. When cleavage is distinctly unequal, the larger cells are called **macromeres** and usu-

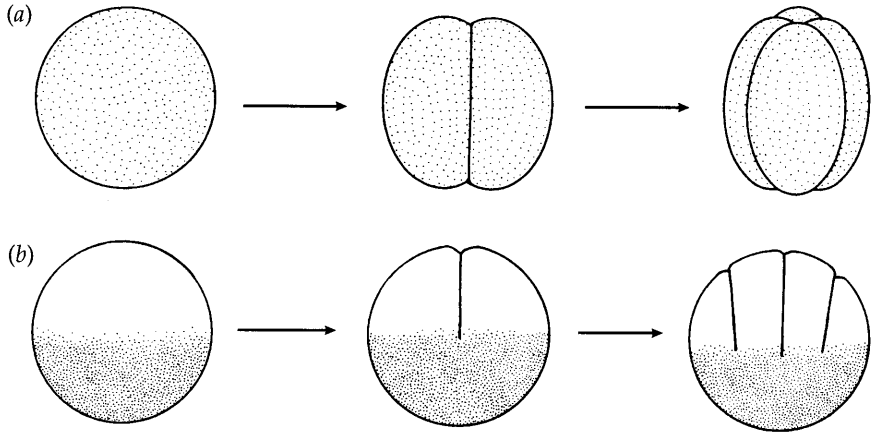


Figure 1.2 Types of early cleavage in developing zygotes. *(a)* Holoblastic cleavage. The cleavage planes pass completely through the cytoplasm. *(b)* Meroblastic cleavage. The cleavage planes do not pass completely through the yolky cytoplasm. (From Brusca and Brusca 1990.)

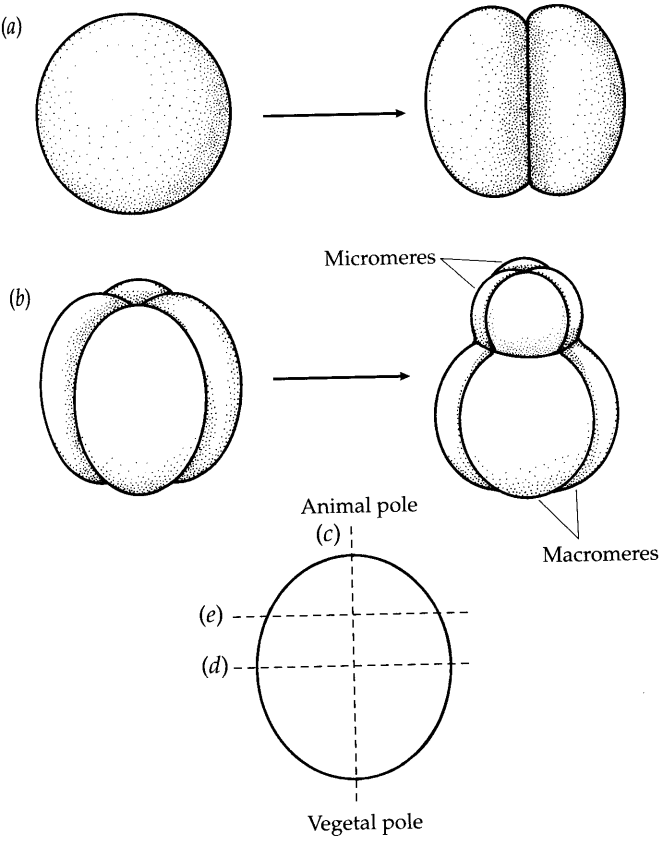


Figure 1.3 Planes of holoblastic cleavage. *(a)* Equal cleavage. *(b)* Unequal cleavage produces micromeres and macromeres. *(c–e)* Planes of cleavage relative to the animal-vegetal axis of the egg or zygote. *(c)* Longitudinal (= meridional) cleavage parallel to the animal-vegetal axis. *(d)* Equatorial cleavage perpendicular to the animal-vegetal axis and bisecting the zygote into equal animal and vegetal halves. *(e)* Latitudinal cleavage perpendicular to the animal-vegetal axis but not passing along the equatorial plane. (From Brusca and Brusca 1990.)

ally lie at the vegetal pole. The smaller cells are called **micromeres** and are usually located at the animal pole.

Cleavage planes that pass parallel to the animal-vegetal axis produce **longitudinal** (= **meridional**) divisions; those that pass at right angles to the axis produce **transverse** divisions. Transverse divisions may be either **equatorial**, when the embryo is separated equally into animal and vegetal halves, or simply **latitudinal** when the division plane does not pass through the "equator" of the embryo.

RADIAL AND SPIRAL CLEAVAGE. Most animals display one of two basic cleavage patterns defined on the basis of the orientation of the blastomeres about the animal-vegetal axis. These patterns are called **radial cleavage** and **spiral cleavage** and are illustrated in Figure 1.4. Radial cleavage involves strictly meridional and transverse divisions. Thus, the blastomeres are arranged in rows either parallel or perpendicular to the animal-vegetal axis. The placement of the blastomeres shows a radially symmetrical pattern in polar view.

Spiral cleavage is quite another matter. Although not inherently complex, it can be difficult to describe. The first

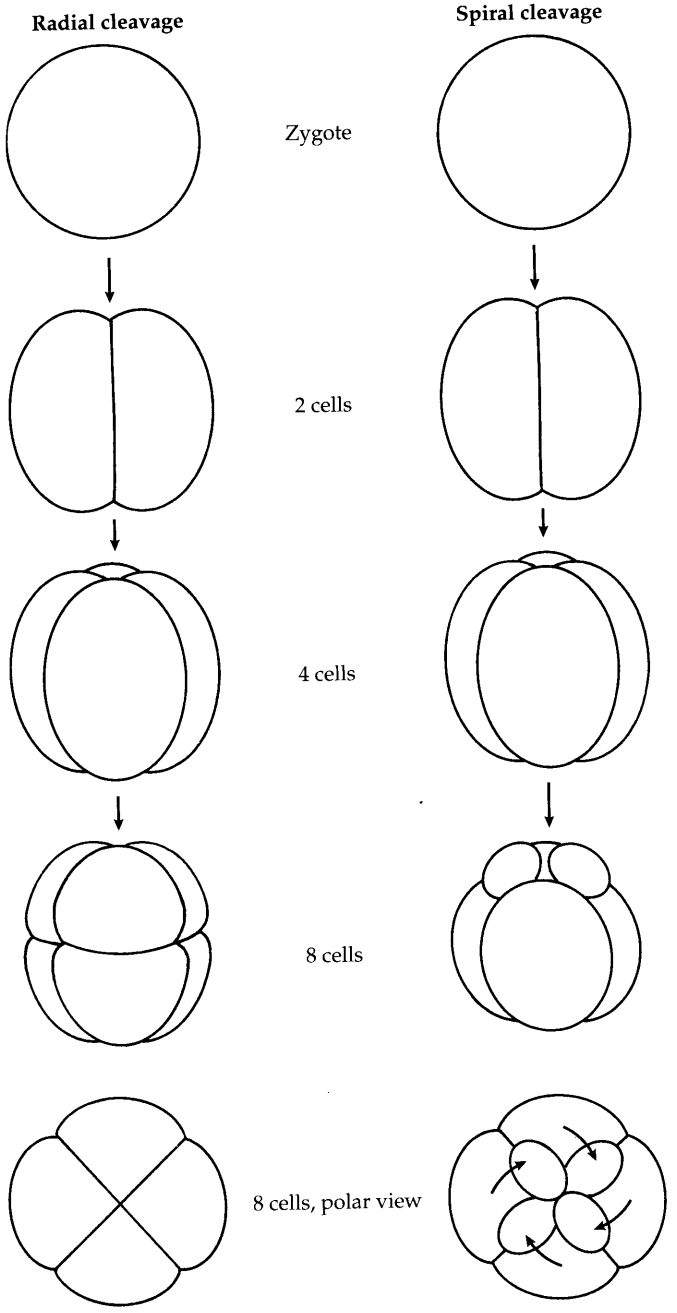
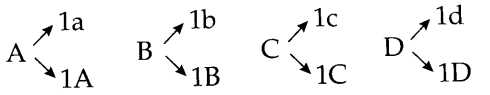


Figure 1.4 Comparison of radial versus spiral cleavage through the 8-cell stage. During radial cleavage, the cleavage planes all pass either perpendicular or parallel to the animal-vegetal axis of the embryo. Spiral cleavage involves a tilting of the mitotic spindles, commencing with the division from four to eight cells. The resulting cleavage planes are neither perpendicular nor parallel to the axis. The polar views of the resulting 8-cell stages illustrate the differences in blastomere orientation. (From Brusca and Brusca 1990.)

two divisions are meridional and usually equal to subequal. Subsequent divisions, however, result in the displacement of blastomeres in such a way that they lie in the furrows between one another. This condition is a result of the formation of the mitotic spindles at acute angles rather than parallel to the axis of the embryo; hence the cleavage planes are neither perfectly meridional nor perfectly transverse. The division from 4 to 8 cells involves a displacement of the cells near the animal pole in a clockwise (**dextrotropic**) direction (viewed from the animal pole). The next division, from 8 to 16 cells, occurs with a displacement in a counterclockwise (**levotropic**) direction; the next is clockwise, and so on, "twisting" back and forth until approximately the 64-cell stage. (In reality, divisions are frequently nonsynchronous; not all of the cells divide at the same rate. Thus, a particular embryo may not proceed from 4 cells to 8, to 16, and so on as neatly as in our generalized example.)

An elaborate coding system for spiral cleavage was developed by E. B. Wilson (1892) during his extensive studies on the polychaete worm *Neanthes succinea* conducted at Woods Hole Biological Station. Wilson's system is usually applied to spiral cleavage in order to trace cell fates and compare development among various taxa. The following account of spiral cleavage is a general one, but it provides a point of reference for considering the patterns seen in different animal groups. Although this coding system may seem a bit confusing at first, it will quickly become evident that it is a rather simple and elegant means by which one may follow the developmental lineage of each and every cell in a developing embryo.

At the 4-cell stage, following the initial meridional divisions, the cells are given the codes A, B, C, and D and are labeled clockwise in that order when viewed from the animal pole (Figure 1.5*a*). These four cells are referred to as a quartet of macromeres, and may be collectively coded as simply Q. The D cell commonly is slightly larger than the others, providing a starting point for the coding process. The next division is more-or-less unequal, with the four cells nearest the animal pole being displaced in a dextrotropic fashion, as explained above. These four smaller cells are called the first quartet of micromeres (collectively the lq cells) and are given the individual codes of 1a, 1b, 1c, and 1d. The numeral "1" indicates a member of the first micromere quartet to be produced; the letters correspond to their respective macromere origins. The capital letters designating the macromeres are now preceded by the numeral "1" to indicate that they have divided once and produced a first micromere set (Figure 1.5*b*). We may view this 8-cell embryo as four pairs of daughter cells that have been produced by the divisions of the four original macromeres, as follows:



One "rule" that will aid you in tracing the cells and their codes through spiral cleavage is that the *only* code numbers that are changed through subsequent divisions are the prefix numbers of the macromeres. These are changed to indicate the number of times these individual macromeres have divided, and to correspond to the number of micromere quartets thus produced. So, at the 8-cell stage, we can designate the existing blastomeres as the 1Q (= 1A, 1B, 1C, 1D) and the lq (= 1a, 1b, 1c, 1d).

It should be mentioned that although the macromeres and micromeres are sometimes similar in size, these terms are nonetheless always used in describing spiral cleavage. Much of the size discrepancy depends upon the amount of yolk present at the vegetal pole in the original egg; this yolk tends to be retained primarily in the larger macromeres.

The division from 8 to 16 cells occurs levotropically and involves cleavage of each macromere and micromere. The macromeres (1Q) divide to produce a second quartet of micromeres (2q = 2a, 2b, 2c, 2d), and 4 daughter macromeres, whose prefix numeral is changed to "2." The first micromere quartet also divides and now comprises eight cells, each of which is identifiable not only by the letter corresponding to its parent macromere but now

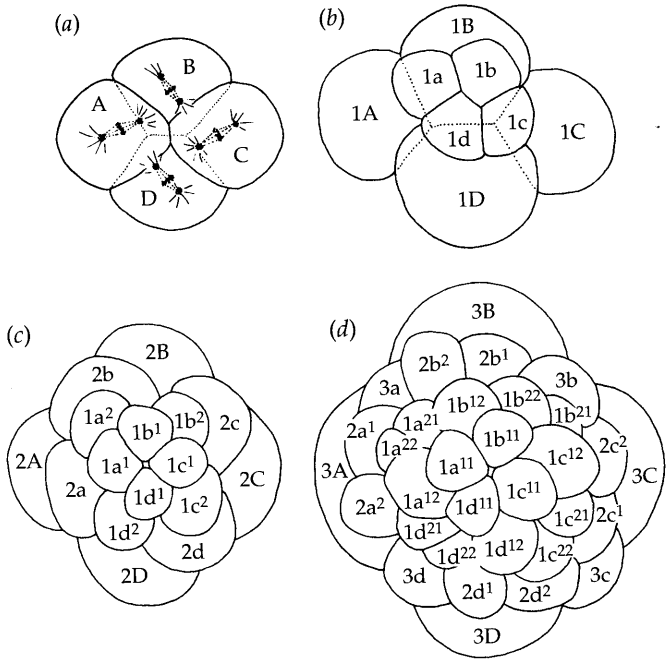


Figure 1.5 Spiral cleavage from 4 to 32 cells (assumed synchronous) labeled with E. B. Wilson's coding system. All diagrams are viewed from the animal pole surface. (From Brusca and Brusca 1990.)

by the addition of superscript numerals. For example, the 1a micromere (of the 8-cell embryo) divides to produce two daughter cells coded the $1a^1$ and the $1a^2$ cells. The cell that is physically nearer the animal pole of the embryo receives the superscript "1," the other cell the superscript "2." Thus, the 16-cell stage (Figure 1.5*c*) includes the following cells:

Derivatives of the 1q: $1a^1$ $1b^1$ $1c^1$ $1d^1$; $1a^2$ $1b^2$ $1c^2$ $1d^2$

Derivatives of the 1Q: $2q = 2a$ $2b$ $2c$ $2d$; $2Q = 2A$ $2B$ $2C$ $2D$

The next division (from 16 to 32 cells) involves dextrotropic displacement. The third micromere quartet (3q) is formed, the daughter macromeres are now given the prefix "3" (3Q), and all of the 12 existing micromeres divide. Superscripts are added to the derivatives of the first and second micromere quartets according to the rule of position as stated above. Thus, the $1b^1$ cell divides to yield the $1b^{11}$ and $1b^{12}$ cells; the $1a^2$ cell yields the $1a^{21}$ and $1a^{22}$ cells; the 2*c* yields the $2c^1$ and $2c^2$, and so on. Do not think of these superscripts as double-digit numbers (e.g., "twenty-one" and "twenty-two") but rather as two-digit sequences reflecting the precise lineage of each cell ("two-one" and "two-two").

The elegance of Wilson's system is that each code tells the history as well as the position of the cell in the embryo. For instance, the code $1b^{11}$ indicates that the cell is a member (derivative) of the first quartet of micromeres; that its parent macromere is the B cell; that the original 1b micromere has divided twice since its formation; and that this particular cell rests uppermost in the embryo relative to its sister cells. The 32-cell stage (Figure 1.5*d*) is composed of the following:

Derivatives of the 1q: $1a^{11}$ $1b^{11}$ $1c^{11}$ $1d^{11}$; $1a^{12}$ $1b^{12}$ $1c^{12}$ $1d^{12}$; $1a^{21}$ $1b^{21}$ $1c^{21}$ $1d^{21}$; $1a^{22}$ $1b^{22}$ $1c^{22}$ $1d^{22}$

Derivatives of the 2q: $2a^1$ $2b^1$ $2c^1$ $2d^1$; $2a^2$ $2b^2$ $2c^2$ $2d^2$

Derivatives of the 2Q: $3q = 3a$ $3b$ $3c$ $3d$; $3Q = 3A$ $3B$ $3C$ $3D$

The division to 64 cells follows the same pattern, with appropriate coding changes and additions of superscripts. The displacement is levotropic and results in the following cells:

Derivatives of the 1q: $1a^{111}$ $1b^{111}$ $1c^{111}$ $1d^{111}$; $1a^{112}$ $1b^{112}$ $1c^{112}$ $1d^{112}$; $1a^{121}$ $1b^{121}$ $1c^{121}$ $1d^{121}$; $1a^{122}$ $1b^{122}$ $1c^{122}$ $1d^{122}$; $1a^{211}$ $1b^{211}$ $1c^{211}$ $1d^{211}$; $1a^{212}$ $1b^{212}$ $1c^{212}$ $1d^{212}$; $1a^{221}$ $1b^{221}$ $1c^{221}$ $1d^{221}$; $1a^{222}$ $1b^{222}$ $1c^{222}$ $1d^{222}$

Derivatives of the 2q: $2a^{11}$ $2b^{11}$ $2c^{11}$ $2d^{11}$; $2a^{12}$ $2b^{12}$ $2c^{12}$ $2d^{12}$; $2a^{21}$ $2b^{21}$ $2c^{21}$ $2d^{21}$; $2a^{22}$ $2b^{22}$ $2c^{22}$ $2d^{22}$

Derivatives of the 3q: $3a^1$ $3b^1$ $3c^1$ $3d^1$; $3a^2$ $3b^2$ $3c^2$ $3d^2$

Derivatives of the 3Q: $4q = 4a$ $4b$ $4c$ $4d$; $4Q = 4A$ $4B$ $4C$ $4D$

Notice that no two cells share precisely the same code, so exact identification of individual blastomeres and their lineages is always possible.

The Problem of Cell Fates

Tracing the fates of cells through development has been a popular and productive endeavor of embryologists for over a century. Such studies have played a major role in enabling researchers not only to describe development but also to establish homologies among attributes in different animals. Although the cells of embryos eventually become established as functional parts of tissues or organs, there is a great deal of variation in the timing of the establishment of cell fates and in how firmly fixed the fates eventually become. Even in the adult stages of some animals (e.g., sponges) the cells retain the ability to change their structure and function, although under normal conditions they are relatively specialized. Furthermore, many groups of animals have remarkable powers to regenerate lost parts, wherein cells may dedifferentiate and then generate new tissues and organs. But in other cases, cell fates are quite firmly fixed and cells are able only to produce more of their own kind.

By carefully watching the development of any animal, one can predict that certain cells are going to form certain structures. In some cases, cell fates are determined very early during cleavage—as early as the 2- or 4-cell stage. If one experimentally removes a blastomere from the early embryo of such an animal, that embryo will fail to develop normally; the fates of the cells have already become fixed, and the missing cell cannot be replaced. Animals whose cell fates are established very early are said to have **determinate cleavage**. On the other hand, the blastomeres of some ani-

mals can be separated at the 2-cell, 4-cell, or even later stages, and each separate cell will develop normally; in such cases the fates of the cells are not fixed until relatively late in development. Such animals are said to have **indeterminate cleavage**. Eggs that undergo determinate cleavage are often called **mosaic ova**, because the fates of regions of undivided cells can be mapped. Eggs that undergo indeterminate cleavage are often called **regulative ova**, in that they can "regulate" to accommodate lost blastomeres.

In any case, formation of an animal's basic body plan is in most cases complete by the time the embryo comprises about 10^4 cells (usually after 1 or 2 days). By this time, all available embryonic material has been apportioned into specific cell groups, or "founder regions." These regions are few in number and are large, each becoming a territory within which still-more intricate developmental patterns unfold. As these zones of undifferentiated tissue are established, the unfolding genetic code drives them to develop into their "preassigned" body tissues, organs, or other structures. Graphic representations of these regions are called **fate maps**.

In the past it has been a general practice to equate mosaic eggs and determinate cleavage with spirally cleaving embryos, and to equate regulative ova and indeterminate cleavage with radially cleaving embryos. However, surprisingly few actual tests for determinacy have been performed, and what evidence is available suggests that there are many exceptions to this generalization. That is, some embryos with spiral cleavage appear indeterminate, and some with radial cleavage appear determinate. Much more work remains to be done on these matters, and for the present the relationships among these features of early development are questionable.

In spite of the variations and exceptions, there is a remarkable underlying consistency in the fates of blastomeres among embryos that develop by typical spiral cleavage. Many examples of these similarities are discussed in later chapters, but we illustrate the point by noting that the germ layers of spirally cleaving embryos tend to arise from the same groups of cells. The first three quartets of micromeres and their derivatives give rise to ectoderm (the outer germ layer), the 4a, 4b, 4c, and 4Q cells to endoderm (the inner germ layer), and the 4d cell to mesoderm (the middle germ layer). Many students of embryology view this uniformity of cell fates as strong evidence that taxa sharing this pattern are related to one another in some fundamental way and that they share a common evolutionary heritage.

Blastula Types

The product of early cleavage is called the **blastula**, which may be defined developmentally as the embryonic form preceding the formation of embryonic germ layers. Several types of blastulae are recognized among invertebrates. A **coeloblastula** frequently results from radial cleavage of ova with relatively small amounts of yolk (Figure 1.6*a*). This blastula is a hollow ball of cells, the wall of which is usually one cell-layer thick. The space within the sphere of cells is the **blastocoel**, or **primary body cavity**. Spiral cleavage often results in a solid ball of cells called a **stereoblastula** (Figure 1.6*b*); obviously there is no blastocoel at this stage. Meroblastic cleavage typically results in a cap or disc of cells (the **blastodisc**) at the animal pole above an uncleaved mass of yolk. This arrangement is appropriately termed a **discoblastula** (Figure 1.6*c*). Some centrolecithal ova undergo odd cleavage patterns to form a **periblastula**, similar in some respects to a coeloblastula, that is centrally filled with noncellular yolk (Figure 1.6*d*).

Gastrulation and Germ Layer Formation

Through one or more of several methods, the blastula develops toward a multilayered form, a process called **gastrulation** (Figure 1.7). The structure of the blastula dictates to some degree the nature of the process and the form of the resulting embryo, the **gastrula**. Gastrulation is the formation of the embryonic germ layers, the tissues on which all subsequent development eventually depends. In fact, we may view gastrulation as the embryonic analogue of the transition from protozoan to metazoan grades of complexity. It achieves separation of those cells that must interact directly with the environment (i.e., locomotory, sensory, and protective functions) from those that process materials ingested from the environment (i.e., nutritive functions).

The initial inner and outer sheets of cells are the **endoderm** and **ectoderm**, respectively; a third germ layer, the **mesoderm**, is produced in most animals between the ecto-

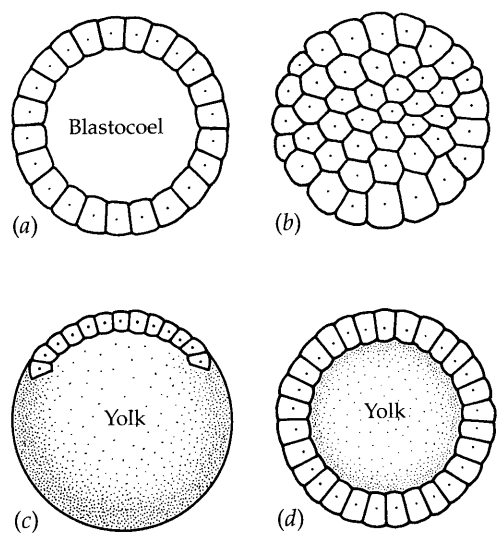


Figure 1.6 Types of blastulae. These diagrams represent sections along the animal–vegetal axis. *(a)* Coeloblastula. The blastomeres form a hollow sphere with a wall one cell layer thick. *(b)* Stereoblastula. Cleavage results in a solid ball of blastomeres. *(c)* Discoblastula. Cleavage has produced a cap of blastomeres that lies at the animal pole, above a solid mass of yolk. *(d)* Periblastula. Blastomeres form a single cell layer enclosing an inner yolky mass. (From Brusca and Brusca 1990.)

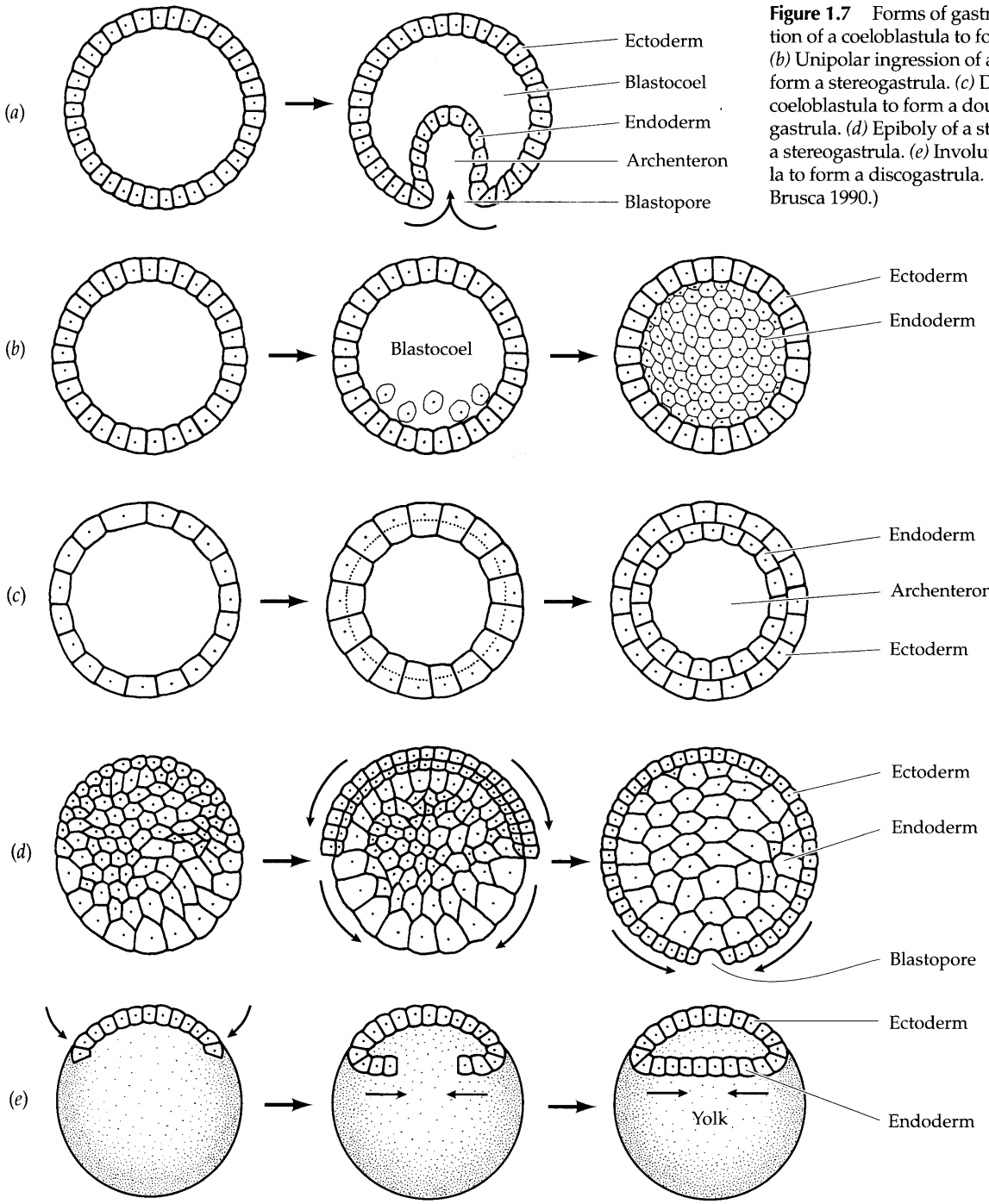


Figure 1.7 Forms of gastrulation. *(a)* Invagination of a coeloblastula to form a coelogastrula. *(b)* Unipolar ingression of a coeloblastula to form a stereogastrula. *(c)* Delamination of a coeloblastula to form a double-layered coelogastrula. *(d)* Epiboly of a stereoblastula to form a stereogastrula. *(e)* Involution of a discoblastula to form a discogastrula. (From Brusca and Brusca 1990.)

derm and the endoderm. One of the principle examples of the unity among the metazoa is the consistency of the fates of these germ layers. For example, ectoderm always forms the nervous system and the outer skin and its derivatives; endoderm the main portion of the gut and associated structures; and mesoderm the coelomic lining, the circulatory system, most of the internal support structures, and the musculature. The process of gastrulation, then, is a critical one in establishing the basic materials and their locations for the building of the whole organism.

Coeloblastulae often gastrulate by **invagination**, a process commonly used to illustrate gastrulation in general zoology classes. The cells in one area of the surface of the blastula (frequently at or near the vegetal pole) grow inward as a sac within the blastocoel (Figure 1.7*a*). These invaginated cells are now called the endoderm, the sac thus formed is the embryonic gut, or **archenteron**, and the opening to the outside is the **blastopore**. The outer cells are now called ectoderm, and a double-layered, hollow **coelogastrula** has been formed.

The coeloblastulae of many cnidarians undergo gastrulation processes that result in a solid **stereogastrula**. Usually the cells of the blastula divide such that the cleavage planes are perpendicular to the surface of the embryo. Some of the cells detach from the wall and migrate into the blastocoel, eventually filling it with a solid mass of endoderm. This process is called **ingression** (Figure 1.7*b*) and may occur only at the vegetal pole (unipolar ingression) or over virtually the whole blastula (multipolar ingression). In a few instances (e.g., certain hydroids) the cells of the blastula divide with cleavage planes that are parallel to the surface, a process called **delamination** (Figure 1.7*c*). Delamination also produces a layer or mass of endoderm surrounded by a layer of ectoderm.

Stereoblastulae that result from holoblastic cleavage generally undergo gastrulation by **epiboly**. Because stereoblastulae have no blastocoel into which the presumptive endoderm can migrate by any of the above methods, gastrulation involves a rapid growth of presumptive ectoderm around the presumptive endoderm (Figure 1.7*d*). Cells of the animal pole proliferate rapidly, growing down and over the vegetal cells to enclose them as endoderm. The archenteron typically forms secondarily as a space within the endoderm.

Figure 1.7*e* illustrates gastrulation by **involution**, a process that usually follows the formation of a discoblastula. The cells around the edge of the disc divide rapidly and grow beneath the disc, thus forming a double-layered gastrula with ectoderm on the surface and endoderm below. There are several other types of gastrulation, mostly variations or combinations of the above processes.

Mesoderm and Body Cavities

Some time following gastrulation, a middle layer forms between the ectoderm and the endoderm. This middle layer may be derived from ectoderm, as it is in members of the diploblastic phyla Cnidaria and Ctenophora, or from endoderm, as it is in all of the triploblastic phyla. In the first case the middle layer is said to be **ectomesoderm**, and in the latter case **endomesoderm**, or "true" mesoderm. Thus, the triploblastic condition, by definition, includes entomesoderm. In most texts, the term *mesoderm* in a general sense refers to endomesoderm rather than ectomesoderm.

In diploblastic and certain triploblastic phyla (the acoelomates), the middle layer does not form thin sheets of cells; rather, it produces a fairly solid but loosely organized **mesenchyme** consisting of a gel matrix (the **mesoglea**) that contains various cellular and fibrous inclusions. In a few cases (e.g., the hydrozoans) a virtually noncellular mesoglea lies between the ectoderm and endoderm.

One of the major trends in the evolution of the triploblastic metazoa has been the development of a fluid-filled cavity between the outer body wall and the digestive tube—that is, between the derivatives of the the ectoderm and the endoderm. The evolution of this structural device created a radically new architecture, a tube-within-a-tube design in which the inner tube (the gut and its associated organs) was freed from the constraint of being attached to the outer tube (the body wall) except at the ends. The fluid-filled cavity not only served as a mechanical buffer between these two largely independent tubes, but it also allowed for the development and expansion of new structures within the body, served as storage chambers for various body products (such as gametes), provided a medium for circulation, and was in itself an incipient hydroskeleton.

Three major grades of construction are recognized among the triploblastic metazoa: **acoelomate**, **pseudocoelomate**, and **eucoelomate**. The acoelomate grade (Greek *a*, "without," and *coel*, "cavity") occurs in two triploblastic phyla, Platyhelminthes and Nematoda. In these animals, the mesoderm forms a more or less solid mass of tissue between the gut and the body wall (Figure 1.8*a*). In most other triploblastic phyla, an actual space develops as a fluid-filled cavity between the body wall and the gut. In many phyla

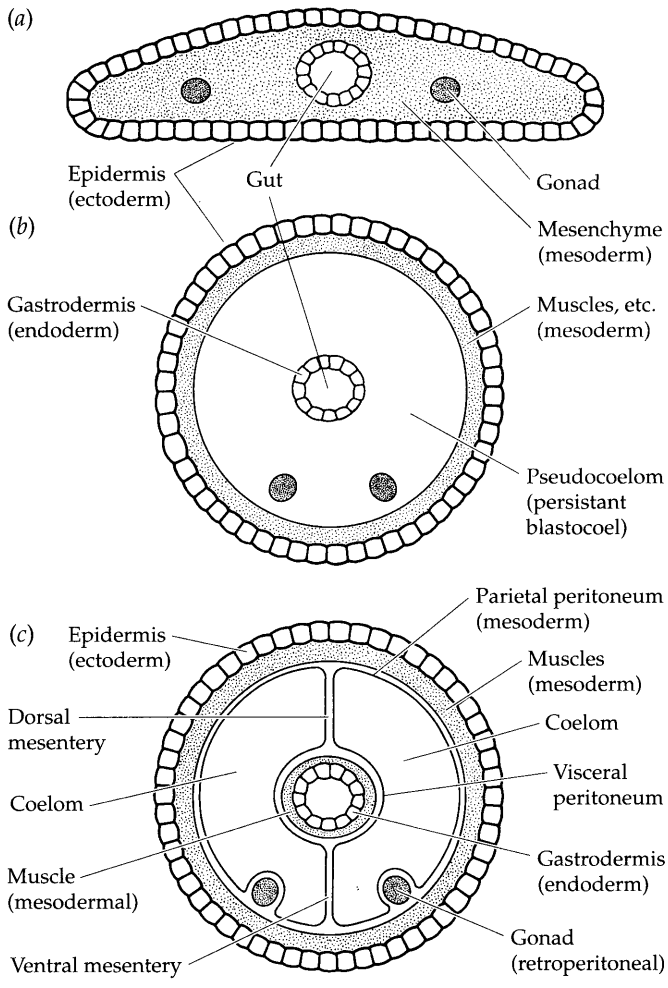


Figure 1.8 Principal body plans of triploblastic metazoa (diagrammatic cross sections). *(a)* Acoelomate. *(b)* Pseudocoelomate. *(c)* Eucoelomate. (From Brusca and Brusca 1990.)

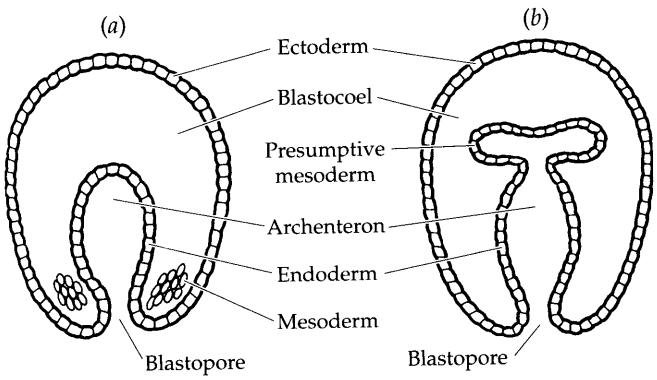


Figure 1.9 Methods of mesoderm formation in late gastrulae (frontal sections). *(a)* Mesoderm formed from derivatives of a mesentoblast. *(b)* Mesoderm formed by archenteric pouching. (From Brusca and Brusca 1990.)

(e.g., annelids, molluscs, and echinoderms), this cavity arises within the mesoderm itself and is completely enclosed within a thin cellular lining called the **peritoneum**, which is derived from the mesoderm. Such a cavity is called a true **coelom**, or eucoelom. Notice that the organs of the body are not actually free within the coelomic space, but are separated from it by the peritoneum (Figure 1.8*c*).

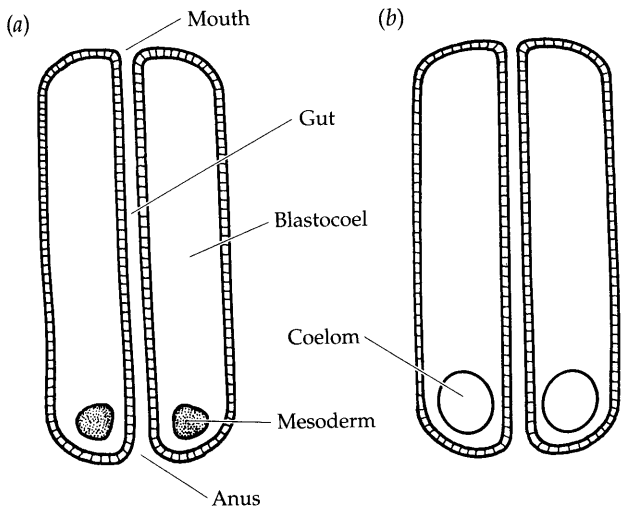
Several phyla of triploblastic metazoa (nematodes, rotifers, and others) possess a body cavity that is neither formed from the mesoderm nor fully lined by peritoneum or any other form of mesodermally derived tissue. Such a cavity is called a **pseudocoelom** (Greek *pseudo*, "false") (Figure 1.8*b*). Unlike the enclosed organs of true coelomates, the organs of pseudocoelomate animals lie free within the body cavity and are bathed directly in its fluid. The embryonic origin of the body spaces in pseudocoelomate animals is unclear. In some cases it appears to be a persistent blastocoel; in other cases its origin is quite unknown.

In eucoelomate animals, mesoderm generally originates in one of two basic ways. In most phyla that undergo spiral cleavage (e.g., annelids, molluscs), a single micromere—the 4d cell, known as the **mesentoblast**—proliferates as mesoderm between the walls of the developing archenteron (endoderm) and the body wall (ectoderm) (Figure 1.9*a*). The other cells of the 4q (the 4a, 4b, and 4c cells) contribute to endoderm. In some other taxa (e.g., echinoderms and chordates), the mesoderm arises from the wall of the archenteron itself (that is, from preformed endoderm), either as a solid sheet or as pouches (Figure 1.9*b*).

The formation and subsequent development of mesoderm is intimately associated with the formation of the body cavity in coelomate metazoa. In those instances where mesoderm has been produced as solid masses derived from a mesentoblast, the body cavity arises through a process called **schizocoely**. Normally in such cases, paired pockets of mesoderm gradually enlarge and become hollow, eventually becoming thin-walled coelomic spaces (Figure 1.10*a,b*). The number of such paired coeloms varies among animal phyla and is frequently associated with segmentation, as it is in annelid worms (Figure 1.10*c*).

The other general method of coelom formation is called **enterocoely**; it accompanies the process of mesoderm formation from the archenteron. In the most direct sort of enterocoely, mesoderm production and coelom formation are one and the same process. Figure 1.11*a* illustrates this process, called **archenteric pouching**. A pouch or pouches form in the gut wall. Each pouch eventually pinches off from the gut as a complete coelomic compartment. The walls of these pouches are defined as mesoderm. In some cases the mesoderm arises from the walls of the archen-

Figure 1.10 Coelom formation by schizocoely (frontal sections). *(a)* Precoelomic conditions with paired packets of mesoderm. *(b)* Hollowing of the mesodermal packets to produce a pair of coelomic spaces. *(c)* Progressive proliferation of serially arranged pairs of coelomic spaces. The process as depicted is characteristic of metameric annelids. (From Brusca and Brusca 1990.)



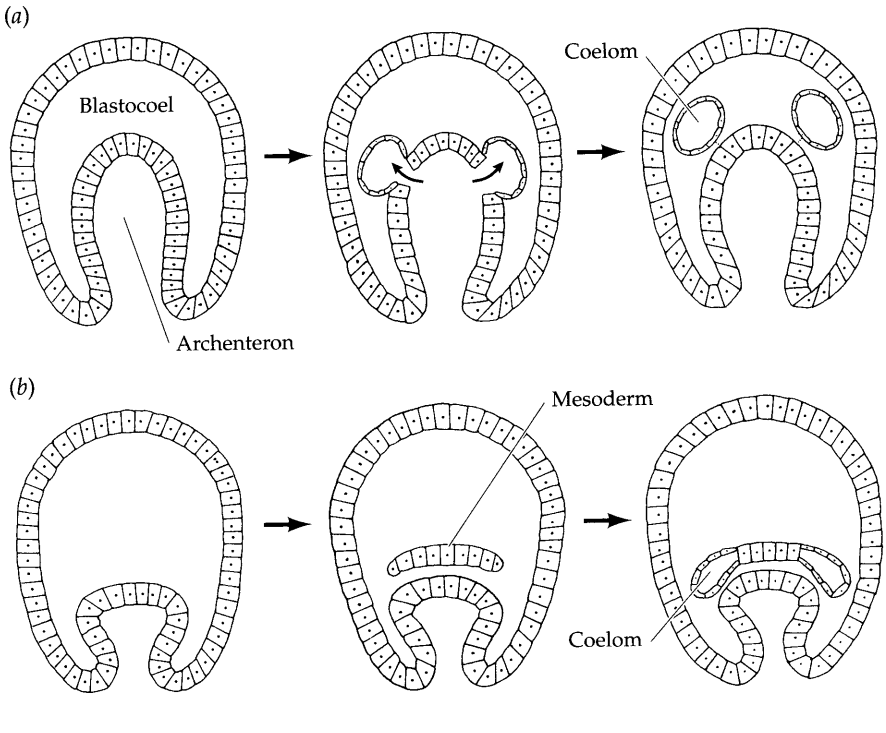


Figure 1.11 Coelom formation by enterocoely (frontal sections). *(a)* Archenteric pouching. *(b)* Proliferation and subsequent hollowing of a plate of mesoderm from the archenteron. *(c)* The typical tripartite arrangement of coeloms in a deuterostome embryo. (From Brusca and Brusca 1990.)

teron as a solid sheet or plate that later becomes bilayered and hollow (Figure 1.11*b*). Some authors consider this process to be a form of schizocoely (because of the "splitting" of the mesodermal plate), but it is in fact a modified form of enterocoely. Enterocoely frequently results in a tripartite arrangement of the body cavities, which are designated **protocoel**, **mesocoel**, and **metacoel** (Figure 1.11*c*).

Body Symmetry

A fundamental aspect of an animal's body plan is its overall shape or geometry. So in order to discuss anatomical architecture and function, we must acquaint ourselves with a basic aspect of body form: symmetry. **Symmetry** refers to the arrangement of body structures relative to some axis of the body. Animals that can be bisected or split along at least one plane, so that the resulting halves are similar to one another, are said to be **symmetrical**. For example, a shrimp can be bisected vertically through its midline, head to tail, to produce right and left halves that are mirror images of one another. Animals that have no **plane of symmetry** are said to be **asymmetrical**. Many sponges, for example, have an irregular growth form and so lack any clear plane of symmetry.

Most animals possess some kind of symmetry, but within this context a great variety of body design has evolved. The simplest form of symmetry is **spherical symmetry**; it is seen in an animal that assumes the form of a sphere, with its parts arranged concentrically around, or radiating from, a central point (Figure 1.12). A sphere has an infinite number of planes of symmetry that can pass through its center to divide the organism into like halves. Spherical symmetry is rare in nature and, in the strictest sense, is found only in certain protozoa. Creatures with spherical symmetry share an important functional attribute with asymmetrical organisms: both groups lack **polarity**. That is, no clear differentiation along an axis exists, other than from the center of the body toward its surface. In all other forms of symmetry, some level of polarity has been achieved, and with polarity comes specialization of body regions and structures.

A body displaying **radial symmetry** has the general form of a cylinder, with one main axis around which the various body parts are arranged (Figure 1.13). In a body displaying perfect radial symmetry, the body parts are arranged equally around the axis, and any plane of sectioning that passes along that axis results in similar halves (rather like a cake being divided and subdivided into equal halves and quarters). Nearly perfect radial symmetry occurs in the simplest sponges, in many cnidarian polyps, and in oocytes (Figure 1.13). Perfect radial sym-

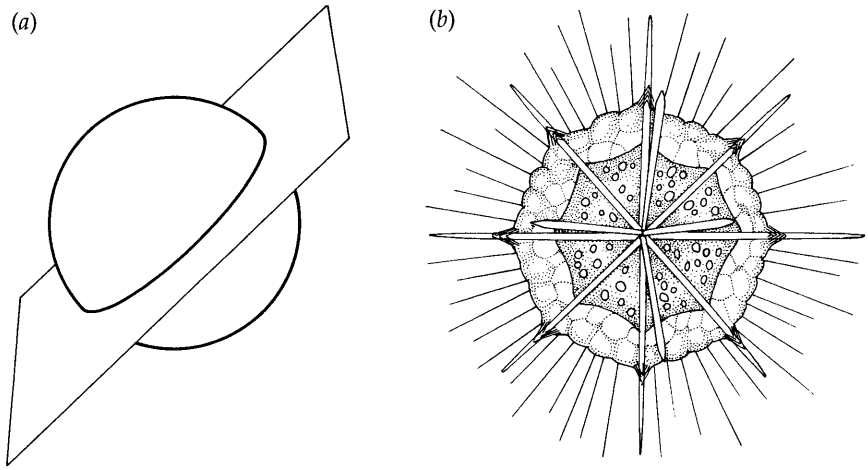


Figure 1.12 Spherical symmetry in animals. *(a)* In spherical symmetry, any plane passing through the center divides the organism into like halves. *(b)* A radiolarian protozoan. (From Brusca and Brusca 1990.)

metry is relatively rare, however, and most radially symmetrical animals have evolved modifications on this theme. **Biradial symmetry**, for example, occurs where portions of the body are specialized and only two planes of sectioning can divide the animal into similar halves. Common examples of biradial organisms are sea anemones and ctenophores.

One adaptively significant feature of radial symmetry is that such animals can confront their environment in numerous directions. A radially symmetrical animal has no front or back end; it is organized about an axis that passes through the center of its body, like an axle through a wheel. When a gut is present, this axis passes through the mouth-bearing (**oral**) surface to the opposite (**aboral**) surface. Radial symmetry is most common in sessile species (e.g., sponges and sea anemones) and drifting pelagic species (e.g., jellyfishes and ctenophores). Given these lifestyles, it is clearly advantageous to be able to confront the environment equally well from a variety of directions. In such creatures one generally finds feeding structures and sensory receptors placed in such a way that they contact the environment more-or-less equally in all directions from the body axis. Furthermore, many fundamentally bilaterally symmetrical animals have become "functionally" radial in certain ways associated with sessile lifestyles. For example, their feeding structures may be in the form of a whorl of radially arranged tentacles, an arrangement allowing more efficient contact with their surroundings.

The body parts of **bilaterally symmetrical** animals are oriented about an axis that passes from the front (**anterior**) to the back (**posterior**) end. There is a single plane of symmetry, passing along the axis of the body to separate right and left sides, the **midsagittal plane** (or median sagittal plane). A longitudinal plane passing perpendicular to the sagittal plane and separating the backside (**dorsal**) from the underside (**ventral**) is called a **frontal plane**. Any plane that cuts across the body, from side to side, is called a **transverse plane** (or, more simply, a cross section) (Figure 1.14). In bilaterally symmetrical animals, the term **lateral** refers to the sides of the body, or to structures away from and to the right and left of the midsagittal plane. The term **medial** refers to the midline of the body, or to structures on or near the midsagittal plane.

Whereas spherical and radial symmetry are typically associated with sessile or drifting animals, bilaterality is generally found in animals with controlled mobility. In these animals, the anterior end of the body confronts the environment first. With the evolution of bilateral symmetry and unidirectional movement, one finds an associated concentration of feeding and sensory structures at the anterior end. The formation of a head end is called **cephal-**

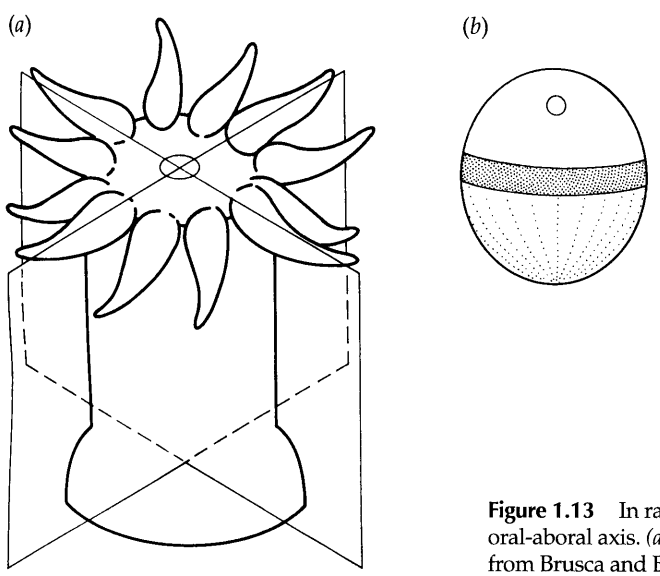


Figure 1.13 In radial symmetry, the body parts are arranged radially around a central oral-aboral axis. *(a)* A representation of perfect radial symmetry. *(b)* Sea urchin oocyte. (*a* from Brusca and Brusca 1990.)

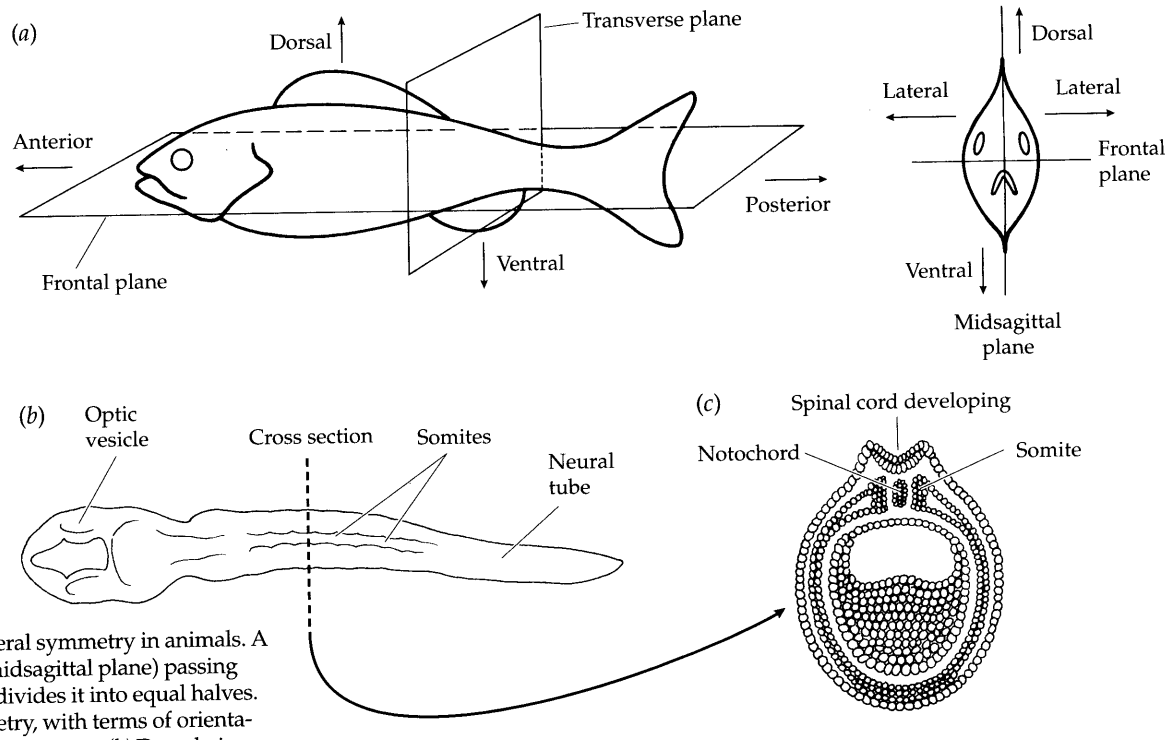


Figure 1.14 Bilateral symmetry in animals. A single plane (the midsagittal plane) passing through the body divides it into equal halves. *(a)* Bilateral symmetry, with terms of orientation and planes of symmetry. *(b)* Dorsal view of amphibian larva. *(c)* Cross section of the amphibian larva at the transverse plane indicated.

ization. Furthermore, with the differentiation of dorsal and ventral surfaces, the ventrum often becomes locomotory and the dorsum often is specialized for protection. A variety of secondary asymmetrical modifications of bilateral (and radial) symmetry have occurred, for example, the spiral coiling of gastropods and hermit crabs. Most asymmetrical modifications result from the displacement of certain body parts because of the habit of being fastened on one side rather than on the ventral surface, or from unequal development of certain paired structures.

Development and Evolution

Homology

Evolution consists of hereditable changes that alter development. When we say that the one-toed horse is derived from a five-toed ancestor, we are saying that changes have occurred in the development of the limb cartilage cells. Some genes involved in chondrocyte growth, placement, or differentiation have been altered. The origin of any new structure or structural modification does not take place in an adult, but by modifications of embryonic or larval development.

Some of the best evidence for evolution is provided by featues that are homologous between embryos of different organisms. **Homologies** are seen when unity of form persists in a diversity of structures that share a common origin—structures inherited from a common ancestor. Because evolution involves *descent with modification*, we should not necessarily expect structures in related organisms to be identical, only similar. The bones of a human hand, a bat wing, a bird wing, and a seal flipper are all composed of the same fundamental elements, but the elements are arranged differently. The concept of homology is one of the most crucial ideas in biology today. As David Wake (1995) has written:

> Homology is the central concept for *all* biology. Whenever we say that a mammalian hormone is the "same" as a fish hormone, that a human sequence is the "same" as a sequence in a chimp or a mouse, that a HOX gene is the "same" in a mouse, a fruit fly, a frog, and a human—even when we argue that discoveries about a roundworm, a fruit fly, a frog, a mouse, or a chimp have relevance to the human condition—we have made a bold and direct statement about homology.

Homology was originally defined as "the same organ in different animals under every variety of form and function" (Owen, 1843). In recent years, this definition has been defined more carefully. First, modern definitions of homology have extended the levels at which homology may be ascertained. In addition to the organs and skeletal parts recognized by Owen, one can now seek homologies between different organisms by looking at their genes and proteins. Second, modern definitions stress that homologous features can only exist between organisms derived from a common ancestor. Thus, one such definition (Futuyma, 1986) proposes that homology is the possession in two or more species of a trait derived, with or without modification, from the same trait in their common ancestor.

Similar structures need not be homologues. Characteristics are homologous only if they have "continuity of information" from their common origin. Such continuity means that there is a genealogical relationship. Thus, characteristics of two organisms can be homologous only if the same character (or its precursor) was present in their common ancestor. To give a cultural example, one could discuss whether the pyramids of Egypt and Mexico are homologous (van Valen 1982). If they share a common ancestor, they would be considered homologous structures (each diverging from the same ancestral pyramid design). If they do not share a common ancestor, they would be seen an example of **convergence**. Convergent structures have similar characteristics but are not derived from a common ancestor. The bivalved shells of clams and the bivalved shells of brachiopods (lamp shells) evolved independently and are therefore not homologous. Such products of convergence are often referred to as **analogues**. The wing of a mosquito and the wing of a bird are another pair of analogous structures. They perform the same functions and look similar, but their parts are not linked by continuity with a common ancestor.

Distinguishing convergent structures (which evolve independently in different groups to perform similar functions) from homologous structures (which are derived from a common ancestor) is a major task in determining which organisms are closely related. Identifying homologies provides a powerful means of unraveling evolutionary history and classifying organisms.

Synapomorphy and Symplesiomorphy

Synapomorphies are shared homologues inherited from an immediate common ancestor. These "shared derived traits" separate one group from all others. The mammary glands of different species of mammals may differ from one another, but the presence of mammary glands themselves is a synapomorphy that characterizes the mammals as a group distinguishable from all other vertebrates. Mammary glands constitute a shared derived trait. This particular trait did not arise *de novo*. Rather, the mammary gland evolved from other types of glands found in reptiles. Thus, at some deeper level mammals and reptiles also share a homology (the glandular precursor of a mammary gland). Another example is the presence of hair, also a defining trait (synapomorphy) of mammals. Hair is derived from evolutionary modifications of reptilian scales. All mammals have hair, and *no other group* of animals has it.

A related term, **symplesiomorphy**, is used for homologous features inherited from ancestors more remote than the immediate common ancestor. Thus, hair and mammary glands are synapomorphic characters that define the emergence of mammals among vertebrates, but they are symplesiomorphic traits shared by species groups *within* the class Mammalia. Because symplesiomorphies are shared ancestral traits, they tell us nothing about relationships among the groups that share them. Thus, among the vertebrate classes, the mammals are distinguished by the synapomorphies of hair and mammary glands. Similarly, the jawed vertebrates are shown to be more closely related to each other than they are to the agnathans (jawless fishes) because they share the derived trait (synapomorphy) of articulating jaws. However, *within* the class Mammalia, the presence of hair and mammary glands are shared ancestral traits—symplesiomorphies—and are of no use in evaluating relationships among the orders of mammals.

Synapomorphies in embryonic and larval stages provide some of the best evidence for evolutionary descent from a common ancestor. Although the adult barnacle looks nothing like a crab or lobster, the presence of a nauplius larva in barnacle development indicates that barnacles should be grouped with the crustaceans, because the nauplius larva is a unique synapomorphy defining the taxon Crustacea. Similarly, although an adult tunicate doesn't look like any vertebrate (or like anything else on this planet), the presence of a notochord—a synapomorphy that defines the phylum Chordata—in the larvae of both groups shows the affinity of tunicates and vertebrates.

Homology (synapomorphies and symplesiomorphies) can also be seen at the molecular level. Such relationships can be observed in the homologous genes whose protein products control cell division. Even between very divergent species (such as humans and yeasts), these genes share very similar nucleotide sequences. Some of these genes are so similar that the gene for the human protein can replace the homologous gene in yeast and allow the yeast cells to divide. The presence in numerous phyla of a large number of very similar genes involved in cell division strongly suggests that all of these genes were derived from a common ancestor and are thus homologous.

Although these homologous genes are usually common to many phyla, there are often small differences in their nucleotide sequences. These differences may have little or no effect on the mechanics of cell function, but they can be used as synapomorphies to separate the living kingdoms into smaller groups. For instance, if there is a particular base pair change in the gene encoding the small subunit (18S) ribosomal RNA, and that base pair substitution is found only in a certain group of animals, then that group of animals can be hypothesized to be united by that substitution. By cataloging many of these structural and molecular synapomorphies, one can attempt to reconstruct the relationships among the various taxa. One such reconstruction is shown in Figure 1.15.

Researchers can also compare the rates of these nucleotide sequence changes with the fossil record in an attempt to calculate "clocks" of gene evolution. On the basis of protein and gene homologies, one extensive study recently concluded that prokaryotes and eukaryotes diverged about 2 billion years ago, and that animals, plants, and fungi did not diverge from each other until nearly a billion years later (Doolittle et al. 1996). The plants may have diverged first, leaving a common ancestor for animals and fungi

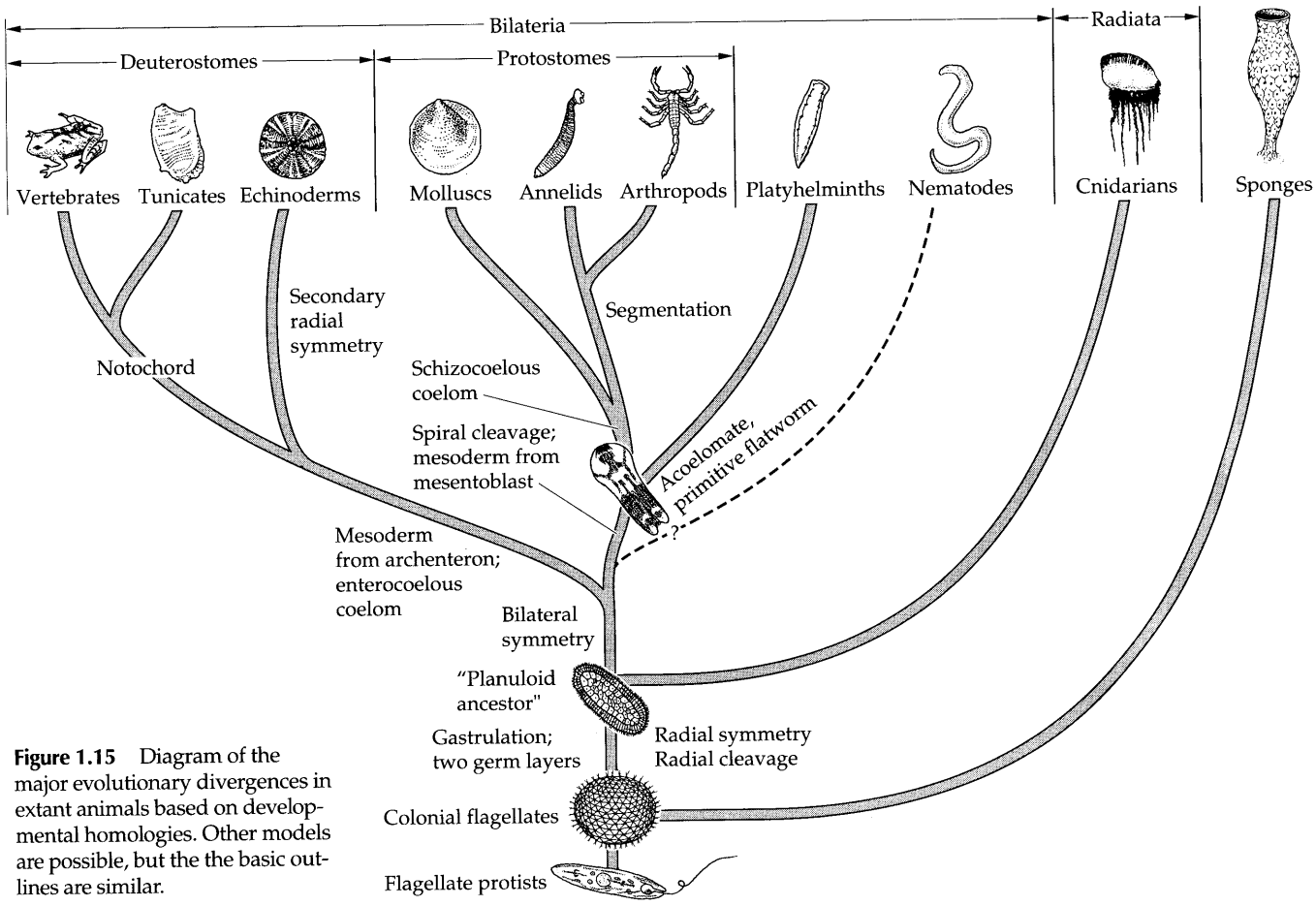


Figure 1.15 Diagram of the major evolutionary divergences in extant animals based on developmental homologies. Other models are possible, but the the basic outlines are similar.

(Figure 1.16*a*). Most studies have implicated the choanoflagellates as the protists most likely to have shared a common ancestor with the animals. One recently published hypothesis of evolutionary divergence within animals, based on paleontological data (Valentine et al. 1996), is shown in Figure 1.16*b*. These studies are not without their critics. Assumptions have been made in reading the fossil record, in choosing which changes are important and which are not, in deciding which changes are the result of evolutionary convergence and which show common ancestry, and in choosing the mathematical algorithms that integrate the different sets of data. Still, one can get a sense of the outline of how the major living groups evolved. For more information on how these relationships are detected and depicted, see Brusca and Brusca (1990) and Raff (1996).

Levels of Homology

Any assignment of homology must specify the *level* at which this assignment is being made (see Bolker and Raff 1996). For example, bat wings and bird wings are homologous if they are viewed as tetrapod forelimbs. That is to say, the bony structures of these forelimbs are similar because they are derived from the common ancestor of all tetrapods. However, bird and bat wings are not homologous when viewed as functional wings. Wings emerged in the birds, and bat wings emerged *independently* in one group of mammals. On the other hand, the gliding wing of the albatross and the paddle-like wing of the penguin are homologous as wings, since both are derived from an ancestral avian winged structure.

The level of homology is of critical concern when assessing the relationship between molecular and structural homologies. For example, the Pax6 protein may be present in every photoreceptor in the animal kingdom. Thus, it has been claimed that, on the molecular level, all photoreceptors share a homology, derived from a primordial photoreceptor containing the Pax6 protein (Quiring et al. 1994). However, on the structural level, the compound eye of the fly, the "inverted" cephalopod eye, and the mammalian eye are definitely analogous structures, each formed in a very different manner and having very different anatomies. Similarly, the fly leg and the chick leg are obviously analogous. The arthropod appendage develops from the ectodermal cells of an imaginal disc that everts during metamorphosis and secretes a cuticular exoskeleton. The chick leg forms from interactions between a particular region of trunk ectoderm with a particular region of mesoderm, which form a cartilagenous endoskeleton

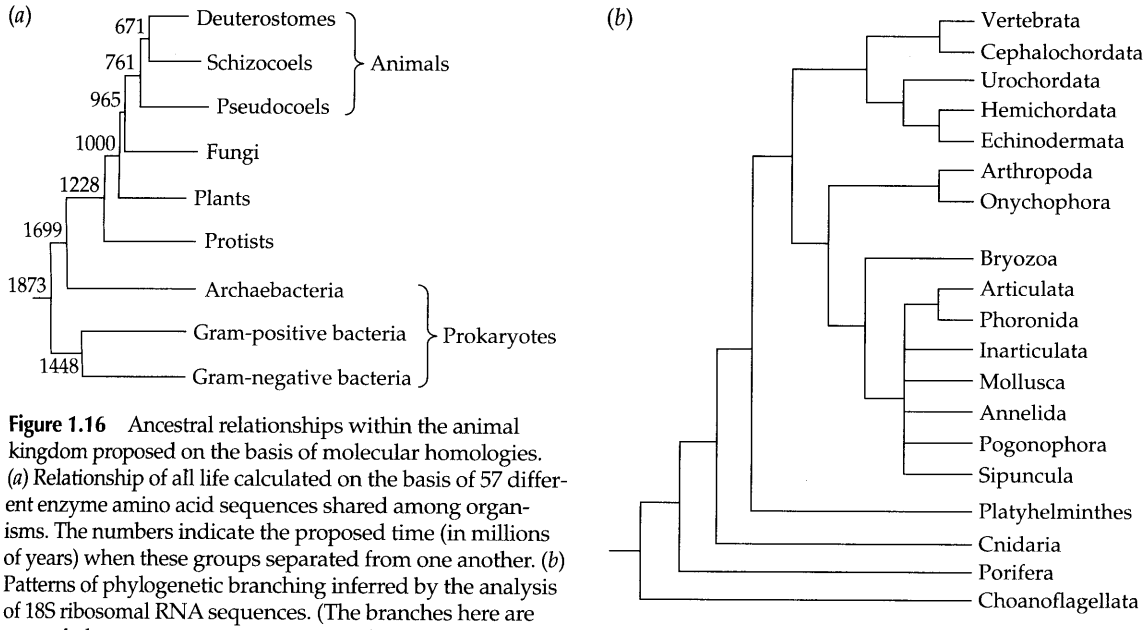


Figure 1.16 Ancestral relationships within the animal kingdom proposed on the basis of molecular homologies. (*a*) Relationship of all life calculated on the basis of 57 different enzyme amino acid sequences shared among organisms. The numbers indicate the proposed time (in millions of years) when these groups separated from one another. (*b*) Patterns of phylogenetic branching inferred by the analysis of 18S ribosomal RNA sequences. (The branches here are not scaled to represent any time intervals.) (*a* from Doolittle et al. 1996; *b* from Valentine et al. 1996.)

that gradually is replaced by bone. The anatomical development and adult anatomy of fly and chick legs have hardly anything in common. However, the chick and the fly apparently use the same sets of genes to specify both the placement of the limbs along the body axis and the polarity of the limb axes. Some key regulatory genes are homologous, whereas the structures are analogous.

Developmental Homologies

Homologies can relate embryology and evolution, and biologists have used embryological homologies in several ways. One way embryological homology can be used is to show the relationships among taxa. As mentioned earlier, synapomorphies (derived homologues) can sometimes be seen in embryonic or larval states more readily than in adults. The larvae of tunicates demonstrate their affinity to vertebrates, and the spirally cleaving embryos of annelids show their affinity to molluscs. Also, adult structures that do not appear to be derived from a common ancestor may be found to have the same embryological origins. The most celebrated of these homologies is that between the middle ear bones of mammals (the stapes, malleus, and incus bones) and the articulation region of the reptilian jaw. Although the adult structures differ enormously, the embryonic development of the mammalian ear bones parallels the fossil record of cartilage changes in the reptilian jaw apparatus.

Homologies also link development and evolution by showing how developmental changes in identical structures can produce evolutionary novelties. One mechanism that produces variety among homologous structures is **allometric growth**. Allometric growth is seen when different growth rates develop in different parts of the organism. In the male fiddler crab, *Uca pugnax*, the mass of the waving claw increases six times faster than the mass of the rest of its body. Thus, unlike other crabs (and unlike the females of its own species), this animal's claw becomes enormous, although the structure is homologous to the normal claw. Allometric growth is important in distinguishing the different morphologies of ants, giving the workers ("soldiers") larger jaws.

Another way to produce an evolutionary change is by **heterochrony**, the phenomenon wherein animals change the rate of their development or the relative time of appearance of features inherited from their ancestors. For instance, some salamanders have accelerated the production of gonads relative to the rest of the embryo, causing the animal to become a sexually mature adult at a much earlier stage. In *Bolitoglossa occidentalis*, the adult stage is reached while this amphibian still has webbed feet and is very small. Its minute body size and feet that can be used to produce suction enable *B. occidentalis* to climb trees, a niche rarely occupied by salamanders. This species is thought to have evolved from a related species that passes through a juvenile stage similar to the adult stage of *B. occidentalis*.

Another way embryonic homologies have been used is to look at the expression patterns of homologous genes during development. As mentioned earlier, the *Pax6* gene appears to be expressed in the developing eye throughout the animal kingdom. Instead of having developed independently in several groups of organisms, it is possible that all the different types of animal eyes each evolved from a common ancestor that expressed the *Pax6* gene (Quiring et al. 1994). Similarly, a gene called *tinman* (because the mutant lacks a heart) appears to be expressed in heart primordia in both flies and vertebrates (Scott 1994). Not only are these genes homologous, but the patterns of their expression ap-

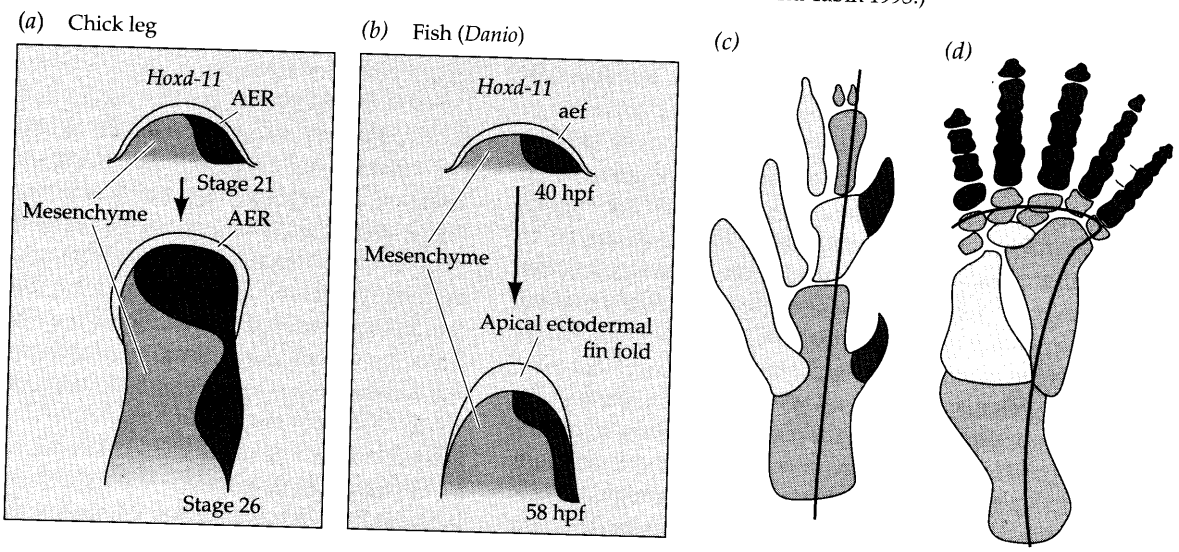
pear to be similar. This level of homology has important implications for the mechanisms of evolution, and it implies powerful conservatism within the animal kingdom.

A variation of this way of using homologies in embryonic gene expression to study evolution is to consider certain pathways as homologous. Here the "characteristic" being compared is not a structure or a molecule, but a biochemical pathway (De Robertis and Sasai 1996; Gilbert et al. 1996). For instance, the neural tube in vertebrates (deuterostomes) is specified by certain proteins blocking the action of a protein called bone morphogenesis protein 4 (BMP4). Interestingly, the same proteins appear to specify the neural tube in flies (protostomes)—also by blocking BMP4. The pathways by which the neural tube is constructed in the ventral portion of the fly embryo and the dorsal portion of the vertebrate embryo appear to be remarkably constant despite the 500 million years of divergence between these two groups. This similarity suggests that there may have been only one original way of making a neural tube, and that it was not invented separately in protostomes and deuterostomes.

Another way homologous genes have been used to examine evolution is in studies that indicate how, in related organisms, homologous structures may take different forms because the expression of homologous genes has been altered during development. For instance, there have been enormous debates about the origin of the amphibian leg from the fish fin. As Richard Owen pointed out, there is considerable homology between the bones of the fish fin and the tetrapod limb, the pectoral and pelvic fins of the fish being homologous to the fore and hindlimbs, respectively. While specific homologies were able to be made between the proximal elements (zeugopod; tibia and fibula) of the fin and limb, homologies between the autopod of the limb (the hand or foot at the distal end) and the rays of the fins "did not hold water." While there seems to be homology for the proximal elements of the limb, the autopod seems to be something new.

Recent studies have strongly suggested that the expression of a particular cluster of genes called the *Hox* genes may be crucial in the change from fin to limb. In the early limb bud of chicks and mice, certain *Hox* genes are expressed only in the posterior end of the limb bud. This is similar to the situation in the zebrafish fin bud (Figure 1.17; Sordino et al. 1995). However, in the development of the foot, there is a second phase, where the expression of these genes changes. Instead of being restricted to the posterior of the limb bud, the *Hox* genes are expressed across the distal mesoderm. This band of expression is coincident with the "digital arch" from which the digits form. These studies show that, whereas the *Hox* gene expression pattern is "homologous" between fish fin and chick leg in the proximal regions, the expression in the late bud distal mesenchyme is new. It also confirms the paleontological-developmental studies of Shubin and Alberch (1986), who proposed that the path of digit formation was not (as previously believed) through the fourth digit (making the fin rays homologous the other digits), but through an arch of distal wrist condensations (metapterygia) that begins posteriorly and turns anteriorly across the distal mesenchyme. Thus, the border of *Hox* gene expression follows the metapterygial axis that Shu-

Figure 1.17 Differences in the expression of the *Hox* gene *Hoxd-11* in fish fin and tetrapod leg. (*a*) Regions of *Hoxd-11* expression in the mouse hindlimb from an early bud stage to a later one. During the later stages, the *Hoxd-11* expression pattern extends across the anterior-posterior border of the progress zone. (*b*) In the zebrafish pectoral fin, *Hoxd-11* expression continues posteriorly, but does not extend anteriorly. (*c, d*) Origin of digits as an evolutionary novelty. (*c*) Diagrammatic representation of a primitive fish fin showing a central axis (black) with rays radiating anteriorly (light gray) and posteriorly (dark gray). (*d*) Current view of autopod formation. The axis originally extends posteriorly, but then curves anteriorly across the metapterygial cartilage. The tibia is considered to branch anteriorly, but the digits are not homologous to any rays. (*a, b* after Sordino et al. 1995; *c, d* after Nelson and Tabin 1995.)



bin and Alberch hypothesized as being the origin of digits. The reoriented, distal, phase of this *Hox* gene expression pattern represents a new and "derived" condition (i.e., a synapomorphy). This, in turn, might have evolved due to changes in the regulation of these *Hox* genes. We are finally coming to a point in biology where changes in gene expression on the molecular level can be linked to evolutionary change at the phylogenetic level.

A deeper understanding of evolutionary processes will emerge as we come to understand how changes in developmental processes create new structures and new combinations of old structures. We will not have this knowledge until we know the developmental processes occurring in the various animal phyla. In 1894, Wilhelm Roux, one of the founders of experimental embryology, predicted that once the physiology of development was known, comparisons between the phyla could delineate the paths by which life evolved on earth. We are finally at the point of being able to fulfill his prediction. But before we can do so, we must learn more about the various ways that embryos have evolved. Fortunately, the study of embryology is among the world's more fascinating subjects. There are few real "crimes against nature," but making embryology boring must count as one of them.

Literature Cited

Bolker, J. A. and R. A. Raff. 1996. Developmental genetics and traditional homology. *BioEssays* 18: 489–494.

Brusca, R. C. and G. J. Brusca. 1990. *Invertebrates*. Sinauer Associates, Sunderland, MA.

De Robertis, E. M. and Y. Sasai. 1996. A common plan for dorsoventral patterning in Bilateria. *Nature* 380: 37–40.

Doolittle, R. F., D.-F. Feng, S. Tsang, G. Cho and E. Little. 1996. Determining divergence times of the major kingdoms of living organisms with a protein clock. *Science* 271: 470–477.

Futuyma, D. J. 1986. *Evolutionary Biology*, 2nd Ed. Sinauer Associates, Sunderland, MA.

Gilbert, S. F. 1997. *Developmental Biology*, 5th Ed. Sinauer Associates, Sunderland, MA.

Gilbert, S. F., J. M. Opitz and R. A. Raff. 1996. Resynthesizing evolutionary and developmental biology. *Dev. Biol.* 173: 357–372.

Nelson, C. E. and C. Tabin. 1995. Footnote on limb evolution. *Nature* 375: 630–631.

Owen, R. 1843. *Lectures on Comparative Anatomy and Physiology of the Invertebrate Animals, delivered at the Royal College of Surgeons in 1843.* Longman, Brown, Green and Longman, London.

Quiring, R., U. Waldorf, U. Kotler and W. J. Gehring. 1994. Homology of the *eyeless* gene of *Drosophila* to the *Small eye* gene of mice and aniridia in humans. *Science* 265: 785–789.

Raff, R. A. 1996. *The Shape of Life: Genes, Development, and the Evolution of Animal Form.* University of Chicago Press, Chicago.

Roth, V. L. 1988. The biological basis of homology. In *Ontogeny and Systematics*. C. J. Humphries (ed.), Columbia University Press, New York, pp. 1–26.

Roux, W. 1894. The problems, method, and scope of developmental mechanics. Trans. W. H. Wheeler. In *Biological Lectures of the Marine Biological Laboratory, Woods Hole*, Ginn, Boston, pp. 149–190.

Scott, M. P. 1994. Intimations of a creature. *Cell* 79: 1121–1124.

Shubin, N. H. and P. Alberch. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evol. Biol.* 20: 319–387

Sordino, P., F. van der Hoeven and D. Duboule. 1995. *Hox* gene expression in teleost fins and the origin of the vertebrate digits. *Nature* 375: 678–681.

Valentine, J. W., D. H. Erwin and D. Jablonski. 1996. Developmental evolution of metazoan body plans: The fossil evidence. *Dev. Biol.* 173: 373–381.

van Valen, L. 1982. Homology and causes. *J. Morphol.* 173: 305–312.

Wilson, E. B. 1892. The cell lineage of *Nereis*. *J. Morphol.* 6: 361–480.