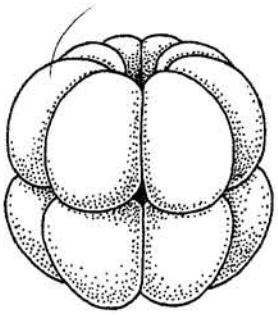
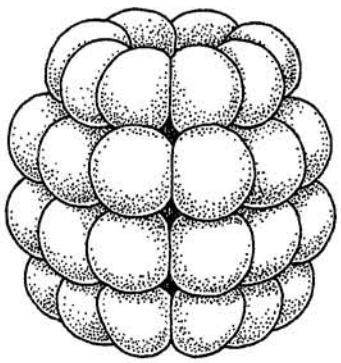
CHAPTER 2

Invertebrate Classification and Relationships

"According to my opinion, (which I give every one leave to hoot at . . .) classification consists in grouping beings according to their actual *relationship,* i.e., their consanguinity, or descent from common stocks."
Charles Darwin (1843)





Introduction

About 1 million animal species have been described and named so far, but at least another 4 to 10 million species probably await discovery and description; many will undoubtedly become extinct without being discovered. Probably several hundred million other species were here previously but are now extinct. At one time, presumably, there were no animals. The marvelous variety of animal life-forms seen today and in the fossil record evolved gradually, beginning over 3 billion years ago; the Earth itself is over 4.5 billion years old.

Multicellular life seems to have taken quite a long time to evolve from single-celled ancestral forms: Fossils of the earliest known unicellular eukaryotes (see Chapter 3) are about 1.8 to 1.9 billion years old, but the oldest known fossils of multicellular animals (called *metazoans*) or their burrows are no more than 544 to 580 million years old, members of the so-called Ediacaran fauna. Moreover, none of those Ediacara animals from 550 or so million years ago had shells, bones, or other hard parts, and their relationship to modern animals, if any, is unclear. The first sizable metazoans that are clearly related to modern animals appear abruptly in the Cambrian period. The best-studied fossils are from the Burgess Shale of British Columbia, first discovered only in 1909 but formed some 525 million years ago (mya) in the mid-Cambrian. Many of the animals were soft-bodied and others had hard parts, but their most conspicuous feature is their substantial diversity. A similar fauna was discovered more recently in China, from older sedimentary rocks formed in the early Cambrian, about 540 mya. This amazingly sudden appearance and apparently rapid

diversification of complex animals over several millions of years has been called the **Cambrian explosion.**

There is now some evidence that the Cambrian explosion reflects an incomplete fossil record. For example, what appear to be arthropod-like metazoan embryos have recently been described from southern China in rocks formed about 570 mya (Fig. 2.1), suggesting that large-bodied forms related to modern animals existed well before the recorded Cambrian explosion. More dramatically, some recent molecular studies suggest that most basic animal body plans existed at least 100 million years before any were preserved as fossils. This suggestion is based on differences in the amino acid sequences of particular proteins or differences in the nucleotide sequences of particular genes (e.g., cytochrome c) that are widespread among various animal groups, coupled with estimates of how long it should have taken for the proteins or underlying gene sequences to have diverged that far from each other. If the interpretations of these data are correct, the basic animal groups may have begun diverging as long ago as 1 billion years, but without leaving any historical record for the first 400 to 500 million years of their evolution. Possibly these early animals were simply too small and lacking in hard parts to be fossilized. Perhaps it was the gradual increase in atmospheric oxygen above some critical concentration, due to increases in photosynthesis, that permitted larger body sizes and hard, impermeable outer body coverings to evolve, creating novel opportunities for fossilization. Or perhaps the particular environmental conditions needed for fossil formation simply did not exist before about 600 mya. If the molecular data are correct, the explosion of animal body plans recorded in the Cambrian period reflects an increase in the numbers and kinds of fossilizable animals, not the sudden invention of new animal designs. Or perhaps the molecular analyses are misleading and there really was an explosion of animal body plans somewhere around 540 mya, attributable perhaps to dramatically increased pressures of predation and competition.

Figure 2.1

Multicellular fossilized embryo (~ 500 μm diameter) from deposits in southern China formed about 570 million years ago. We don't know what this embryo would have developed into, but it has been tentatively identified as that of a bilaterally symmetrical, multicellular animal. If this interpretation is correct, then a diversity of multicellular animal life undoubtedly existed long before the Burgess Shale record of the Cambrian explosion.

In any event, nearly all of today's major animal groups (phyla) are represented among the Cambrian fossils formed some 525–540 mya; without ancestral stages and stages that are intermediate between the various animal groups, the fossil record provides no clues about how the phyla are related to each other. Studying the fossil record can tell us something about evolution *since* the Cambrian explosion, but nothing about the ancestors from which these fossilized animals evolved. However, if we make the very reasonable assumption that all animals have ancestral forms in common, and that as animals evolved from those common ancestors they became less and less alike, we can infer evolutionary relationships, with varying degrees of certainty. Such inferences are based on morphological, developmental, physiological, biochemical, and genetic similarities and differences among animal groups.

Before we can consider the evolutionary interrelationships among different groups of organisms, we must sort the millions of animal species into categories, which can be done only after determining the degrees of similarity and difference that will define each category. It is important to keep in mind that all classification schemes are, at least in part, artificial attempts to impose order. Humans decide which characteristics will separate one family from another within the same order, which characteristics will separate one order from another within the same class, and so forth. As we will see throughout this book, many organisms do not fit cleanly into any one group; it is relatively simple to decide upon the categories to be used but often far more difficult to determine the category to which a given organism belongs. Once the organisms are assigned to taxonomic categories, it becomes possible to consider the evolutionary relationships among and within those categories. In this chapter, we will consider some of the schemes that have been developed to sort animals into groups.

Classification by Cell Number, Embryology, and Body Symmetry

Invertebrates have been categorized in many ways. One of the most basic divisions is based upon whether individuals are single celled or composed of many cells. True animals are multicellular, generally diploid organisms that each develop from a blastula; these organisms are referred

In a second group of animals, the region between the outer body wall musculature and the endoderm of the gut is a fluid-filled cavity (Fig. 2.3b); in some species, this cavity is derived from the **blastocoel,** an internal space that develops in the embryo prior to gastrulation (Figs. 2.4b,c and 2.5). This type of body cavity is termed a **pseudocoel,** and the organism housing it is said to be **pseudocoelomate.** The name is a bit misleading. The *pseudo* is not intended to disparage the *coel;* the body cavity is genuine. The *pseudo* prefix merely draws attention to the fact that this body cavity is not a true coelom, which, as we will see, is a precisely defined internal cavity formed through one of several quite different processes and always lined completely with tissue derived from embryonic mesoderm.

This brings us to the third group of triploblastic animals, those with a true **coelom:** an internal, fluid-filled body cavity lying between the gut and the outer body wall musculature and lined with tissue derived from embryonic mesoderm. The animals possessing such a body cavity are **coelomates** (or **eucoelomates;** *eu* = G: real, true). Coelom formation may occur by either of two quite dissimilar mechanisms; mode of coelom formation traditionally is used to assign coelomates to one of two major subgroups: protostomes or deuterostomes. Among **protostomes,** coelom formation occurs by gradual enlargement of a split in the mesoderm (Fig. 2.4). This process is termed **schizocoely** (*schizo* = G: split). Among **deuterostomes,** on the other hand, the coelom typically forms through evagination of the archenteron into the blastocoel of the embryo (Figs. 2.4 and 2.5). Because the coelom of deuterostomes is formed from a part of what eventually becomes the gut, coelom formation in this group of animals is termed **enterocoely** (*entero* = G: gut).

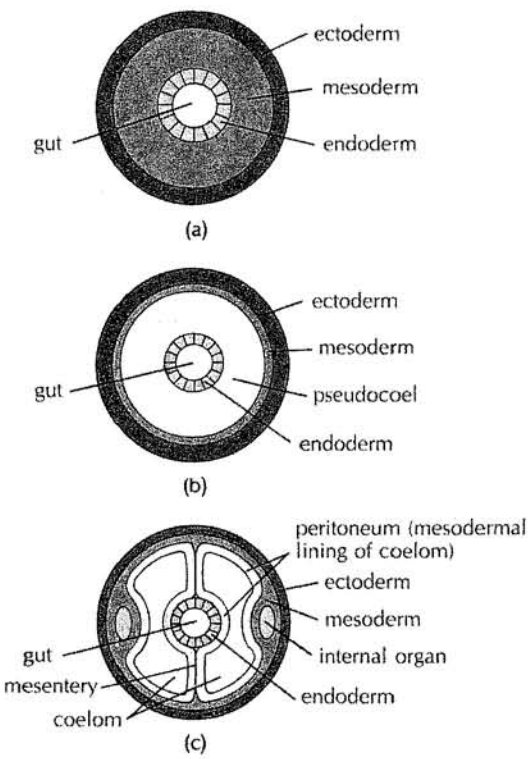


Figure 2.3

(a) Diagrammatic cross section through the body of an acoelomate. The space between the gut and the outer body wall musculature is completely filled with tissue derived from embryonic mesoderm. (b) Cross section through the body of a pseudocoelomate. The gut derives entirely from endoderm and is therefore not lined with mesoderm. (c) Cross section through the body of a coelomate. The entire coelomic space is bordered by tissue derived from embryonic mesoderm.

Whether the coelom is formed by schizocoely or enterocoely, the end result is similar. The organism is left with a fluid-filled internal body cavity lying between the gut and the outer body wall musculature, and unlike the cavity of pseudocoelomates, this cavity is lined by a mesodermally derived epithelium. The fact that internal cavities develop by any of three distinctly different mechanisms (enterocoely, schizocoely, or persistence of embryonic blastocoel) suggests that such cavities have been independently evolved at least three times. If so, the selective pressures favoring the evolution of internal body cavities must have been substantial.

Indeed, selective advantages are easy to imagine. For example, with an internal body cavity the gut is somewhat independent from muscular, locomotory activities of the body wall. Also, the animal gains internal space into which can bulge digestive organs, gonads, and developing embryos, and an internal fluid that can serve to distribute oxygen, nutrients, and hormones or neurosecretory substances throughout the body, facilitating the evolution of larger body sizes. Perhaps most significantly, fluid-filled body cavities can lead to more effective locomotory systems, as discussed in Chapter 5.

To summarize, triploblastic animals can be acoelomates, pseudocoelomates, or coelomates, depending on whether they possess an internal, fluid-filled body cavity and on whether this body cavity is lined by mesodermally derived tissue. These are 3 distinctive types of organization. However, what they tell us about the evolutionary relationships among animals in the different categories, or even among animals within each of the categories is uncertain; in particular, it is becoming increasingly obvious that coelomic cavities can be lost as well as gained, that acoelomates are unlikely to have evolved from a single common ancestor, and that the acoelomate body plan may not be *primitive* (i.e., closest to the ancestral triploblastic condition). There is a growing suspicion that the earliest triploblastic animals were coelomate, and that the acoelomate condition may represent a number of independent losses of the body cavity.

In contrast, the distinction between protostomes and deuterostomes, based partly on how the coelom is created during development, seems more secure; the validity of these two groups has so far been largely upheld by molecular data, suggesting that protostome species are indeed more closely related to each other than to any deuterostome species. But mode of coelom formation is only one

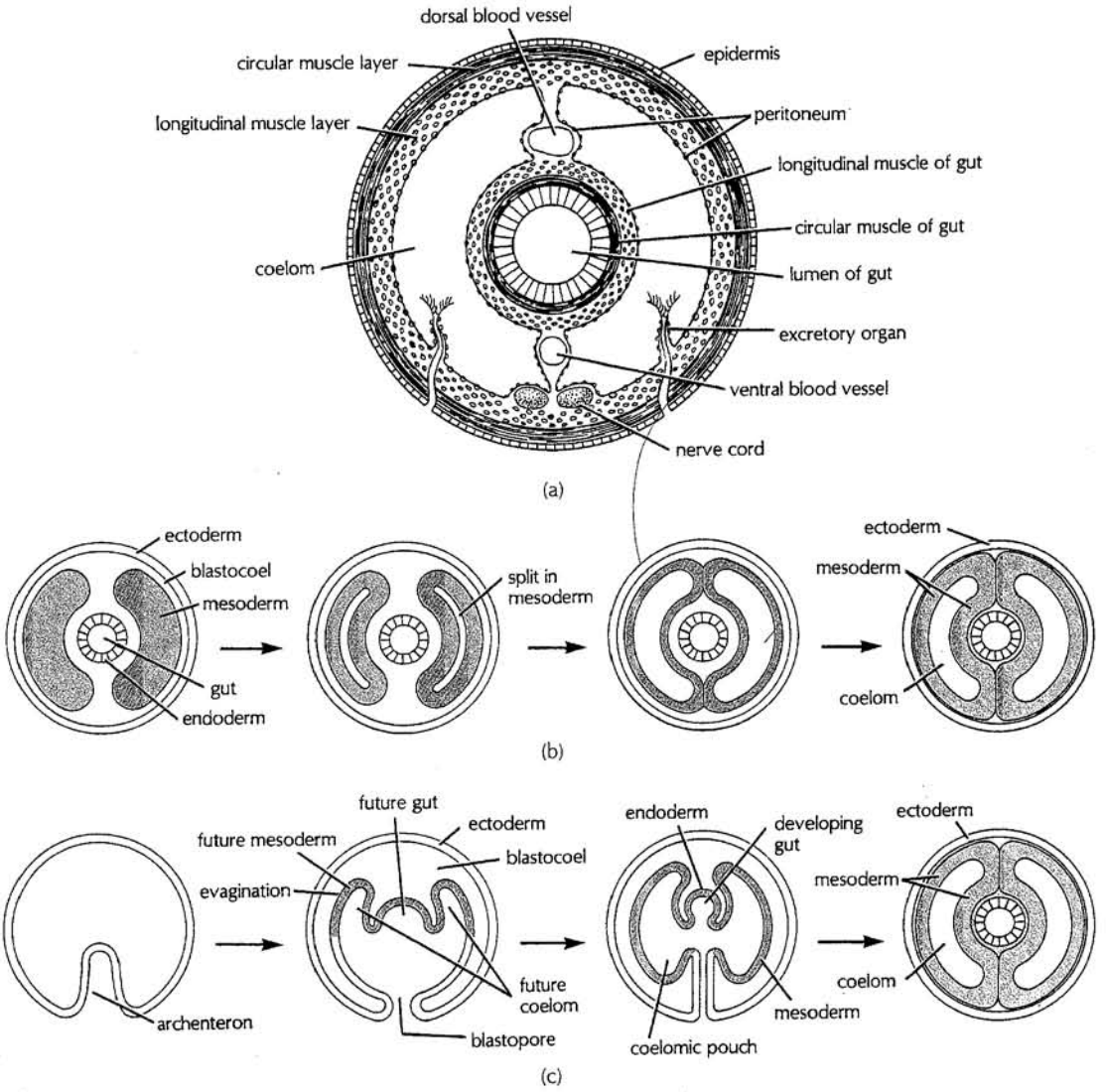


Figure 2.4

(a) Detailed cross section through the body of a coelomate. The tissues bordering the coelomic space include the musculature of the gut; the mesenteries, which suspend the various organs in the coelom; and the peritoneum, which lines the coelomic cavity. (b) Coelom formation by schizocoely—that is, by an actual split, or schism, in the mesodermal tissue. (c) Coelom formation by enterocoely, in which the archenteron evaginates into the embryonic blastocoel.

of several characteristics distinguishing protostomes from deuterostomes. In fact, the terms *protostome* and *deuterostome* were actually coined to reflect differences in the embryonic origin of the mouth (*stoma* = G: mouth). Among the protostomes, the mouth (and sometimes the anus) forms from the blastopore (the opening from the outside into the archenteron)—hence the term *protostome,* meaning "first mouth," since the mouth forms from the first opening that appears during embryonic development. Among the deuterostomes, the mouth never develops from the blastopore: although the blastopore may give rise to the anus, as in some protostomes, the deuterostome mouth always forms as a second, novel opening elsewhere on the embryo—hence the term *deuterostome,* meaning "second mouth."

What other characteristics distinguish protostomes from deuterostomes? In addition to differing in the mode of coelom formation and in the embryological origin of the mouth, they also typically differ in the number of coelomic cavities formed as they develop. Among protostomes, the number of coelomic cavities is highly variable: For example, an annelid worm can have as many coelomic cavities as it has segments—hundreds in some species. Among deuterostomes, however, the original coelomic cavity generally subdivides to form 3 pairs of coelomic pouches (i.e., the deuterostome coelom is commonly *tripartite*). Protostomes and deuterostomes also differ with respect to the orientation of the spindle axes of the cells during cleavage, the point in development at which cell fates become irrevocably fixed, and how the mesoderm originates.

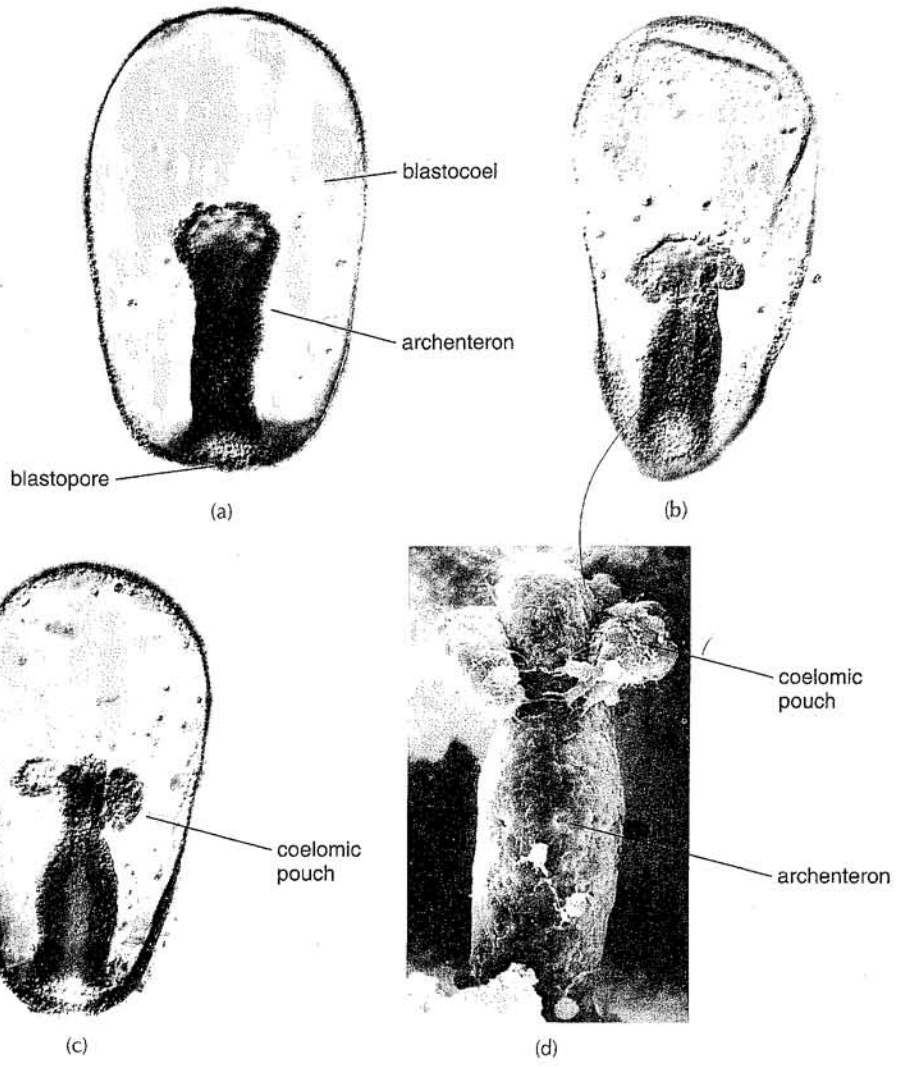


Figure 2.5

(a–c) Enterocoely in a sea star, showing the coelomic pouches forming from the sides of the archenteron and splitting off. (d) The coelomic pouches are clearly shown in this scanning electron micrograph. The pouches gradually enlarge to form the coelom. (a–d) *Courtesy of B.J. Crawford, from Crawford and Chia, 1978* Journal of Morphology *157:99. Reprinted by permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.*

Cleavage is usually either radial or spiral, depending on the orientation of the mitotic spindles relative to the egg axis. Generally, yolk is asymmetrically distributed within an egg, and the nucleus occurs in, or moves to, the region of lower yolk density. This is the **animal pole,** and it is here that the polar bodies are given off during meiosis. The opposite end of the egg is termed the **vegetal** (not vegetable!) **pole.**

In **radial cleavage** (deuterostomes), the spindles of a given cell, and thus the cleavage planes, are oriented either parallel or perpendicular to the animal-vegetal axis. Thus, daughter cells derived from a division in which the cleavage plane is parallel to the animal-vegetal axis end up lying in the same plane as the original mother cell (Fig. 2.6a,b). The two daughter cells resulting from a division perpendicular to the animal-vegetal axis come to lie directly one atop the other, with the center of the upper cell lying directly over the center of the underlying cell (Figs. 2.6c–f and 2.7).

In contrast, the spindle axes of cells undergoing **spiral cleavage** (protostomes) are oriented (after the first two cleavages) at 45° angles to the animal-vegetal axis (Fig. 2.6j–k). Moreover, the division line may not pass through the center of the dividing cell. As a result, by the eight-cell stage we often see a group of smaller cells **(micromeres)** lying in the spaces between the underlying larger cells **(macromeres)** (Fig. 2.6k–m). Cell division continues in this fashion, with the cleavage planes always oblique to the polar axis of the embryo.

Cleaving embryos of protostomes and deuterostomes also differ with respect to when their cells become fully committed to a particular fate. Among deuterostomes, one can separate the cells of a two-cell or four-cell embryo, and each cell will typically develop into a small but complete

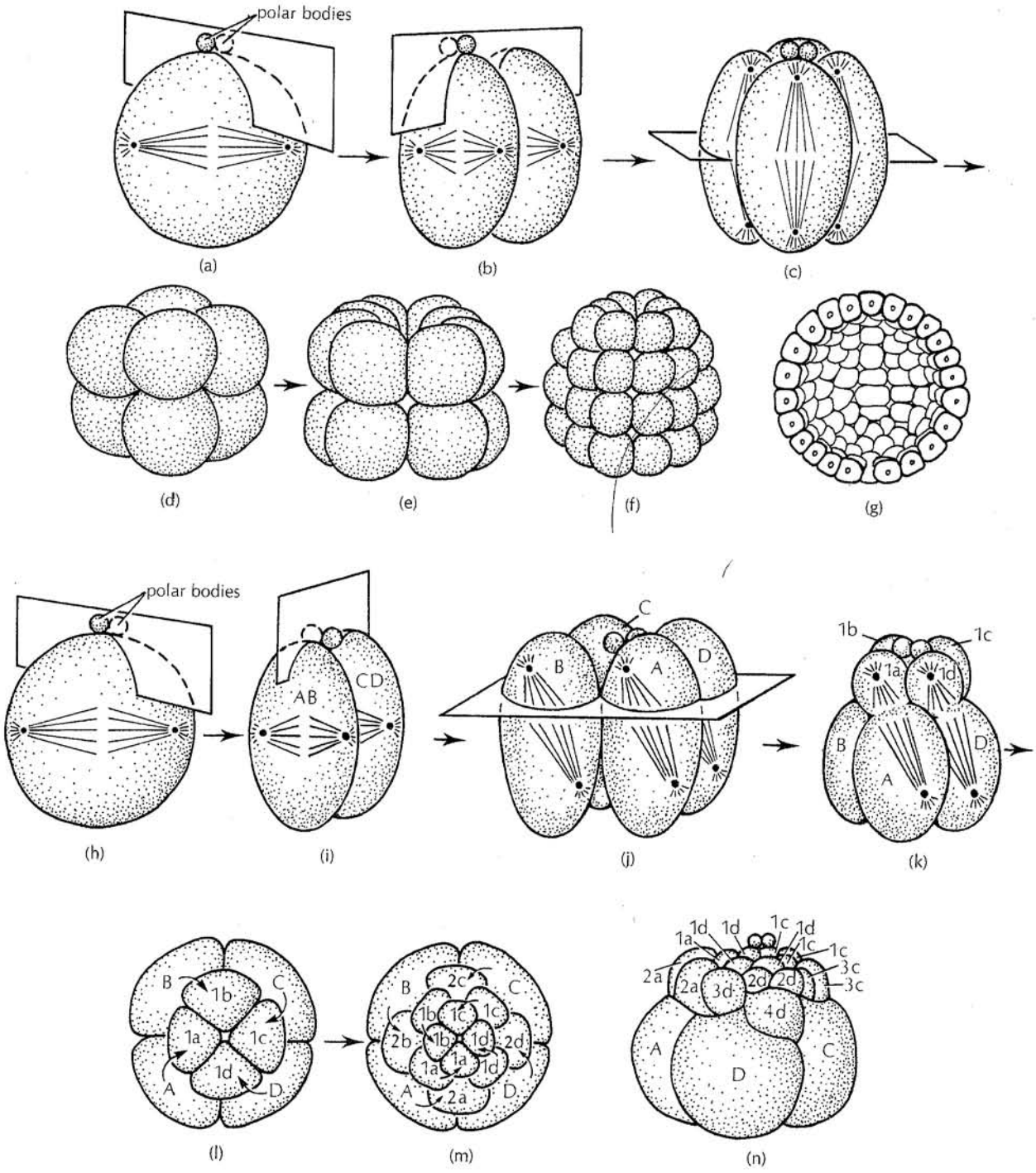


Figure 2.6

(a–g) Radial cleavage, as seen in the sea cucumber *Synapta digitata*. In (g), part of the embryo has been removed to reveal the blastocoel. (h–n) Spiral cleavage. The first two cleavages (h,i) are identical with those seen in radially cleaving embryos, forming four large blastomeres (j). The cleavage plane during the next cleavage, however, is oblique to the animal-vegetal axis of the embryo and does not pass through the center of a given cell (k). This produces a ring of smaller cells (micromeres) lying between the underlying larger cells (macromeres), as shown in (l). The lettering system illustrated was devised by embryologist E. B. Wilson in the late 1800s to make possible a discussion of particular cell origins and fates. The number preceding a letter indicates the cleavage in which a particular micromere was formed. Capital letters refer to macromeres, while lowercase letters refer to micromeres. With each subsequent cleavage, the macromeres divide to form one daughter macromere and one daughter micromere, while the micromeres divide to form two daughter micromeres. The 32-cell embryo of the marine snail *Crepidula fornicata* is shown in (n). Note the 4d cell, from which most of the mesodermal tissue of protostomes will ultimately derive.

After Richards.

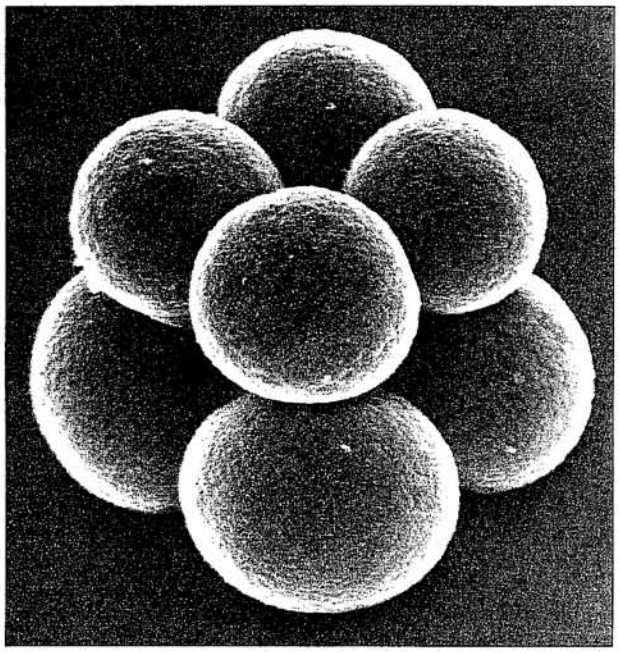


Figure 2.7

Scanning electron micrograph of radial cleavage (8-cell stage) in the cephalochordate *Branchiostoma belcheri* (chapter 22).

Courtesy of N. Kajita. From Hirakow, R. and N. Kajita. 1990. J. Morphol. 203:331–44. Reprinted by permission of Wiley-Liss, Inc. a subsidiary of John Wiley & Sons, Inc.

and fully functional animal. Thus, deuterostomes are said to show **indeterminate** (or **regulative**) cleavage; each cell retains—sometimes as late as the eight-cell stage—the capacity to differentiate the entire organism if that cell loses contact with its associates. Among protostomes, in contrast, the developmental potential of each cell is irrevocably determined at the first cleavage; separate the blastomeres of a two-celled protostome embryo and each cell will, in most species, give rise only to a short-lived, malformed monster. Protostome cleavage is therefore said to be **determinate** or **mosaic.** Protostome embryonic development can never produce identical twins, which in deuterostomes arise from the natural separation of blastomeres during early cleavage.

A further difference between the two groups of coelomates concerns the source of mesoderm. Among protostomes, much of the mesodermal tissue derives from a single cell of the 64-cell embryo, located at the edge of the blastopore. This is not true of deuterostomes, which produce mesoderm from the walls of the archenteron.

During their first 1 or 2 cleavages, some protostomes form **polar lobes** (not to be confused with polar bodies, which arise during egg maturation). A polar lobe is a conspicuous bulge of cytoplasm that forms prior to cell division. The lobe contains no nuclear material. After cell division is complete, the bulge is resorbed into the single daughter cell to which it is still attached (Fig. 2.8). Although the functional significance of this phenomenon for the embryo is still not fully understood, polar-lobe formation has provided developmental biologists with an intriguing system through which to study the role of cytoplasmic factors in determining cell fate. In the basic experiment, the fully formed polar lobe is detached from an embryo, and the development of the lobeless embryo is subsequently monitored. Polar-lobe formation is characteristic of only some protostome species (some annelids and some molluscs) but is never encountered among deuterostomes.

Finally, the ciliary bands involved in feeding and locomotion among deuterostome larvae (and adults) are typically monociliated (Fig. 2.9a), while those found among larval protostomes are typically composed of multiciliated cells (Fig. 2.9b). Details of particle capture also differ among protostome and deuterostome larvae (Fig. 2.9c).

Classification schemes in biology always seem tidy: The developmental features distinguishing ideal protostomes from ideal deuterostomes are summarized in Table 2.1. Unfortunately, biologists often find it far simpler to construct logical classification systems than to neatly distribute animals within them. For example, flatworms (phylum Platyhelminthes) are acoelomate; in all other respects, however, they develop as perfectly good protostomes, showing, for example, spiral cleavage and development of the mouth from the blastopore. Are they protostomes? As faith in the phylogenetic significance of body cavities is diminishing, the definition of "protostome" is being broadened to include both acoelomate and pseudocoelomate animals. Even so, few protostome species exhibit all of the other listed protostome characteristics. Not all protostomes exhibit spiral cleavage, for example. Crabs, insects, and squid show neither spiral or radial cleavage; they are grouped with protostomes primarily because their cleavage patterns are assumed to have evolved from a spiral ancestry. Similarly, although the blastopore generally becomes the mouth during protostome development, in some protostome species it becomes instead the anus, as in deuterostomes. And some deuterostome species (e.g., the sea squirts) show the fully determinate cleavage pattern typically associated with protostomes, while some protostome species show the indeterminate cleavage pattern typically associated with deuterostomes. Finally, some species exhibit a combination of protostome and deuterostome characteristics. Because all animal groups have had ancestral forms in common at some time during their evolution, because evolution is an ongoing process, and because embryos as well as adults are subject to the modifying forces of natural selection, some species are likely to have developmental characteristics that fall outside the mainstream. The affinities of the "misfits" must remain uncertain, at least until additional embryological and molecular studies can be completed. In any event, those species exhibiting entirely or primarily protostome characteristics are most likely to be more closely related to each other than to those species exhibiting purely deuterostome characteristics.

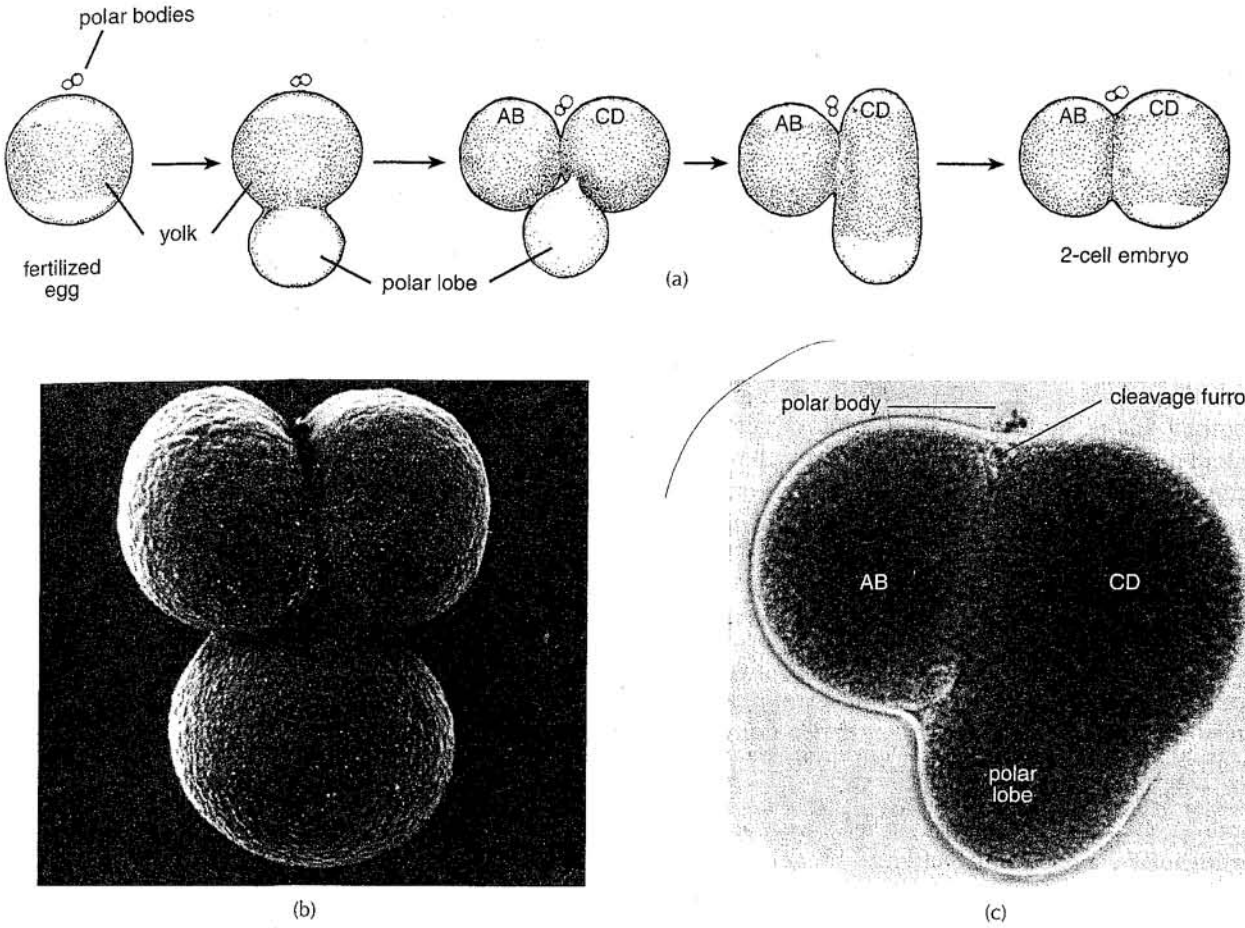


Figure 2.8

(a) Polar lobe formation during the development of a protostome. Following resorption of the polar lobe, the two blastomeres are clearly unequal in size because the cytoplasm held within the polar lobe does not participate directly in the process of cleavage. (b) Scanning electron micrograph of the two-celled embryo of the marine snail *Nassarius reticulatus*. The polar lobe (at bottom) is nearly equal in size to the blastomere into which it will be resorbed. (c) Polar-lobe formation during first cleavage in the blue mussel, *Mytillus edulis*, as seen with light microscopy. The newly formed cleavage furrow is visible between the AB and CD blastomeres. The polar lobe is clearly affiliated with only one of the daughter cells (the CD blastomere). A polar body (a product of meiotic division prior to cleavage) can be seen at the animal pole of the embryo.

(b) *Courtesy of M. R. Dohmen.* (c) *Carolina Biological Supply Company/PhotoTake.*

Table 2.1 Summary of the Developmental Characteristics of Idealized Protostomous and Deuterostomous Coelomates

Developmental characteristic	Protostomes	Deuterostomes
Mouth origin	From blastopore	Never from blastopore
Coelom formation	Schizocoely	Enterocoely
Arrangement of coelomic cavities	Variable in number	Generally in 3 pairs
Mesoderm origin	4d cell (Fig. 2.6n)	Other
Cleavage pattern	Spiral, determinate	Radial, indeterminate
Polar-lobe formation	Present in some species	Not present in any species
Larval ciliary bands	Compound cilia from multiciliated cells	Simple cilia, 1 cilium per cell
	Downstream particle capture	Upstream particle capture

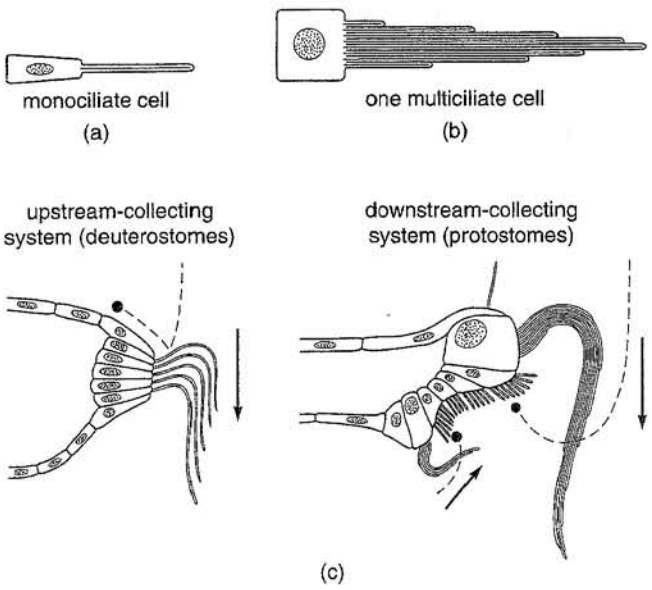


Figure 2.9

(a) A monociliated cell, characteristic of ciliated deuterostome larvae. (b) A multiciliated cell with a compound cilium, typical of protostome larvae. (c) The upstream and downstream particle-collection systems characterizing the ciliated larvae of all deuterostomes and at least most protostomes, respectively. In the upstream-collection system, individual cilia temporarily reverse their direction of beat—probably in response to mechanical contact with food particles—so that particles are directed to the upstream surface of the ciliary band.

From C. Nielsen, 1987. Acta Zoologica (Stockholm), *68:205–262. Reprinted by permission.*

Classification by Evolutionary Relationship

Probably the most familiar classification scheme is the taxonomic framework established about 250 years ago (1758) by Carolus Linnaeus. The system is hierarchical; that is, one category contains groups of lesser categories, which in turn contain still more groups of lesser categories, and so on:

Kingdom
Phylum
Class
Order
Family
Genus
Species

Many subgroups are superimposed upon this basic framework. One encounters among arthropods, for example, subclasses within classes, suborders within orders, infraorders within suborders, and even sections within infraorders, and families are grouped together within superfamilies. Any named group of organisms (e.g., sea urchins, banana slugs) that is sufficiently distinct to be assigned to such a category is called a **taxon.**

The members of any given taxon show a high degree of similarity—morphological, biochemical, genetic, and sometimes behavioral—and are presumed to be more closely related to each other than to the members of any other taxon at the same taxonomic level. The members of a particular order of snails, for example, are all presumed to have evolved from a single ancestor that is not an ancestor of snails in other orders. Similarly, all the members of any particular phylum are presumed to have evolved from a single ancestral form. Such groups, at every taxonomic level, are said to be **monophyletic** (G: single-tribed). At present, there is considerable debate about whether each taxon must also include all descendants of that ancestor. A group that does not do so is said to be **paraphyletic.** By this definition, the invertebrates form a paraphyletic group, since their vertebrate descendants are excluded.

Phylum is generally the highest taxonomic level that will concern us in this text. Invertebrate animals are presently distributed among at least 23 phyla (32 phyla in this textbook), each representing a unique body plan. Remarkably, no new phylum-level body plans have arisen in the past 600 million years, despite substantial radiation following each of the 5 major and about 10 smaller extinctions taking place during that time. In the most devastating extinction event to date, about 250 million years ago at the Permian-Triassic boundary, nearly 95% of existing species-level animal diversity was lost. In the subsequent 250 million years many new species evolved, often representing new orders and classes, but no new phylum-level body plans appeared.

The category of **species** has additional biological significance. Theoretically, the members of one species are reproductively isolated from members of all other species. The species, therefore, forms a pool of genetic material that only members of that species have access to and that is isolated from the gene pool of all other species.

The scientific name of a species is binomial (has two parts): the **generic name** and the **specific name.** The generic and specific names (i.e., the **species name**) are usually italicized in print and underlined in writing. The generic name begins with a capital letter, but the specific name does not. For example, the proper scientific name for one of the common shallow-water marine snails found off Cape Cod, Massachusetts, is *Crepidula fornicata.* Related species are *Crepidula plana* and *Crepidula convexa.* Once the generic name is spelled out, it may be abbreviated when used subsequently, as long as no confusion results (if an author is referring to the two genera *Crepidula* and *Conus,* for example, neither genus name can be abbreviated as "*C.*"). Thus, *Crepidula fornicata, C. plana,* and *C. convexa* are common shallow-water marine gastropods found near Woods Hole, Massachusetts. They all belong to the phylum Mollusca and are contained within the class Gastropoda, family Calyptraeidae. The family Calyptraeidae contains other genera besides *Crepidula;* the class Gastropoda contains other families besides the Calyptraeidae; and the phylum Mollusca contains other classes besides the Gastropoda. The taxonomic classification system is indeed hierarchical.

An additional name often follows the species name of an organism. This additional name is capitalized but is

not italicized and may be contained in parentheses. This is the name of the person who first described the organism. A barnacle common along the coast of the southeastern United States, for example, is *Balanus amphitrite* Darwin, first described by Charles Darwin. Linnaeus's name is often abbreviated as L., since he is associated with the descriptions of so many species. If the organism was originally described as being in a different genus than the one in which it is currently placed, the describer's name is enclosed within parentheses. Thus, the snail *Ilyanassa obsoleta* (Say) was described by a man named Say, who originally assigned the species to another genus (the genus *Nassa*). This snail was later determined to be sufficiently dissimilar from other members of the genus *Nassa* to warrant its assignment to a different genus. Occasionally, a person's name is followed by a date, identifying the year in which the species was first described. For example, the shrimplike animal known as "*Euphausia superba*, Dana 1858" was first described by Dana in 1858, and it has remained in the genus *Euphausia* since it was originally named.

A list of all groups containing invertebrates is presented in Figure 2.10, showing where each phylum fits into the framework discussed so far in this section. The number following each listing gives the page on which the group is first discussed. The distribution of described species among the various animal phyla is summarized in Figure 2.11. Note that the percentage of species contained

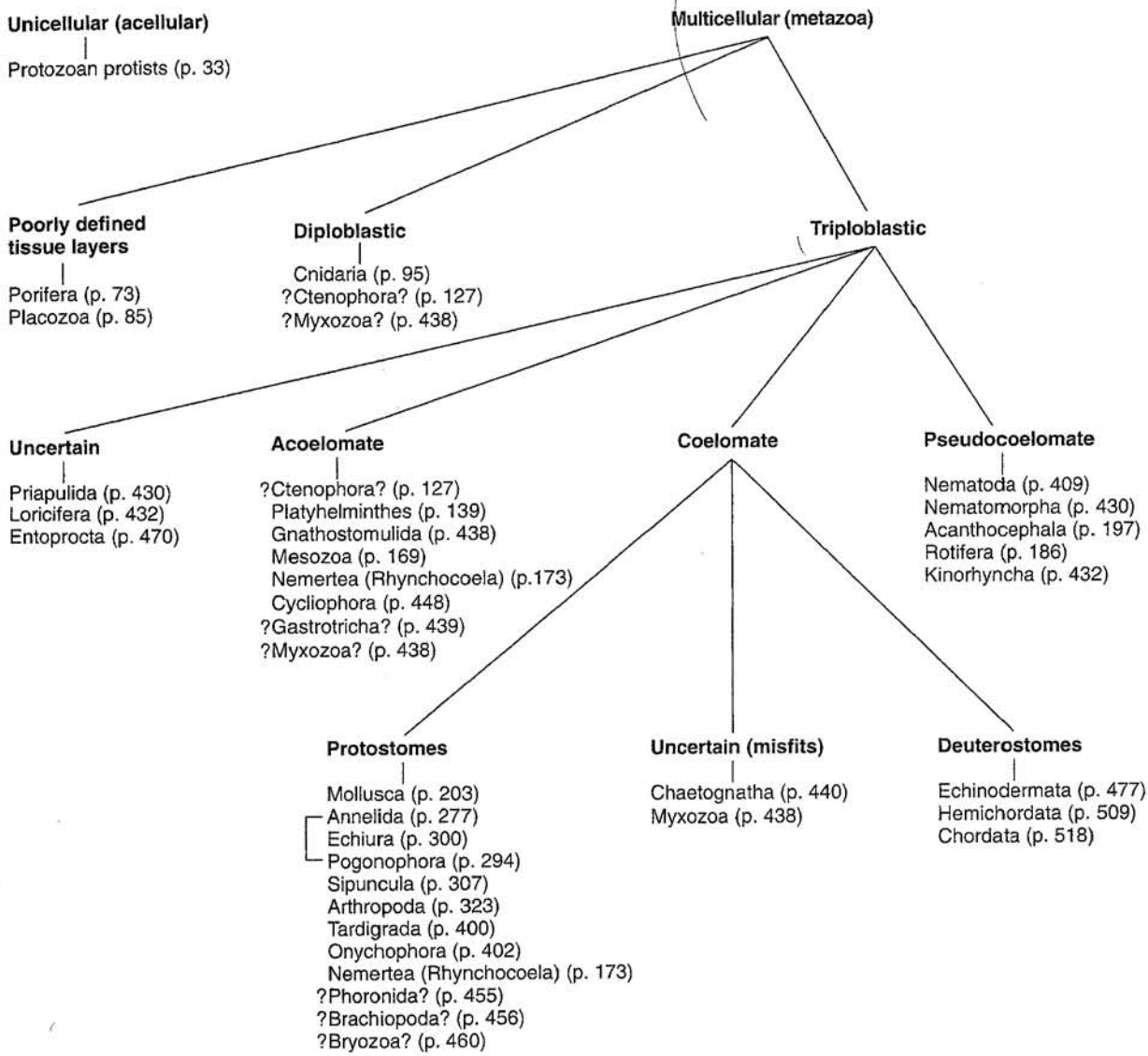


Figure 2.10

Arrangement of the major groups according to the factors discussed in this chapter. Brackets indicate groups recently merged into a single phylum. Note that placement of some groups within this framework is uncertain (indicated by "?"), and that some groups (e.g., ctenophores) appear in two places. At least some of the pseudocoelomates and acoelomates may have evolved from coelomate ancestors.

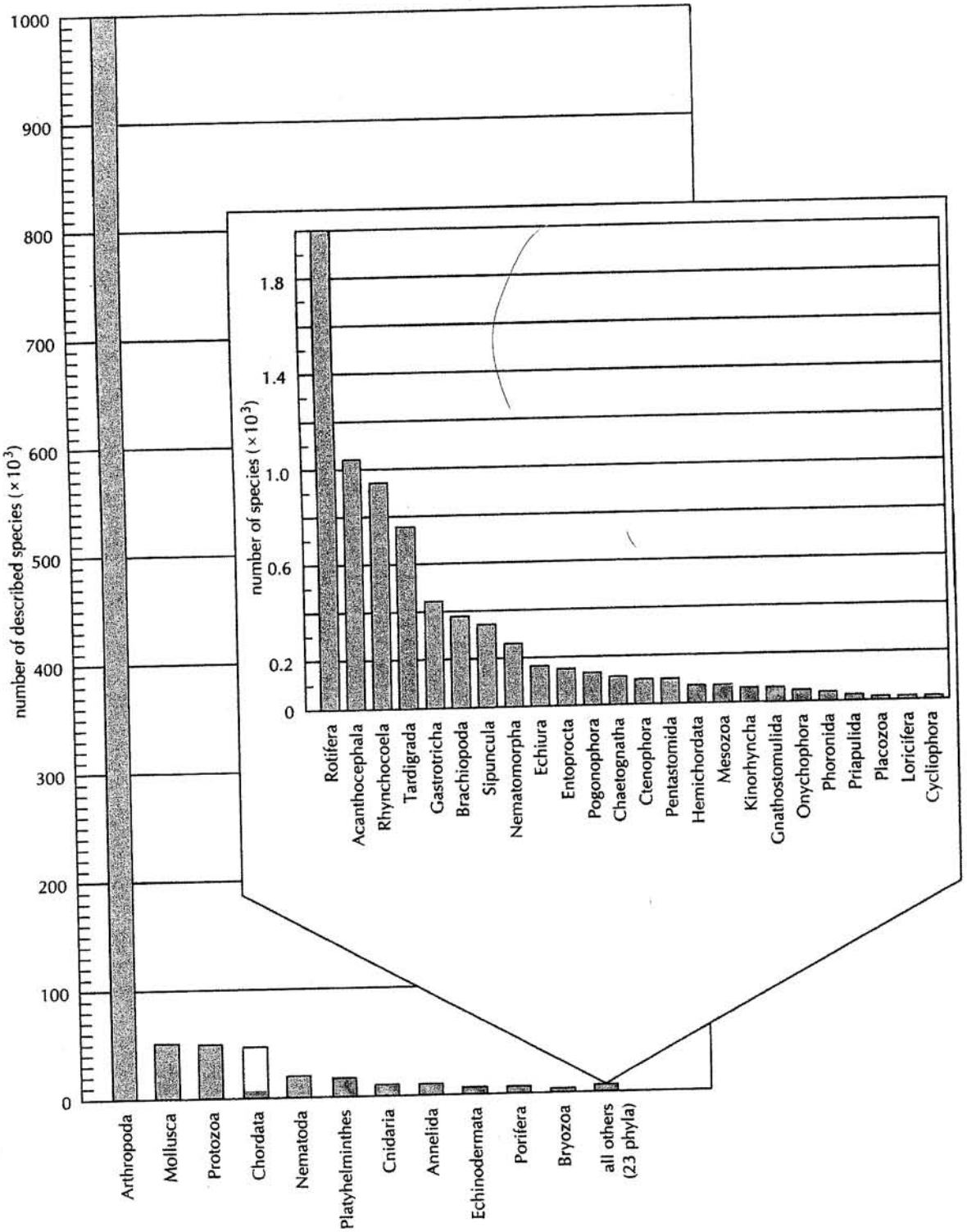


Figure 2.11

Graphic representation of the distribution of described species among the 34 major groups of invertebrates. In this text, protozoans are divided among more than one dozen phyla. Metazoan phyla containing fewer than 2,000 described species are presented in the inset. Note the different scale on the Y-axis of the inset. The open (unshaded) area of the bar labeled "Chordata" represents vertebrate species. All other species in all other phyla are invertebrates.

within our own phylum—the phylum Chordata—is quite small (only about 5% of all described species) and that this phylum contains some invertebrates as well as vertebrates.

Deducing Evolutionary Relationships

"... it is clear that a number of key ideas about metazoan phylogeny and body plan evolution will need to be reconsidered, and that at least some traditional views may require major modification." T. Lacalli, 1997. *Invertebrate Biology* 116:363–70.

An ideal taxonomic classification scheme reflects degrees of phylogenetic relatedness; that is, all members of a given taxonomic group should have descended from a single ancestral species and thus be more closely related to each other than to the members of any other group.

Biologists have long made logical, reasoned guesses about the origins of various animal groups, based upon studies of developmental patterns, studies of morphological and biochemical characteristics, and careful examination of animals preserved in the fossil record. Comparative molecular analyses of protein structure and of DNA and ribosomal RNA sequences among species are altering some of these views substantially.[1] Ferreting out probable relationships is no easy task. Indeed, there is no universally accepted procedure for deducing evolutionary relationships; considerable disagreement on this point is well reflected in the appropriate literature of the past 30 to 40 years.[2] In part, the controversy concerns the relative importance of phenotypic similarities among taxa, phenotypic differences among taxa, and the degree to which one is willing to admit (and deal with the fact) that phenotype may be a very misleading indicator of underlying genetic similarities and differences. Through the process of **convergence,** distantly related animals may come to resemble each other rather closely. The features that resemble each other through convergence are referred to as **analogous,** as opposed to homologous. For example, the eye of an octopus (a cephalopod mollusc) is remarkably like that of a human, but these visual organs are believed to be analogues, not homologues, and not to indicate any close evolutionary relationship between vertebrates and molluscs. Although we may share some genes associated with eye formation, we are unlikely to have inherited our eyes directly from any molluscan ancestor. Which features indicate evolutionary closeness and which do not? Should we try to make this distinction? How can we know if we've decided correctly?

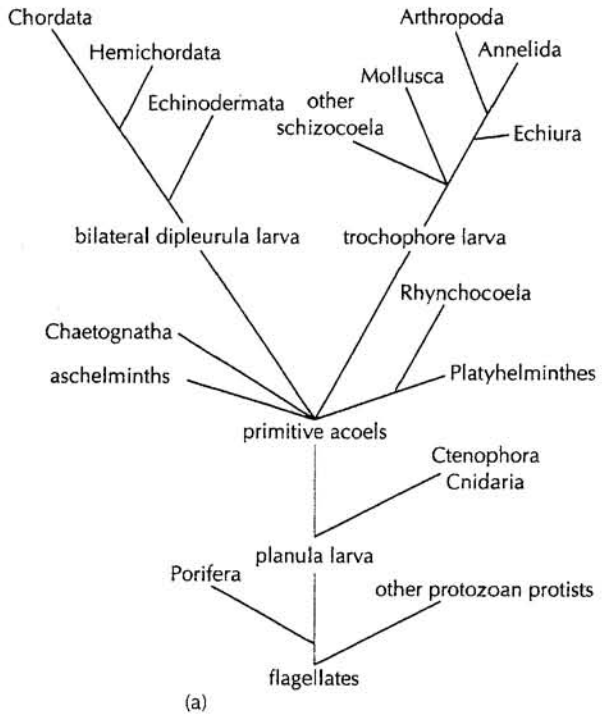
Moreover, in the evolutionary process, structures sometimes become less complex rather than more complex. Suppose, for example, you discover a new species of wingless insect. How can you tell whether this species evolved before insect wings evolved or whether it instead descended from a winged ancestor and lost the wings over time? It is often very difficult to determine which of two character states is the original (*primitive,* or *plesiomorphic*) condition and which is the advanced (*derived,* or *apomorphic*) condition.

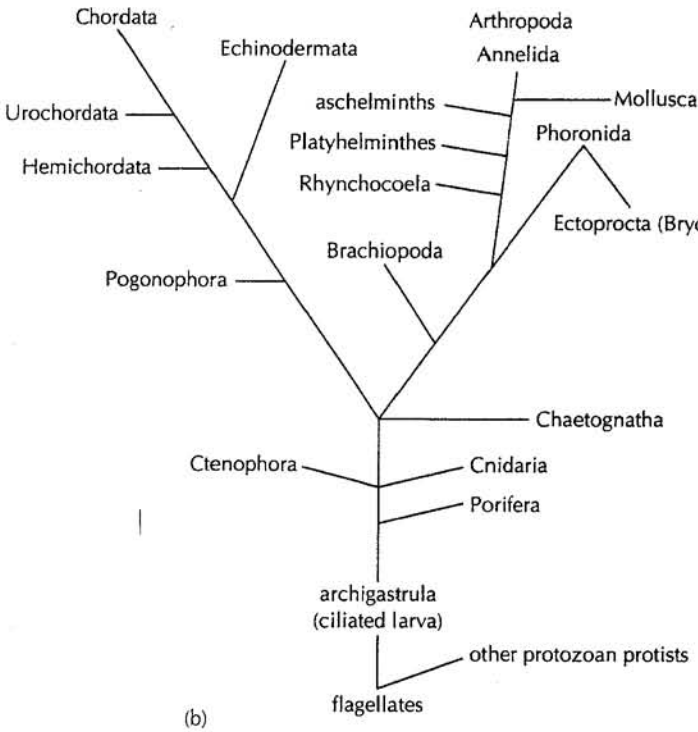
Until very recently, evolutionary relationships have been deduced entirely through anatomical and ultrastructural studies, with phenotypes serving as reflections of the underlying genotypes. During the past 10 years or so, however, biochemical and molecular studies have allowed us to examine genotypic diversity directly. Particularly remarkable are recent interspecific comparisons of nucleotide sequences of genes coding for ribosomal RNA (rRNA), comparisons made feasible through development of the polymerase chain reaction (PCR) in the mid-1980s. The PCR permits biologists to generate very quickly and inexpensively many copies of specific DNA sequences; a billion copies of a single DNA molecule can be obtained in about a day, producing sufficient material for analysis.

Molecular studies often produce some remarkable and surprising results, results that differ considerably from those of earlier, organismal studies. These results are frequently controversial, both inside and outside the molecular community; in some cases, there is considerable disagreement among workers about the procedures used to prepare and analyze the data, and about how the results of molecular studies should be interpreted, as discussed later in this chapter. But even before molecular biologists joined the fray, proposed phylogenetic relationships were controversial. A variety of phylogenetic trees (called **dendrograms;** *dendro* = G: a tree) have been proposed over the years. Seven of these dendrograms are illustrated in Figure 2.12. None of the proposed schemes represents idle speculation; all reflect hard work and detailed and careful reasoning. The two oldest schemes (Fig. 2.12a,b) assume that all multicellular animals descended from some form of single-celled protist, most likely a colonial flagellate, and they view sponges (phylum Porifera) as the earliest experiments in multicellularity with no close relationship to any other existing phyla. One more recent proposal, based upon molecular comparisons of 18S ribosomal RNA sequences, derives all other animals from a different protist, a slime mold (see p. 62), and separates the cnidarians (jellyfish and sea anemones, for example) markedly from all other animal groups. Another recent scheme (Fig. 2.12c) portrays many different early metazoans as independently evolved from many different protozoan ancestors and many more advanced animals as independently evolved from many different flatworm ancestors. The hypothesized relationships among annelids, arthropods, and molluscs also differ considerably among the different viewpoints; compare, for example, Figure 2.1a and e. The more closely you look at the different schemes, the more fascinating the comparisons

1. See *Topics for Further Discussion and Investigation,* no. 5, at the end of the chapter.

2. See *Topics for Further Discussion and Investigation,* nos. 1 and 2.





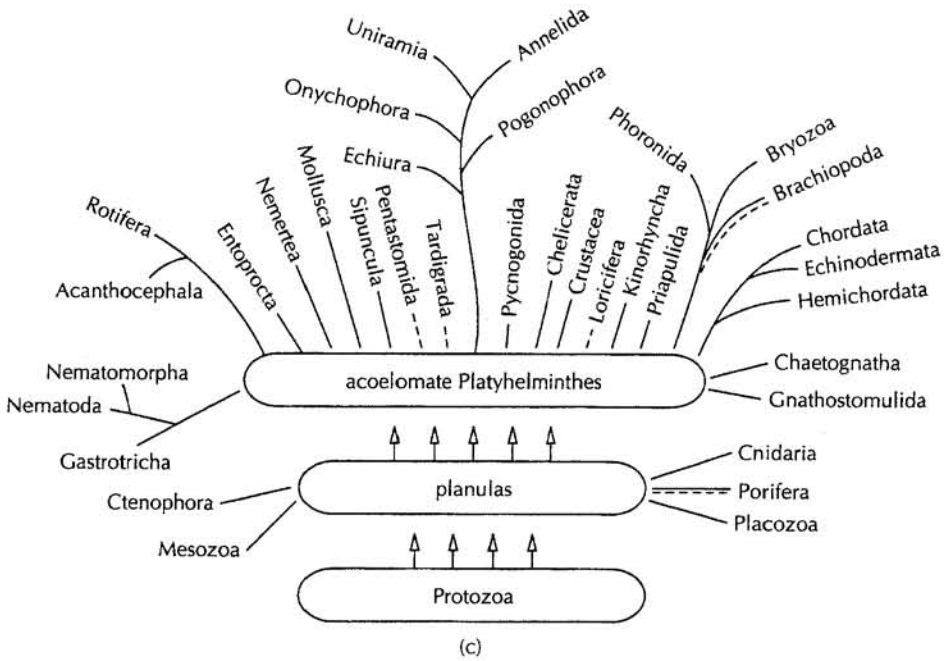


Figure 2.12

(a–g) Seven schemes proposed to illustrate presumed phylogenetic relationships among animals. (a) According to Hyman, 1940. (b) According to Marcus, 1958, from Clark, R. B. *Dynamics in Metazoan Evolution.* New York: Oxford University Press, 1964. (c) Willmer, P. 1990. *Invertebrate Relationships.* New York: Cambridge University Press. (d) From Claus Nielsen, 1994, in *American Zoologist* 34:492–501. Reprinted by permission. (e) Based on 18S rRNA molecular analyses of Cavalier-Smith et al., 1996. *Canadian J. Zoology* 74:2031–2045. Each horizontal line represents data for a single species (maximum likelihood tree using 1,749 nucleotide positions). (f) Based on a review of 18S rRNA data by Aguinaldo and Lake, 1998. *American Zoologist* 38:878–887. In this scheme, protostomes are divided into two distinct groups: Members of one group (the Ecdysozoa) all molt an external article, while members of the second group (the Lophotrochozoa) do not. (g) Based on a combination of 276 morphological characters and 151 18S rRNA sequences (from 151 animal species). (P) indicates the 4 platyhelminth flatworm groups. Blue shading indicates components in which morphological and molecular evidence are especially in disagreement.

(g) *Modified from J. Zrzavý, S. Mihulka, P. K. Kepka, A. Bezděk, and D. Tietz, 1998.* Cladistics, *14:249–285.*

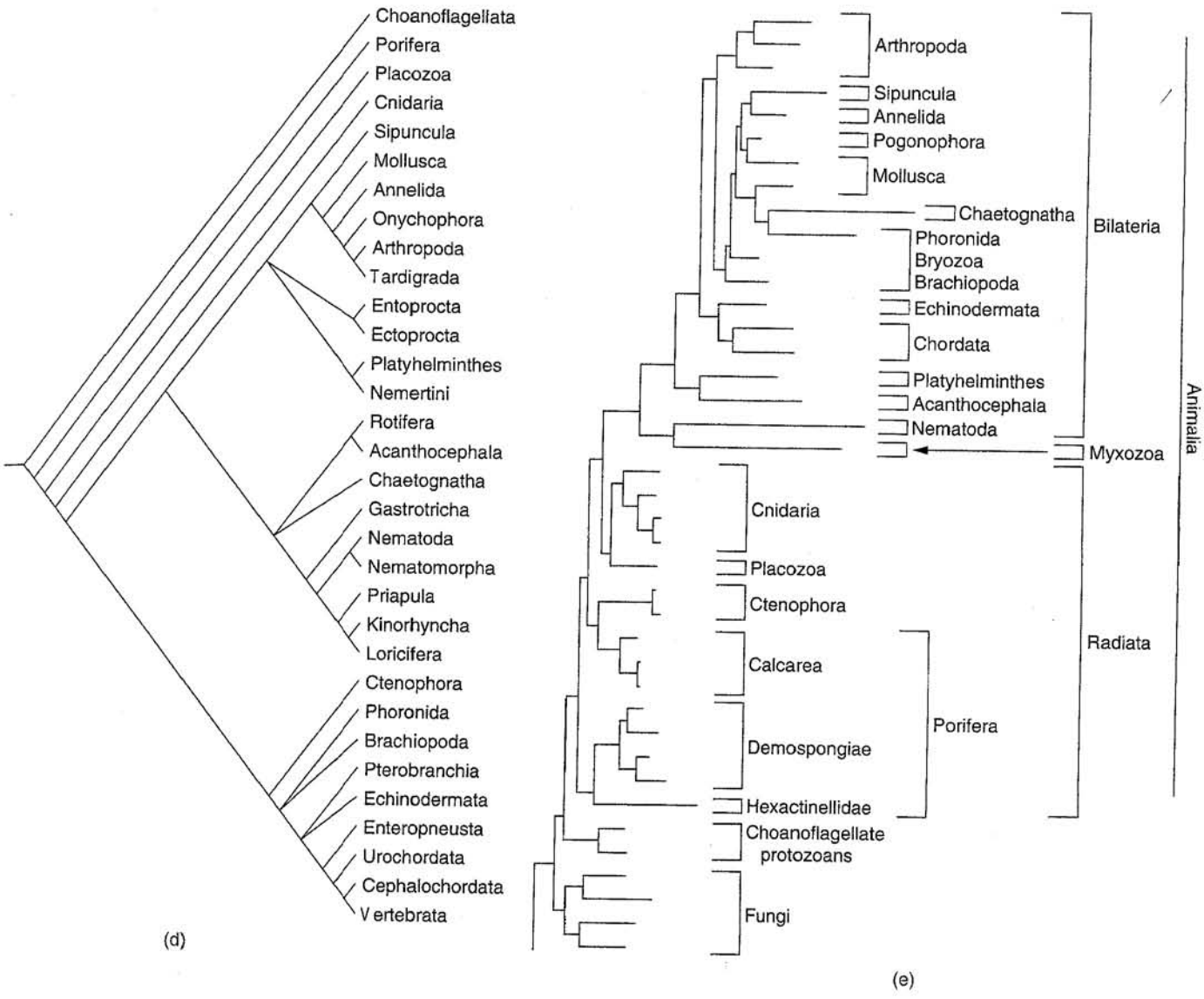


Figure 2.12 Continued on page 20.

become; it is well worth returning to Figure 2.12 at intervals as you read the rest of this book.

At least some of the differences among the various schemes may be attributed to insufficient data. As additional information about the various groups is gradually obtained, the evidence in favor of one scheme over some others may become more compelling, or additional modifications may be proposed.

Classification schemes reflecting evolutionary relationships are certainly not static, and the assignment of a given animal or group of animals to a particular position within the taxonomic hierarchy is not an irrevocable event. Studies of an animal's early development, for example, can reveal new information about the nature of the organism's internal body cavity, information that may affiliate that organism with an entirely different group of animals from those with which it was previously categorized. Controversies can also diminish—or increase—when data from the fossil record are added to data from extant species. Or a detailed study might call the usefulness of particular characters into question. If, for example, a certain embryonic cleavage pattern arose only once in evolution, then those animals that develop in this particular way must be closely related. But if evidence is found that this particular pattern evolved independently in several groups of animals, then that trait conveys little, if any, phylogenetic information.

Classifications also change when biologists discover organisms having characteristics not shared with any existing groups. For example, two arthropod classes (the Remipedia and Tantulocarida, p. 396) and two small but remarkably distinct phyla of recently discovered marine animals called loriciferans (p. 432) and cycliophorans (p. 448) have been established in the last 20 years or so. Cycliophorans were first described in 1995.

Sometimes classifications change when biologists reexamine previously studied material, or acquire new material. A small but fascinating group of gutless worms,

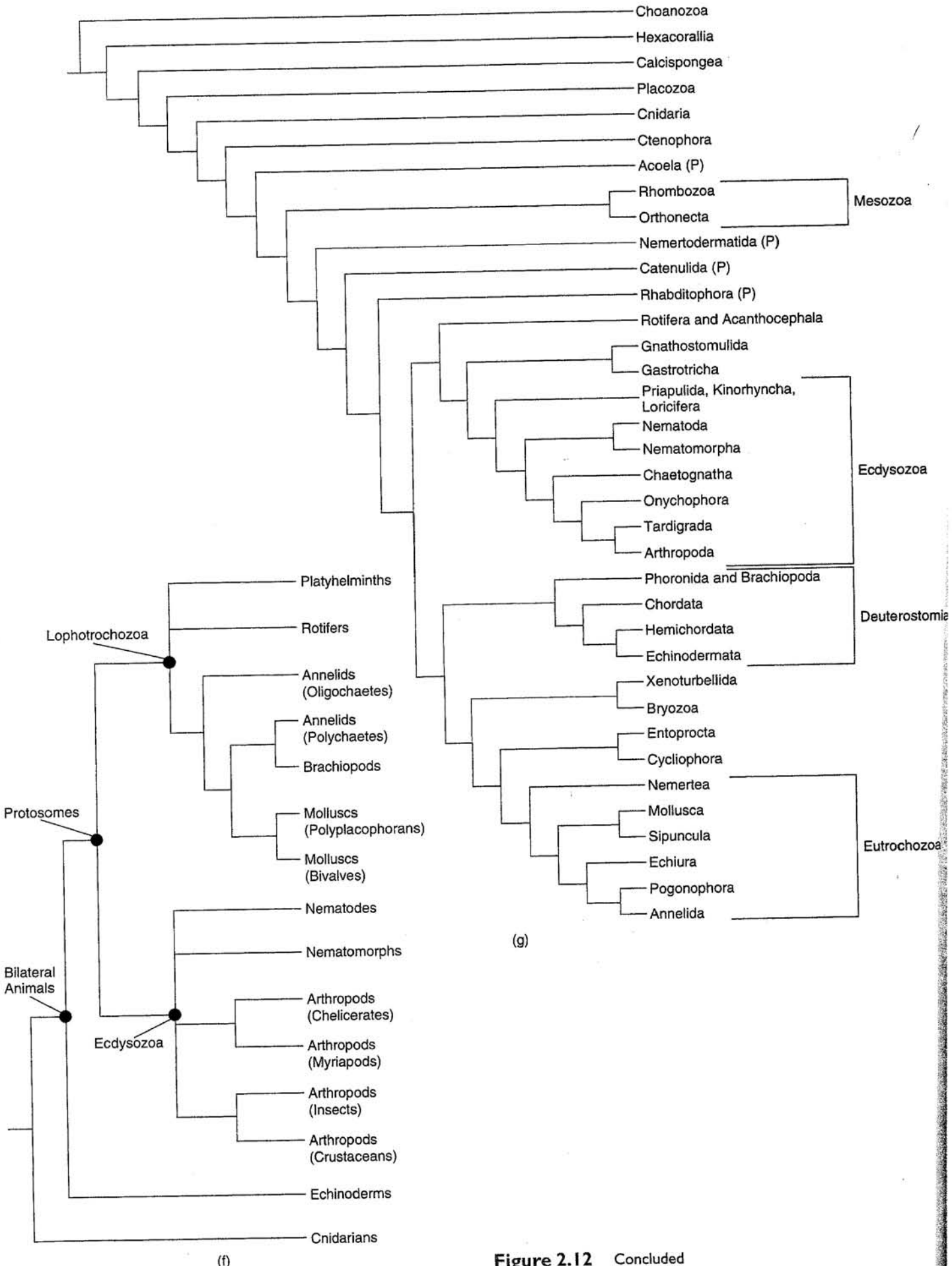


Figure 2.12 Concluded

for example, the pogonophorans (p. 294) were originally characterized as unquestionable deuterostomes, based on adult morphology. Years later, specimens with a small additional body part were obtained—the posterior part of the animal had detached unnoticed from previous specimens—and the animals were quickly reclassified as a phylum of protostomes. Indeed, largely on the basis of features of that small terminal portion, pogonophorans have recently been incorporated into the phylum Annelida, a group that contains earthworms and leeches.

Finally, molecular studies comparing selected gene sequences among representatives of different groups are quickly altering our understanding of many invertebrate relationships. While molecular data often support previous conclusions based on morphology, such as the monophyly of living animals and the distinction between protostomes and deuterostomes, they frequently suggest relationships quite different from those based on morphological criteria. Where molecular data produce phylogenies very different from those based on morphology, decisions will have to be made about which evidence is more likely to be correct. And it is worth noting that molecular studies, as powerful as they are, will never resolve all phylogenetic issues, no matter how sophisticated these studies become. For one thing, when species diversified too rapidly, molecular studies are unable to resolve the order of divergence. Moreover, molecular studies will never be able to tell us the precise sequence of steps that took place as one form gave rise to another or what selective pressures brought about these morphological changes. And molecular studies can never tell us what ancestral, unfossilized animals looked like. Perhaps molecular, paleontological, ecological, and morphological evidence can be used in concert to deduce relationships, but we will still need to decide how much weight to give each line of evidence when the different approaches imply different evolutionary scenarios.

Phylogenetic relationships have been argued about for over 150 years. Such arguments will likely continue long into the future.

Why Determine Evolutionary Trees?

One goal of classification schemes is simply to facilitate discussions about different groups of animals, and ideally to arrange those groups in the correct evolutionary context. But knowing with certainty the precise pattern of evolutionary change that gave rise to the present diversity of animal form would give us far more than a convenient and stable classification system. Finding one species of coral, for example, that produces a particular chemical defensive compound of great biomedical potential, we might know which other species were most likely to synthesize related compounds. We would also be better able to understand the sequence of genetic changes involved in body plans evolution, and would be able to tell with certainty how many times certain traits had evolved independently within any particular group of animals.

For example, Figure 2.13 shows one recent hypothesis regarding the evolutionary relationships among 12 sea star species in two genera within the phylum Echinodermata. Some of the sea star species (shown in black) produce microscopic, swimming larval forms that spend many days or weeks dispersing in the sea while feeding on unicellular protists before metamorphosing to adult form and habitat. Other species either release larvae that do not feed while dispersing (shown in light blue)—the larvae are endowed by the parent with enough yolk to fuel their entire planktonic development and the process of metamorphosis—or brood their offspring within or underneath the body (shown in dark blue), so that the developing young neither feed nor disperse; instead, they simply crawl out from the parent as miniature sea stars.

A convincing phylogeny for these species can tell us much about life history evolution within the group. If the scenario in Figure 2.13 (one of several presented in the original paper) is correct, the ancestor to all of these 12 species had free-living, feeding larvae, and feeding larvae have been lost independently at least 4 times, once on the way to *Patieriella pseudoexigua* and *Asterina pseudoexigua pacifica*, and once on the way to *A. gibbosa*, for example. Similarly, dispersive larvae, whether they are feeding or not, have been lost during the evolution of these sea stars at least 3 times, once on the way to *A. pseudoexigua pacifica* and once on the way to *P. exigua*, *P. vivipara* and *P. parvivipara*, for example. Similar arguments are being made for the evolution of life histories, behaviors, parasitic associations, morphological features, and biochemical or physiological attributes in a wide range of other animal groups. Thus, there is a lot riding on our ability to convincingly ascertain exactly how animals are related to each other.

How Evolutionary Relationships Are Determined

"Even with a consistent method, the best tree need not be the correct tree." R. Raff et al. 1997. *Ann. Rev. Ecol. Syst.* 25:351–75.

If all living metazoans evolved from a single ancestral form many millions of years ago, then all animals are related to each other: No matter how distant, there must be some genealogical connection between flatworms, snails, squid, annelid worms, insects, lobsters, sea urchins, and baleen whales. Trace your own ancestry far enough back, and you must find an invertebrate in your family tree.

Trying to unravel the evolutionary connections among the major animal groups is one of life's greatest puzzles and presents one of the greatest of intellectual challenges. In particular, there are many difficulties in deciding how best to go about arranging and sorting the puzzle pieces, and in judging the accuracy of the picture

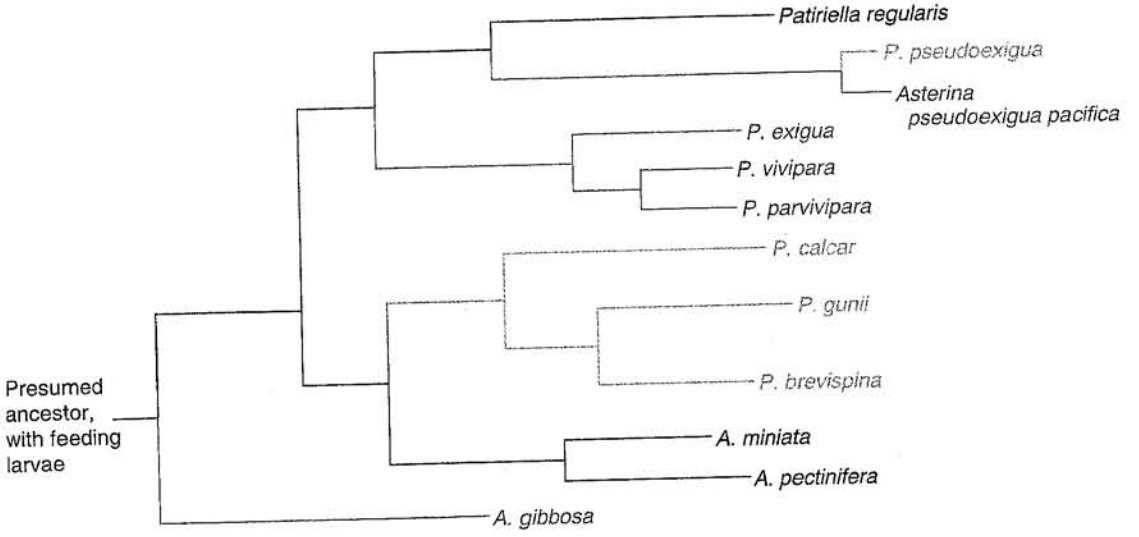


Figure 2.13
One proposed phylogenetic hypothesis for 12 species in the sea star genera *Patiriella* and *Asterina*. The tree was constructed with the goal of understanding the process of life-history evolution within this group of animals. Species producing microscopic larvae that feed in the plankton are shown in black. Species producing microscopic planktonic larvae that do not feed are shown in light blue. Species producing embryos that neither feed in the plankton nor disperse during development are shown in dark blue.
From M.W. Hart, M. Byrne, and M.J. Smith, 1997. Evolution 51:1848–1861. Reprinted by permission.

that emerges when the sorting is done. In the next few pages I discuss these and related difficulties. Far more detailed discussions are found in the references listed at the end of this chapter.

Charles Darwin originally referred to what we now call evolution as "descent with modification." The members of any species tend to resemble each other from one generation to the next, as long as there is random mating within the gene pool. But if some individuals become reproductively isolated from other members of the species, they can evolve in quite different directions, particularly if they face different selective pressures—different temperature or salinity regimes, for example, or different sorts of predators or food resources. If species have gradually acquired differences—physical, physiological, biochemical, behavioral, genetic—at constant rates, and if they have continually evolved to resemble their ancestors less and less over time—ideally becoming more and more complex—then it should be easy to deduce evolutionary relationships. But animals do not evolve in so straightforward a way, which opens the door for both sophisticated creativity and controversy.

The centerpiece of any phylogenetic detective work is *homology*. Morphological features that share a common evolutionary origin are said to be *homologous;* the differences in such features among different animal groups reflect descent from ancestors with modification. In many cases, homologous features develop through similar pathways controlled by the same genetic instructions. If you can recognize homology when you see it, evolutionary puzzles should be easily solved. If you can safely assume, for example, that spiral cleavage evolved only once, then spiral cleavage is a homologous trait in all groups that exhibit it: All spirally cleaving animals have descended from a common ancestor and must be more closely related to each other than to animals that show any other cleavage pattern. But what if spiral cleavage is *not* homologous in all groups? Suppose that when eggs cleave there are only a few ways for the daughter cells to sit in stable relation to each other, and that the spiral pattern formed by adjacent cells simply represents one particularly stable geometric arrangement. In that case, different animal groups are likely to have independently converged upon spiral cleavage as an especially successful way to initiate development: Cleavage pattern then misleads us in our thinking about evolutionary relationships, and the molluscs, annelids, flatworms, and other spirally cleaving animals need not be closely related. Similarly, if coelomic cavities evolved only once, then coelomates form a monophyletic group and we then face the issue of determining whether protostomes evolved from deuterostomes or vice versa. But if coelomic cavities originated independently two or more times in different ancestral species, then the coelomate condition conveys only a very garbled phylogenetic message at best.

Even very complex morphologies can independently evolve from very different ancestors to give a close resemblance by *convergence*, as discussed earlier. It is often difficult to decide whether features that look similar in different animal groups are homologous or not.

The second particularly thorny issue concerns the direction, or *polarity*, of evolutionary change. Even if two

characters are considered to be homologous, there is the question of which one represents the original, or *ancestral,* state and which represents the more advanced, or *derived* state. Issues of homology and polarity are at the source of most current debates among systematists. There are three basic approaches to deducing evolutionary relatedness, as described in the following pages.

Phenetics (or Numerical Taxonomy)

One solution to the homology/polarity dilemma is to assume that it is not possible to ascertain either with certainty, and to then set about establishing taxonomic groups that reflect overall similarity alone, regardless of whether that similarity reflects common ancestry or not. In practice, pheneticists measure as many characters as possible—the number of appendages on the head, the type of cleavage exhibited, the number and color of eyes, and whether eggs are fertilized externally or internally, for example—from each group of animals under study, and then apply complex computer algorithms to determine which groups are most alike and which are most different from each other. In its purest form, all characteristics have equal weight in assessing overall degree of similarity: Cleavage pattern is no more or less important than eye color, for example. Two groups will cluster together if they share more similarities with each other than with the members of other groups. If most of the characters compared are in fact homologues, then the resulting scheme of similarities may also reflect degrees of evolutionary relatedness. But the main appeal of the approach is in not having to grapple with issues of character homology and polarity. The approach does not have strong support at present: most biologists *want* a classification system to reflect evolutionary relationships.

Evolutionary Systematics (Classical Taxonomy)

Evolutionary systematics has been practiced for over 100 years. In contrast to pheneticists, the evolutionary systematist wrestles with issues of homology at the outset of an analysis, and also decides which characters are most likely to hold the greatest amount of phylogenetic information; other characters are given less weight (underweighted) in the analysis or ignored altogether. Once what are believed to be homologous characters are used to deduce general relationships, the extent to which the various species under consideration differ from each other and the extent to which they resemble each other are both taken into account in constructing the final classification. To use a familiar noninvertebrate example, evolutionary systematists put birds in a separate class, the Class Aves; birds have clearly evolved from ancient reptilian ancestors, but they have evolved so dramatically far from those ancestors they deserve status as a separate class. The other, more reptile-like descendants of that same ancestor are grouped in a separate class, the Reptilia. It makes intuitive sense to form groups of similar-looking species and to exclude species that look very different, but as you will see below, all systematists do not share this feeling, in large part because the classical approach often leads to the formation of paraphyletic groups. The Reptilia, for example, is paraphyletic because it excludes some descendants of the original reptilian ancestor: the birds, and the mammals. The evolutionary systematist is not troubled by paraphyletic groupings.

Constructing classifications and evolutionary trees by this method is painstakingly slow, and requires decades of experience working with the animals being categorized. Intuition and logic play important roles in all decisions made. Major objections to this process are that it lacks objectivity and a rigorously standardized methodology, and that outsiders have difficulty arguing with the results.

Cladistics (Phylogenetic Systematics)

This approach to deducing evolutionary relationships has gained a large and enthusiastic following over the past 20 years or so. Although not universally accepted, cladistic procedures have become so widely used and so widely discussed (and argued about) that I will go into the philosophical and procedural underpinnings in more detail than I have for the other two approaches, to facilitate class discussions and individual forays into the burgeoning primary literature. Unfortunately, the field of cladistics is terminologically well-endowed. In this treatment, I use as few of those terms as possible; for those wishing to read and discuss the relevant literature, I define the most important terms in Table 2.2.

Among cladists, phylogenies are constructed and assessed using one of several well-defined procedures and a number of widely available, highly sophisticated computer programs. The only characters of importance in establishing evolutionary relationships are so-called **synapomorphies,** shared characters derived from a common ancestor in which the characters originated. The astute reader will notice that this resembles the definition of homologues as well. However, the cladist is interested only in homologous characters that are not present in any earlier ancestors; only evolutionary novelties are used to construct cladistic classifications and to infer evolutionary relationships. In some cases a single morphological characteristic suffices to define a major evolutionary event. Presence of a water vascular system derived from the central coelomic chamber (mesocoel) during embryogenesis, for example, uniquely defines the echinoderms. A particularly dramatic departure from the classical systematist's approach is the cladist's insistence that valid taxa include all descendants of an ancestor. As mentioned earlier, for example, cladists cannot recognize the Reptilia as a valid taxonomic category because it does not include birds and mammals, which have evolved from reptilian ancestors.

Table 2.2 Cladistic Analysis: Some Common Terms Defined

clade: a group of organisms that includes the most recent common ancestor of all its members and all descendants of that ancestor; every valid clade forms a "monophyletic" group (see below).

cladogenesis: the splitting of clades into two or more distinct lineages (*klados* = G: twig, or branch).

anagenesis: change occurring within a lineage.

cladogram: the pictorial representation of branching sequences that are characterized by particular changes in key morphological or molecular characteristics (character states).

homologous characters, homology: characters that have the same evolutionary origin from a common ancestor, often coded for by the same genes. Homology is the basis for all decisions about evolutionary relationships among species.

taxon: any named group of organisms, such as jellyfish or sea urchins or slippershell snails (*Crepidula fornicata*); plural = **taxa.**

monophyletic taxon: a group of species that evolved from a single ancestor and includes all descendants of that ancestor. By definition, every valid clade forms a monophyletic taxon.

parsimony: a principle stating that, in the absence of other evidence, one should always accept the least complex scenario.

polarity: the direction of evolutionary change.

ancestral (primitive) state: the character state exhibited by the ancestor from which current members of a clade have evolved. Also called the "plesiomorphic" state.

derived (ancestral) state: an altered state, modified from the original, or ancestral condition. Also called the "apomorphic" state.

synapomorphy: a derived (advanced) character that is shared by the most recent common ancestor and by two or more descendants of that ancestor. In cladistic methodology, synapomorphies define clades; that is, they determine which species (or other groups) are most closely related to each other. Essentially, synapomorphies are homologous characters that define clades.

homoplasy: the independent acquisition of similar characteristics (character states) from different ancestors through convergence or parallelism. Such homoplastic events create the illusion of homology.

paraphyletic grouping: a group of species sharing an immediate ancestor but not including all descendants of that ancestor.

polyphyletic grouping: an incorrect grouping containing species that descended from two or more different ancestors. Members of polyphyletic groups do not all share the same immediate ancestor. Members of polyphyletic groups may resemble each other because of the independent evolution of similar traits by different ancestors.

Let us consider a simple example of cladistics in action, with 4 groups of imaginary animals. Distinguishing characteristics are shown in Figure 2.14. The direction of evolutionary change (**polarity**) is first determined by comparison with a closely related taxon (the **outgroup**) that lies outside the taxa being studied; this outgroup's characteristics are assumed to represent the ancestral condition. Suppose that through comparison with an imaginary outgroup, we assume that the ancestor to all 4 of the groups shown in Figure 2.14 had a round head, black eyes, a thin mouth, and no ears. Thus we begin by assuming that blue eyes evolved from black-eyed precursors in the immediate ancestor to animals in Group 2. If this assumption is wrong, then our conclusions will be wrong, too.

Figure 2.14b presents a dendrogram (now called a **cladogram;** *clados* = G: a branch) showing the least complex, most **parsimonious** way of explaining the evolutionary history of these groups. Groups 1 and 4 are said to be **sister groups,** both derived from the same ancestor, an animal that was not ancestral to members of the other 2 groups. By the same reasoning, Group 2 is the sister group to the combination of Groups 1 and 4. Try drawing alternative evolutionary scenarios. You will find that of all possible alternatives, the one illustrated does indeed require the fewest evolutionary changes; to derive Group 4 from Group 2, for example, would require a reversion of eye color back to the ancestral black-eyed condition and the independent evolution of a wide mouth.

Published analyses consider dozens of different characters. Many of those characters give conflicting signals, because not all similarities between different animal groups are caused by homology; some similarities arise through convergence or parallelism. All we see are the similarities, not how they arose, so that some similarities lead in one direction while other similarities point toward very different relationships among groups being compared.

Consider the example in Figure 2.15. Two new characters have been added: Members of two groups now have noses and members of two groups have hair. Assuming that the characteristics of Group 1 represent the primitive, or ancestral condition, 3 very different but perfectly reasonable cladograms can be constructed. Two of these

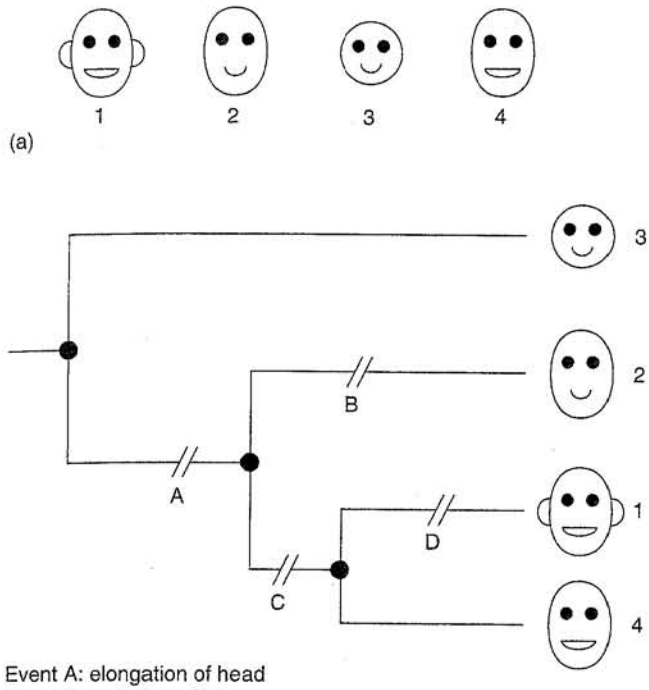


Figure 2.14

Cladistics in action. (a) Imaginary animals are placed into four groups according to differences in head characteristics as shown. Individuals differ in head shape, eye color, mouth shape, and the presence or absence of ears. (b) Evolutionary relationships among the four groups as determined by cladistic principles. Letters represent the evolution of uniquely defining characteristics (synapomorphies) shared by all descendants of the individual in which the characters first evolved. Each filled circle represents an ancestral species that gave rise to the groups stemming from that ancestor.

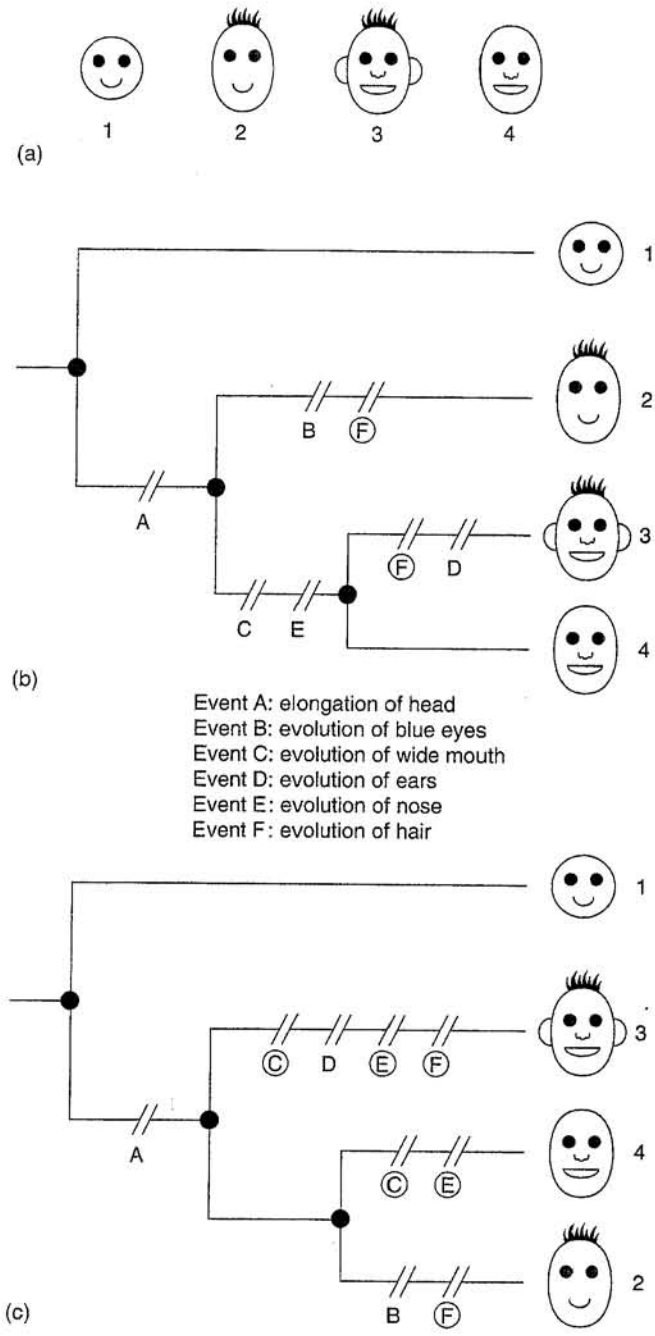


Figure 2.15

The difficulties created by undetected convergent events. (a) As in Figure 2.14, 4 groups of animals differ in head characteristics as shown. Now, however, different sets of characters suggest different evolutionary relationships among the animal groups. Two of these relationships are depicted in (b) and (c). Capital letters indicate key evolutionary events. Circled letters indicate events that must have occurred independently in at least two different ancestors.

are presented in Figure 2.15b and c. In cladogram b, animals 3 and 4 form sister groups, whereas in cladogram c, animals 2 and 4 form sister groups. In the 3rd scenario, which you can work out for yourself, animals 2 and 3 are sister groups. In other words, we can't really tell how these different groups of animals are related. By the principle of parsimony, we favor the first scenario (Fig. 2.15b) because it requires only 7 evolutionary steps (count them); the second scenario requires 9 steps. How many steps are required for the 3rd scenario?

Note that the cladograms in Figure 2.15b and c both postulate convergent evolutionary events (indicated by circled letters). In cladogram b, hair evolved once in Group 2 and a 2nd time, independently, in Group 3. Convergence plays an even larger role in cladogram c; noses, wide mouths, and hair each evolved twice (separately in Groups 3 and 4 for noses and mouths, and separately in Groups 2 and 3 for hair). Other scenarios are possible, too. In Figure 2.15c, we could imagine hair evolving once, along with elongation of the head, and then being lost in the ancestor giving rise to the animals in Group 4. This could in fact be the actual sequence of evolutionary events, of course, but we eliminate it as being a relatively unparsimonious explanation. When different characters

give conflicting signals like this, the scenarios supported by a majority of characters and involving the fewest number of evolutionary transformations are selected for further consideration.

One can test the robustness of particular trees in a variety of ways—using different computer algorithms, for example, and seeing how much the resulting trees resemble each other, or by repeatedly subsampling different elements of the data set and seeing whether the trees change a great deal or only a little as different aspects of the data are randomly included or excluded from the data set. If branching patterns remain stable when different components of the data set are randomly added or removed, that branching pattern is obviously more convincing than if the patterns change with every subsampling of the data. In this sense, the phylogenetic hypotheses that each tree represents are testable. But without additional data, there is really no way to determine which of several competing trees is the most likely one. If convergence is relatively uncommon, then cladistic analyses of morphological characters may produce an accurate tree. But many believe that convergent evolution has been very common, which seems especially likely as many different body plan features are apparently controlled by similar sets of genes in widely different animal groups. If convergence is indeed rampant, then the best trees may well be incorrect trees, because branching patterns will be based on false homologies.

The data contained in DNA molecules may present our best hope of eventually resolving such dilemmas, as discussed in the following text.

Cladistic Treatment of Molecular Data

One great appeal of cladistic methodology is that it accommodates molecular data. Assuming that the gene sequences for particular proteins in different organisms are homologous, each base in the sequence conveys potential information about evolutionary relationships. Consider the short stretch of DNA shown for 4 groups of animals in Figure 2.16. In actual practice, biologists work with sequences that are hundreds or thousands of base-pairs long. If we are convinced that we are starting at exactly the same point in the same gene sequence for each group, then we can read from left to right in our simplified example, checking to see if the bases are the same or different at each position in the sequence. Each difference represents a separate evolutionary event. In Figure 2.16a, for example, all 4 groups have identical bases at positions 1, 2, and 3; these first 3 positions offer no phylogenetically useful information. But Group B has a different base at position 4, an adenine instead of a cytosine. This represents an evolutionary event—a mutation in the gene sequence that occurred only in the immediate ancestor to the animals in Group B. Some of these mutations will alter animal form or function, creating the materials through which natural selection works. Other changes will have no phenotypic effects because the genetic code is degenerate (several triplets code for the same amino acid) or because the mutation occurs in a non-coding region of the DNA or is compensated for (in diploid organisms) by lack of mutation in the homologous chromosome. In our example, position 4 appears to be phylogenetically informative.

But wait: How do we know that the sequences for the 4 groups are correctly aligned? Looking more carefully, we see that after position 3, only one of the remaining bases from Group B animals agrees with those in Group A. Perhaps the original base in position 4 was deleted in the ancestor to Group B; deletions are bona fide mutational events. So let us redraw the sequence data assuming a deletion event at position 4 (Fig. 2.16b). Now we get much better agreement between base pairs in sequences A and B. Similarly, if we assume for Group D that the cytosine at position 5 was not present in the ancestor, but was in fact added through mutation (an insertion), we would realign the sequences for Group D as shown in Figure 2.16c. Now there are no mismatches between the bases in this short DNA sequence.

All sequences must be aligned before the bases can be compared. This alignment is clearly a source of potential error in the subsequent analysis. Once sequences are aligned to the satisfaction of the biologist doing the study, ancestral states are determined through comparison with an outgroup, and the rest of the analysis proceeds much as for analyses using morphological criteria, except that now we are working with hundreds or thousands of characters for each animal group.

These simple examples give you an idea of the sorts of problems one must consider when conducting cladistic analyses. Some of the startling findings based upon cladistic analyses of molecular data are summarized in Figure 2.12f. Compare, for example, the relationships in

(a)

Base Position	1	2	3	4	5	6	7	8
Group A:	A	A	T	C	A	G	A	T
Group B:	A	A	T	A	G	A	G	T
Group C:	A	A	T	C	G	G	A	C
Group D:	A	A	T	C	C	G	G	A

(b)

Group A:	A	A	T	C	A	G	A	T
Group B:	A	A	T	—	A	G	A	G	T

(c)

Group C:	A	A	T	C	G	G	A	C
Group D:	A	A	T	C	G	G	A	

Figure 2.16

Four hypothetical short stretches of a particular gene sequence (e.g., 18S rRNA) taken from 4 different species. Each letter represents a different nucleotide base (A = adenine; G = guanine; C = cytosine; T = thymine). Sequences from different species must be correctly aligned before they can be compared.

Figure 2.12c and f for arthropods, nematodes, and annelids. Almost every month, molecular data are causing biologists to question many of the most cherished and longstanding assumptions about invertebrate evolution. A more detailed example of the use of molecular data in evaluating relationships between major animal groups is given in Research Focus Box 12.1 (page 178).

Uncertainty about Evolutionary Relationships

There is always the temptation to embrace uncritically new technology and complex procedures as giving definitive answers. Indeed, the approach outlined here is so seductive that one is immediately tempted to draw firm conclusions from the cladograms that are generated; the procedures are so sophisticated and so logical that it is easy to forget that the products are working hypotheses. In fact, many biologists have serious reservations about the cladistic approach, and there are many additional controversies within the cladistic community. Even with morphological data, the relationships deduced by computer vary depending on the outgroup used, the characters included in or omitted from the analysis, the computer algorithm used to examine the data, and sometimes even the order in which data are entered into the calculations. The central assumption of parsimony itself periodically falls under attack: Why assume that animals evolve from one form to another in the most direct route possible? In fact, what we know about the evolutionary process suggests this must often not be the case. And is it valid to assume that the characteristics of the outgroup used for comparison always represent the ancestral character states? Even the simplest of animals, and their genomes, have been evolving for hundreds of millions of years.

Molecular data carry their own set of additional complications. Some parts of a given molecule are more likely to change than other parts of the same molecule, and to change at widely different rates within the same animal group, some types of mutations occur with greater frequency than others, different molecules (mitochondrial DNA and 18S rRNA, for example) evolve at different rates within the same animal groups, and homologous molecules evolve at different rates in different animal groups. Of particular interest, gene sequences that evolve unusually rapidly produce longer branches that tend to group closely together—not because the associated animals are close relatives, but only because of the rapid evolution of the sequences in question: "long branches attract." Distinguishing between true evolutionary affinity and such "long branch attraction" problems has not been easy. I already mentioned the additional problems associated with sequence alignment. Also, each position in a molecule can change more than once: Guanine can be replaced by adenine, only to be later replaced by guanine, erasing any sign of the molecular evolution that occurred. And, as with morphological features, molecules can also come to resemble each other through convergence. Indeed, with only 4 possible bases for each position in a DNA molecule, some similarity through convergence is quite likely. Researchers have developed very sophisticated ways of addressing all of these problems, but each manipulation introduces more uncertainty into the analyses.

A major appeal of cladistics is that the data and the methodology are completely up-front and open to examination and criticism. It is also very democratic, not requiring years of experience working with the animals under consideration. Whether this is a step forward or a step backward is an issue for class discussion. But acceptance of the cladistic approach is certain to keep growing. Indeed, cladistics may offer the best hope for forging an eventual consensus about the evolutionary relationships among phyla, particularly as more molecular data from more different molecules and more species are incorporated, and as our understanding about the interpretation of those data improves. But whether cladistics eventually reveals the TRUTH about evolutionary relationships may be impossible to ever evaluate. Even if all biologists should eventually agree on any particular set of relationships, there is really no way to test the accuracy of those conclusions, barring the invention of time travel.

Time Machines: Help from the Fossil Record

Probably the closest we will ever get to time travel is the fossil record. For many years there was great controversy about the evolutionary relationship between insects and crustaceans (crabs, lobsters, shrimp, barnacles, etc.). Crustacean appendages are typically biramous (two-branched), while those of insects are exclusively uniramous (single-branched). Strong arguments were made that the crustacean ancestor bore only biramous appendages, and that one branch from each appendage was lost in the evolution of insects. Other biologists advanced equally strong arguments supporting the independent evolution of crustaceans and insects from separate ancestors, with the insect ancestor never having had biramous appendages. The report of fossilized insects bearing biramous appendages in 1992 finally and immediately laid this long-standing controversy to rest. Subsequently, we have learned that the branching of appendages as they develop is under a very simple genetic control mechanism; in hindsight it seems obvious that the uniramous insects could easily have evolved from ancestors with biramous appendages.

But molecular data can never tell us what any hypothesized ancestor actually looked like; the controversy about the relationships between insects and crustaceans was resolved by physical evidence from the fossil record, not by sophisticated technology or complex computer algorithms. Similarly, when one finds a 570-million-year-old metazoan embryo, we can know with certainty that complex multicellular animals of some

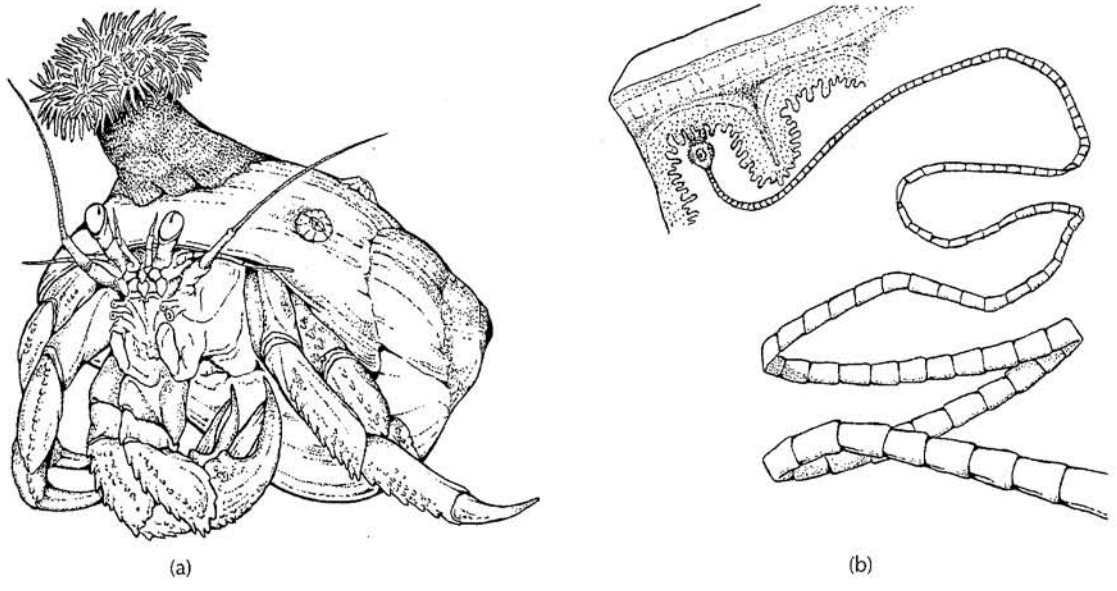
kind existed at that time. Molecular data are leading us to question many evolutionary scenarios and many of the assumptions on which those scenarios are based, and will undoubtedly tell us very exciting things about the genetic changes underlying evolutionary shifts in form and function. Additional fossil material will probably resolve at least some key phylogenetic issues, but issues resolvable by new fossil discoveries are mostly limited to those within phyla, not among phyla: Informative fossils from before the Cambrian explosion will likely remain very limited. Whether or not a firm consensus about evolutionary interrelationships among the various animal phyla emerges remains to be seen; the changes that have occurred in DNA sequences as animals have evolved probably offer our best chance of ever fully resolving these issues.

Classification by Habitat and Lifestyle

Animals also may be categorized on the basis of habitat or lifestyle; such categories reflect degrees of ecological similarity rather than the closeness of evolutionary relationship. For example, one group of animals may be **terrestrial,** living on land, while another is **marine,** living in the ocean. Marine animals, in turn, may be **intertidal** (living between the physical limits of high and low tides and thus exposed to air periodically); **subtidal** (living below the low-tide line and thus exposed to air only under extreme conditions, if ever); or **open ocean** creatures. In addition, animals may be **mobile** (capable of locomotion), **sessile** (immobile), or, perhaps, **sedentary** (exhibiting only limited locomotory capabilities). Some aquatic organisms may be able to move but have negligible locomotory powers with respect to the movement of the medium in which they live; such individuals are said to be **planktonic** (G: forced to drift or wander).

Animals are often categorized as to how they feed or what they eat. For example, some species are **herbivores** (plant eaters), while others are **carnivores** (flesh eaters). Some species remove small food particles from the surrounding medium **(suspension feeders),** while others ingest sediment, digesting the organic component as the sediment moves through the digestive tract **(deposit feeders).**

Members of one species frequently live in intimate association with those of another species. These **symbiotic associations,** or **symbioses,** frequently relate to the feeding biology of one or both of the participants **(symbionts)** in the association (Fig. 2.17). **Ectosymbionts** live near or on the body of the other participant, while **endosymbionts** live within the body of the other participant. When both symbionts benefit, the relationship is said to be **mutualistic,** or an example of **mutualism.** When the benefit accrues to only one of the symbionts and the other is neither benefited nor harmed, the relationship is one of **commensalism,** and the benefiting member is the **commensal.** Last, some animals are **parasites;** that is, they depend upon their **host** for continuation of the species,



(a) (b)

Figure 2.17

(a) A symbiotic relationship between a sea anemone, *Calliactis parasitica,* and a hermit crab, *Eupagurus bernhardus.* The crab deliberately places the anemones on its shell. (b) A tapeworm, *Taenia solium,* shown attached to the intestinal wall of its vertebrate host. (a) *After Hardy.* (b) *After Villee.*

generally subsisting on either the blood or the tissues of the host. A parasite may or may not substantially impair the host's activities. The essence of parasitism is that the parasite is metabolically dependent upon the host and that the association is obligate for the parasite.

The boundaries between parasitism, mutualism, commensalism, and predation are not always distinct. For example, a parasite that eventually kills its host essentially becomes a predator. A parasite that produces a metabolic end product from which the host benefits borders on being mutualistic. Indeed, transitional forms in the process of evolving from one type of relationship to another are not uncommon. Such transitional forms make tidy categorization of animals into human-made schemes difficult; definitions of some categories have been modified by various workers in an attempt to improve the fit, but every rule seems to have an exception.

Topics for Further Discussion and Investigation

1. There are presently 3 major theories of animal classification: the theory of **phenetics** (based entirely on degree of overall anatomical and biochemical similarity, without regard to whether the similarities reflect homology or convergence), the theory of **cladistics** or **phylogenetic classification** (based entirely upon recency of common descent inferred from the mutual possession of particular specialized, derived morphological traits called **synapomorphies**), and the theory of **evolutionary classification** (which attempts to consider both ancestry and the degree to which organisms have subsequently diverged from the ancestral form). Discuss the advantages and disadvantages inherent in any two of these three approaches to the inferring of phylogenetic relationships.

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2. What are the characteristics of the "ideal" classification system, and why is this ideal so difficult to attain?

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3. The fossil record shows a remarkable radiation of animal body plans between about 540 and 570 million years ago in a geologic time period termed the Cambrian. The earliest known metazoans—from the so-called Ediacaran fauna collected in the Ediacara hills of South Australia in the 1940s—are somewhat older. To what extent do the Ediacaran and Cambrian faunas differ, and what might account for those differences?

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4. Molecular analyses allow us a direct look at differences in the genetic structure among species, potentially overcoming some of the problems associated with morphological studies. Moreover, if the chosen molecules are not subject to selection and if mutation rates are constant, degrees of difference between the molecules of 2

different species should indicate the amount of time elapsed since the species diverged from their common ancestor. Why haven't molecular data been able to resolve all previous phylogenetic controversies?

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5. Compare and contrast the relationships among phyla depicted in any three parts of Figure 2.12. For example, note that molluscs (such as snails, clams, and squid) are shown as having an immediate ancestor in common with annelids (such as earthworms and leeches) in (e) and (f) but as evolving independently of annelids in (d).

6. Was there a Cambrian explosion?

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Search the Web

1. http://www.ucmp.berkeley.edu/subway/specex.html

   Click on "Journey into Phylogenetic Systematics" for an introduction to the principles and implications of cladistic analysis, produced at the University of California at Berkeley.

2. http://phylogeny.arizona.edu/tree/phylogeny.html

   The Tree of Life, containing information about phylogeny and biodiversity, and orchestrated by D. R. Maddison and W. P. Maddison at the University of Arizona.

3. http://www.ucmp.berkeley.edu/cambrian/camb.html

   This site, produced by the University of California Museum of Paleontology, concerns the Cambrian explosion. It includes excellent photographs of Burgess Shale fossils.