"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**

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

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 543 to 635 million years old, members of the so-called Ediacaran fauna first discovered in South Australia. Moreover, none of those Ediacaran animals 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 about 543 mya (million years ago). The best-studied invertebrate fossils are from the Burgess Shale of British Columbia, first discovered only in 1909 but formed some 525 mya in the Cambrian. Many of these animals were soft-bodied and others had hard parts, but their most conspicuous feature

---

1. See Topics for Further Discussion and Investigation, no. 3, at the end of the chapter.
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 may be cnidarian-like, echinoderm-like, and arthropod-like metazoan embryos have recently been described from southern China in rocks formed about 580 mya (Fig. 2.1), suggesting that forms related to modern animals existed at least 40 million years 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 increased photosynthetic activity, 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.

In any event, nearly all of today’s major animal 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 these phyla are related to each other. Studying the extensive Cambrian and post-Cambrian 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. In the next few sections, we’ll look at some of those key traits.

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. 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, and to then deduce the evolutionary relationships among and within those groups.

---

2. See Topics for Further Discussion and Investigation, no. 6, at the end of this chapter.

3. See Topics for Further Discussion and Investigation, no. 8, at the end of this chapter.
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 to collectively as the Metazoa, or as metazoans. Other invertebrates are considered either unincellular (single celled) or acellular (without cells)—a distinction discussed further in Chapter 3—and do not develop from anything resembling a metazoan embryo. As we will see in the next several chapters, the point at which an association of cells can be viewed as composing a multicellular organism is not always clear-cut. It is widely agreed that multicellular life evolved from some unicellular organism. Thus, there has been considerable interest in trying to determine how many times multicellularity arose, and from which unicellular ancestors it arose.

Animals may also be classified according to their general body form. Most metazoa show one of two types of body symmetry (Fig. 2.2a,b), at least superficially. Animals like ourselves are bilaterally symmetrical, possessing right and left sides that are approximate mirror images of each other. Bilateral symmetry is highly correlated with cephalization, which is the concentration of nervous and sensory tissues and organs at one end of an animal, resulting in distinct anterior and posterior ends. For an animal that shows cephalization, two mirror images can be produced only when a slice is made parallel to the animal’s long (anterior-posterior) axis, with the cut passing down the midline. Any cut perpendicular to this midline, even when passing through the animal’s center, creates two dissimilar pieces. This is not so for a radially symmetrical organism. Such an animal can be divided into two approximately equal halves by any cut that passes through its center. Thus, most animals belong to either the Radiata or the Bilateria. Asymmetrical invertebrates—those having no ordered pattern to their gross morphology—are uncommon (Fig. 2.2c).

Once again, what seems to be straightforward on the surface is never quite so simple when dealing with actual animals. Many species whose external appearances are the epitome of uncontroversial radial symmetry have asymmetrical internal anatomies. Some sea anemones, for example, are internally bilaterally symmetrical, and even show patterns of gene expression during development that resemble those of other bilateral animals. Perhaps it would have been better to group animals based on degree of cephalization rather than on the basis of body symmetry. I bow, however, to historical precedent.

**Classification by Developmental Pattern**

Developmental pattern has long played a pivotal role in classification schemes, and in deducing evolutionary relationships, as discussed in the next several sections. Multicellular invertebrates have for many years been divided into two groups based upon the number of distinguishable germ layers formed during embryogenesis. Germ layers are groups of cells that behave as a unit during the early stages of embryonic development and give rise to distinctly different tissue and/or organ systems in the adult. In diploblastic animals (diplo = Greek: double), only 2 distinct germ layers form during or following the movement of cells into the embryo’s interior. The outermost layer of cells is called the ectoderm (ecto = G: outer; derm = G: skin) and the innermost layer of cells is called the endoderm (endo = G: inner). Members of only a few phyla (notably the Cnidaria) are generally considered to be diploblastic (Fig. 2.10). Most metazoans are instead triploblastic (trilo = G: triple). During the ontogeny of triploblastic animals, cells of either the ectoderm or, more usually, the endoderm give rise to a third germ layer, the mesoderm (meso = G: middle). This mesodermal layer of tissue always lies between the outer ectodermal tissue and the inner endodermal tissue.

The absence of a distinct, embryonic, third tissue layer does not mean that the adult of a diploblastic species will lack the tissues that are derived from this layer in adults of a triploblastic species. Muscular elements, for example, derive from the mesodermal layer in triploblastic animals, but diploblastic adults also have musculature, despite the absence of a morphologically or behaviorally distinct group of cells that can be termed mesoderm in the early embryo.

Triploblastic animals have been further classified into 3 basic plans of body construction, based on whether they have an internal body cavity independent of the digestive

---

Figure 2.3
(a) Diagrammatic cross section through the body of an acelomate. 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.

tract (gut) and on how this cavity forms during embryogenesis. Although their importance as phylogenetic clues has diminished considerably in recent years, or at least has become more controversial, these developmental characteristics have long played central roles in arguments about how triploblastic metazoans are related to each other. Triploblastic animals lacking an internal body cavity are said to be acelomates ($a = G$: without; coelom = G: a hollow space). Characteristically, the region lying between the outer body wall and the gut of acelomates is solid, being occupied by mesoderm (Fig. 2.3a), and there is no trace of an internal body cavity during embryological development.

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 (Figs. 2.3b, 2.4a); in some species, this cavity is derived from the blastocoel, an internal space that develops in the embryo prior to gastrulation ([Figs. 2.4b(1), c(2), and 2.5a]). This type of body cavity is termed a pseudocoel, and the organism housing it is said to be a 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; $eu = G$: true, proper). Coelom formation may occur by either of 2 quite dissimilar mechanisms a characteristic that has long been 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. 2.4b). 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 embryonic blastocoel (Figs. 2.4c and 2.5). Because the coelom of deuterostomes forms from a part of what eventually becomes the gut, coelom formation in this group of animals is termed enterocoely (entero = G: gut).

Whether the coelom forms 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 3 distinctly different mechanisms (enterocoely, schizocoely, or persistence of embryonic blastocoel) suggests that such cavities have been independently evolved at least 3 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 acelomate, pseudocoelomate, or coelomate, 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 has become increasingly obvious that coelomic cavities can be lost as well as gained,
that acelomates are unlikely to have evolved from a single common ancestor, and that the acelomate body plan may not be primitive (i.e., closest to the ancestral triploblastic condition). Some workers have suggested that the earliest triploblastic animals were acelomate, and that the acelomate condition may thus represent a number of independent losses of the body cavity.

In contrast, the distinction between protostomes and deuterostomes seems secure; the validity of these 2 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 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 may 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.

Cleavage is often referred to as being either radial or spiral, depending on the orientation of the mitotic spindles relative to the egg axis. Generally, yolk is asymmetrically distributed within eggs, 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 (Figs. 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 are oriented (after the first two cleavages) at 45° angles to the animal-vegetal axis (Fig. 2.6j–k). Moreover, the division line does not necessarily 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)
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 4 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 2 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.
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 typically 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 and fully functional animal. Thus, deuterostomes are said to show indeterminate (or regenerative) 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 most 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. Prostome cleavage is therefore said to be determinate or mosaic. Species with determinate development can never produce identical twins, which in deuterostomes arise from the natural separation of blastomeres during early cleavage. Interestingly, both protostomes (e.g., many annelids) and deuterostomes (e.g., many echinoderms) can regenerate body parts as adults, regardless of whether their development is determinate or indeterminate.

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, the embryos of some protostomes form polar lobes (not to be confused with polar bodies, which arise during meiosis). A polar lobe is a conspicuous bulge of cytoplasm that forms prior to cell division and that 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,5 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 it is never encountered among deuterostomes.

Finally, the ciliary bands involved in feeding and locomotion among deuterostome larvae (and adults) are typically monoloculated (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).

The developmental features distinguishing ideal protostomes from ideal deuterostomes are summarized in Table 2.1. Figure 2.10 shows where each animal 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.

Unfortunately, biologists often find it far simpler to construct logical classification systems than to neatly distribute animals within them. As faith in the phylogenetic significance of body cavities has diminished, the definition of “protostome” has been broadened to include both acelomate and pseudocoelomate animals (e.g., flatworms and nematodes, respectively). Few protostome species exhibit all of the other listed protostome characteristics. Not all protostomes exhibit spiral, determinate cleavage, for example.6 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 at least one protostome species (a tardigrade)7 shows the indeterminate cleavage pattern typically associated with deuterostomes.

---
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, Mytilus 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/Photo Take.

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

<table>
<thead>
<tr>
<th>Developmental Characteristic</th>
<th>Protostomes</th>
<th>Deuterostomes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mouth origin</td>
<td>From blastopore</td>
<td>Never from blastopore</td>
</tr>
<tr>
<td>Coelom formation</td>
<td>Schizocoely</td>
<td>Enterocoely</td>
</tr>
<tr>
<td>Arrangement of coelomic cavities</td>
<td>Variable in number</td>
<td>Generally in 3 pairs</td>
</tr>
<tr>
<td>Mesoderm origin</td>
<td>4d cell (Fig. 2.6n)</td>
<td>Other</td>
</tr>
<tr>
<td>Cleavage pattern</td>
<td>Spiral, determinate</td>
<td>Radial, indeterminate</td>
</tr>
<tr>
<td>Polar-lobe formation</td>
<td>Present in some species</td>
<td>Not present in any species</td>
</tr>
<tr>
<td>Larval ciliary bands</td>
<td>Compound cilia from multiciliated cells</td>
<td>Simple cilia, one cilium per cell</td>
</tr>
<tr>
<td></td>
<td>Downstream particle capture</td>
<td>Upstream particle capture</td>
</tr>
</tbody>
</table>
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, developmental, 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). Most modern workers now agree that all monophyletic groups must also include all descendants of the originating 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, and unicellular invertebrates (protists) are distributed among still more phyla. The distribution of described species among the various animal phyla is summarized in Figure 2.11. Note that the percentage of species contained within our own phylum—the phylum Chordata—is quite small (no more than about 5% of all described species) and that this phylum contains both invertebrates and vertebrates.

Remarkably, based on existing fossil evidence, 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 that took place during that time. In the most devastating extinction event to date, 251 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 seem to have appeared. It is possible, of course, that some groups with no fossil record are of more recent origin.

The category of species has particular biological significance, although a single, precise, functional definition has not been found. 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.

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 less inclusive groups, which in turn contain still less inclusive groups, and so on:

- Kingdom
- Phylum
- Class
- Order
- Family
- Genus
- species
Figure 2.10
A modern arrangement of triploblastic animal groups according to the factors discussed in this chapter. The two major animal groupings, protostome and deuterostome, are shaded blue, as are the indications of body cavity types: A = acelomate, Ps = pseudocoelomate, C = coelomate. A "+" indicates that different members of a group belong to different categories (e.g., "C+Ps" means that the group includes both coelomates and pseudocoelomates). No body cavity type designated indicates uncertainty for that group. Some groupings (e.g., Ecdysozoa) are still controversial, and there is not yet complete agreement about membership in the major protostome groups Cycloneuralia and Lophotrochozoa. In some schemes, the lophophorat phyla are included within the Trochozoa. Based on several recent sources.

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 Crepida fornicata. Related species are Crepida plana and Crepida 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 2 genera.
Figure 2.11
Graphic representation of the distribution of described species among the 33 major groups of invertebrates. In this text, protozoans are divided among more than one dozen phyla. Metazoan phyla containing fewer than 2000 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.
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.

The name of the person who first described the organism often follows the species name. It is capitalized, but not italicized. 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 Hyasassa obsoleta (Say) was described by a man named Say, who originally assigned the species to another genus (the genus Nassia). This snail was later determined to be sufficiently dissimilar from other members of the genus Nassia 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.

The system just described has been with us for so long that it seems obvious… and permanent. In 1998, however, a group of influential biologists met with the intention of replacing it. The proposed replacement is called The PhyloCode. Unlike the Linnaean system, The PhyloCode—although it remains hierarchical—is rankless: There will be no classes, orders, or families. It promises to revolutionize systematics.

The following two quotes give a hint of what may lie ahead:

“We argue that taxon names under the Linnaean system are unclear in meaning and provide unstable group-name associations… Furthermore, the Linnaean rank assignments lack justification and invite unwarranted comparisons across taxa.” F. Pleijel and G. W. Rouse. 2003. J. Zool. Syst. Evol. Res. 41:162.


Stay tuned (see Search the Web at the end of this chapter).

Inferring Evolutionary Relationships


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 detailed 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 (rRNA) sequences among species have altered some of these views substantially. "Ferreting out probable relationships is no easy task." In part, the difficulty 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. 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 do not indicate any closer evolutionary relationship between vertebrates and molluscs. 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 2 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 20 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.

8. See Topics for Further Discussion and Investigation, no. 5.

9. See Topics for Further Discussion and Investigation, nos. 1 and 2.
(rRNA), comparisons made feasible through development of the polymerase chain reaction (PCR) in the mid-1980s. The PCR permits biologists to very quickly and inexpensively generate many copies of specific DNA sequences; a billion copies of a single DNA molecule can be obtained in a few hours, 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; 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 have been proposed over the years. Six 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 oldest scheme (Fig. 2.12a) assumes that all multicellular animals descended from some form of single-celled protist, most likely a colonial flagellate, and presents sponges (phylum Porifera) as the earliest experiments in multicellularity with no close relationship to any other existing phyla.

The hypothesized relationships among annelids, arthropods, and molluscs differ considerably among the different viewpoints; compare, for example, Figure 2.12a, d, and f. The more closely you look at the different schemes, the more fascinating the comparisons become; it is well worth returning to Figure 2.12 at intervals as you read the rest of this book. Fig. 2.12c represents one particularly widespread current view, with all acoelomate and pseudocoelomate animals folded into the Protostomia, and the protostomes divided into two major clades: the Ecdysozoa (molting animals) and the Lophotrochozoa (see also Fig. 2.10). Studies of highly conserved Hox gene insertions and deletions (so-called "signature sequences") have added strong support for these ecdysozoan and lophotrochozoan clades. Just as I was completing the manuscript for this revision, however, a colleague showed me a recent paper entitled, "Ecdysozoan clade rejected by genome-wide analysis of rare amino acid replacements." Everything, it seems, is still up for grabs.

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.

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 grouped. 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 animal groups, 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, 2 arthropod classes (the Remipedia and Tantulocarida, p. 417) and 3 small but remarkably distinct phyla of recently discovered marine animals called loriciferans (p. 455), micrognathozoans, and cyclophorans (p. 467) have been established in the last 25 years or so. Cyclophorans were first described in 1995, and micrognathozoans in 2000 (p. 467).

Sometimes classifications change when biologists reexamine previously studied material, or acquire new material. A small but fascinating group of gutless worms, for example, the pogonophorans (p. 304) 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. Such placement has now been supported by molecular data.

Finally, molecular studies comparing selected gene sequences—and, more recently, by analysis of entire genomes—among representatives of different groups are quickly altering our understanding of many invertebrate relationships. While molecular data often support previous conclusions based on morphology and developmental pattern, such as the monophyly of living animals and the distinction between protostomes and deuterostomes, they frequently suggest relationships quite different from those based on other 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,
Figure 2.12
(a–f) Six schemes proposed to illustrate presumed phylogenetic relationships among animals. (a) According to Hyman, 1940. (b) 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 1749 nucleotide positions). (c) Based on a combination of 18S ribosomal (rDNA) sequence data and 276 morphological characters. In this scheme, protostomes are divided into 2 major groups: Members of one group (the Ecdysozoa) all molt an external cuticle, while members of the second group (the Lophotrochozoa) do not. In some treatments (e.g., 2.12e), the Platyzoa is a subgroup contained within the Lophotrochozoa. (Continued on following page.)
components in which morphological and molecular evidence are especially in disagreement.


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...
Figure 2.12  Continued
(e) Based on 18S and 28S ribosomal gene sequence data for 36 lophotrochozoan taxa. Numbers suggest the degree of confidence in particular branching points. (Continued on following page.)

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 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 plan 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 37 species of stick insect (order Phasmdida), a group in which individuals mimic—both morphologically and behaviorally—a variety of sticks and leaves. About 40% of all known stick-insect
Figure 2.12 Continued
(f) Detail of ecdysozoan interrelationships, based on nearly complete 28S and 18S rRNA genes.
species (about 1200 species) are fully winged, but the other 60% (about 1800 species) have either reduced hind-wings or no wings at all. In the figure, species with full or reduced wings are indicated with blue shading.

A convincing phylogeny for these animals can tell us much about the evolution of wings within the group. If the scenario shown in Figure 2.13 is correct, then the earliest stick insects lacked wings, and they diversified into many different species in that wingless condition. We also see that wings must have later appeared at least 4 times independently (indicated by the 4 stars), from at least 4 different wingless ancestors. Wings were then lost at least 2 times in subsequent evolution (indicated by the 2 triangles near the center of the figure). The most remarkable aspect of the scenario presented is that the wings of stick insects in the different groups seem fully homologous with each other and with the wings of other insect species, implying that the genetic instructions for wing development were maintained unexpressed but unaltered for many thousands of generations in wingless stick insects before being reactivated. This is the first published support for the idea that wings can be re-evolved in insect lineages that have lost them.

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**


"... it is very difficult to distinguish true progress in our understanding of metazoan macroevolution from mere change of opinions with the passage of time." R. Jenner, 2003. Unleashing the force of cladistics? Metazoan phylogenetics and hypothesis testing. *Integr. Comp. Biol.* 43:207–18.

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 a great intellectual challenge. 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 that emerges when the sorting is done. These and related difficulties are discussed in the next few pages. 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, 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; our cranium, for example, is homologous with that of cats, dogs, frogs, and whales—the cranium in such animals has a single, common evolutionary origin. Any differences in homologous 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 2 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 whether the character change is the original, or ancestral, state and which represents the more advanced, or derived state. Issues of homology and polarity are at the source of much 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 then set about establishing taxonomic groups that reflect overall similarity alone, regardless of whether that similarity reflects common ancestry or not. In practice, pheneticians measure as many characters as possible—the number of appendages on the head, 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. The main appeal of the approach is in not having to grapple with issues of character homology and polarity, but it now has little support. 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 pheneticians, 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 non-invertebrate 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 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.