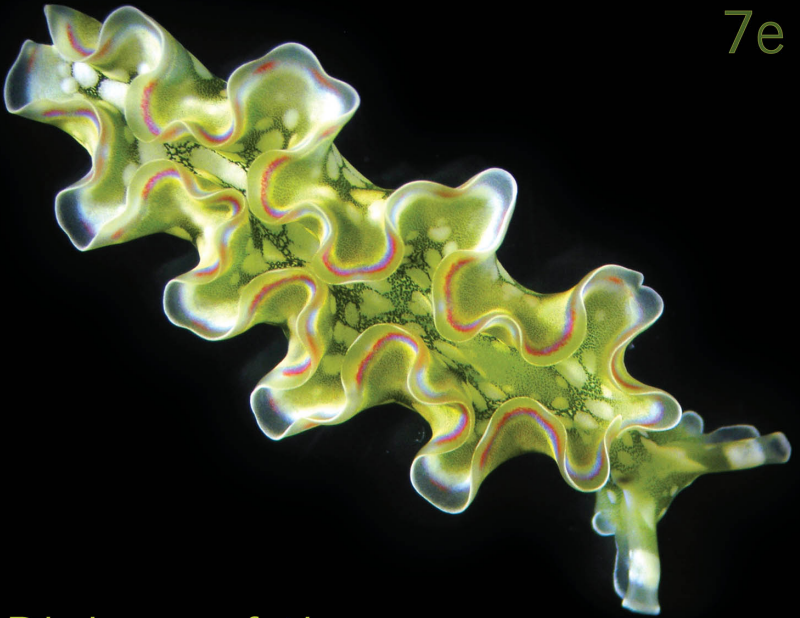


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Biology of the
Invertebrates

Jan A. Pechenik

BIOLOGY OF THE
Invertebrates
seventh edition

JAN A. PECHENIK
Tufts University



BIOLOGY OF THE INVERTEBRATES, SEVENTH EDITION

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*To all who find
invertebrates
fascinating and
worthy of study
And to my family
for their patience
and encouragement.*

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Preface

About This Book

Invertebrate zoology is a fascinating but enormous field. More than 98% of all known animal species are invertebrates, and that proportion is increasing with time as more species are described. Invertebrates are distributed among at least 30 phyla and a mind-boggling number of classes, subclasses, orders, and families. The degree of morphological and functional diversity found within some groups, even within single orders, can overwhelm the beginning student. The enormous size of the field and the great range of potential approaches to the subject make invertebrate biology challenging both to teach and to learn. In preparing the seventh edition of this book, I have endeavored to make the tasks of both teaching and learning easier, and even enjoyable, while nevertheless presenting the latest thinking in the field.

Too many people think of invertebrate zoology as an exercise in memorizing terms and, perhaps, interesting but trivial stories about interesting but irrelevant animals. Too many people think of invertebrate zoology as outdated, and a field in which everything is already known. I hope that this book alters those perceptions by presenting invertebrate zoology as a lively area of ongoing and worthwhile modern biological inquiry.

Like previous editions, the seventh is designed as a nonintimidating, readable introduction to the biology of each group, emphasizing those characteristics that set each group apart from all others. The book is intended to serve as the foundation for further learning—in lecture, laboratory, field, and library—a foundation that is largely manageable by students. Instructors are then free to embellish and expand on that foundation to suit any desired focus: taxonomy and phylogeny, behavior, conservation, environmental biology, diversity of form and function, physiology, ecology, or current research in any of those areas. The book whets the student's appetite and provides the required background, buying instructors the time to discuss more fully whatever they feel are the most interesting and important aspects of the field. This is the guiding principle in my decisions about the

level of detail to provide: I generalize wherever possible to build a firm foundation without intimidation or confusion. Given a chance, the animals themselves soon win most students over.

The most difficult part of writing this book has been deciding what to leave out. My decisions have been reached largely by reading many dozens of research articles on the biology of each group and determining the specific terminology and level of background information that students will need to read those papers. Although all phyla are covered, I have aimed for conciseness, not exhaustiveness, and have emphasized unifying principles rather than the diversity found within each group. Students are best prepared to encounter the diversity of form and function in lecture, laboratory, and field, once they have mastered basic concepts and terminology. I provide a sense of the ecological diversity encountered within each group in a "Taxonomic Detail" section at the end of most chapters, a section that also adds to the value of the book for reference.

The text remains somewhat biased toward functional morphology, bringing animals to life for students and preparing them to make careful observations of living animals in the laboratory and in the field. Most chapters contain a section entitled "Topics for Further Discussion and Investigation," highlighting many of the major research questions that have been and are being addressed for the animals covered in each chapter. For each topic, I have selected references from the primary literature that should be intellectually accessible to any interested, beginning student once he or she has read the relevant textbook chapter. I have had to exclude many excellent papers because they were too advanced, were published in less widely distributed journals, or were review papers rather than primary journal articles. The topics I have chosen, along with the accompanying references, could be used as a basis for lectures, class discussion, term papers, research proposals, or other writing assignments, or simply as a convenient way of easing students into the original literature by having them investigate topics that excite their curiosity. Students gain little by reading and

memorizing predigested summaries of the primary literature; they gain much by reading and discussing that literature. Similarly, I have again decided against adding “end-of-chapter summaries,” arguing that students will learn far more of lasting value by writing and discussing their own summaries than by memorizing mine.

The excitement of invertebrate biology is found in the primary research literature, and a major goal of this book is to motivate and prepare students to read that literature—both the recent literature and that of past decades, before the words “synapomorphy” and “Lophotrochozoa” were common in the literature, and when most workers still thought that Echiura was a phylum and that myxozoans were members of the Protozoa. The *Research Focus Boxes* scattered throughout the book are based on individual papers drawn from the primary literature to illustrate the range of questions that biologists have been asking about invertebrates and the variety of approaches that have been used to address those questions. My goal here is to prepare students to read the primary literature by focusing on how questions are formulated, how data are collected and interpreted, and how each study typically leads to further questions. Students interested in the topic of a particular Research Focus Box might wish to read the original paper on which that Focus Box was based and then use that Focus Box as a model for summarizing other papers on related topics. For Focus Boxes based on older research articles, interested students may wish to follow the topic forward in time, using an indexing service such as the Web of Science. Many instructors now ask their students to write Research Focus Boxes modeled on the ones in this book; such assignments can teach students much of lasting value, particularly if they include guided revision—not an onerous chore for either student or instructor since each Focus Box is only a few pages long. This assignment allows students to put their growing vocabulary to immediate use, and it doesn’t seem to hurt, either, that students feel that they’re learning useful skills in the process.

As further incentive for both instructors and students, Bob Podolski at the College of Charleston has created a Research Focus Box (RFB) posting area on the Society for Integrative and Comparative Biology website (Division of Invertebrate Zoology): <http://www.sicb.org/dl/rfb.php>. Now students can write for a real audience, not just for their instructors. Instructors are encouraged to post their students’ best RFB’s on the website for others to read.

As with previous editions, chapters are self-contained and can be assigned in whatever order best suits the organization of any particular course, once the introductory chapters have been covered. In my own course, I cover some introductory material (particularly chapters 1 and 5) and then begin with annelids and other protostomes. Within each chapter, the material has been arranged in manageable, readable units for the convenience of both student and instructor. For example, a section entitled “Introduction and General Characteristics” might be assigned prior to a lecture on a particular group of organisms, while a section called “Feeding and Digestion” might best be assigned prior to the accompanying laboratory

session; it is always easier to assign additional sections of a text than to tell students what *not* to read within a larger section. I find that periodic scheduled quizzes, designed to reward students for doing the assigned reading, provide excellent motivation. The final chapter (Chapter 24) brings together all of the major phyla by considering general principles of invertebrate reproduction and development, providing students an opportunity to reminisce about all the animals that they have encountered during the term and to begin moving beyond phylum-by-phylum compartmentalization toward synthesis.

This edition has a somewhat greater phylogenetic orientation than its predecessors, but it still avoids prolonged phylogenetic discussion. There is still no consensus concerning many invertebrate interrelationships: Developmental studies, molecular techniques, and cladistic analyses continue to revolutionize our thinking about evolutionary relationships, or at least to challenge many treasured assumptions. Annelids and arthropods may or may not be closely related, segmentation may be a derived rather than an ancestral character in molluscs, the ancestral mollusc may have more closely resembled a bivalve than a gastropod, nematodes are probably closely related to arthropods than to rotifers, insects may have evolved from crustacean ancestors, leeches and earthworms may be derived polychaetes, and phoronids may be modified brachiopods. Similarly, nemertine worms, long considered acoelomates, actually may be unusual coelomates with no direct flatworm affinities. Acoels may be primitive but may not belong in the phylum Platyhelminthes.

For some workers, even the definition of what it means to be a protostome has shifted substantially over the past few years and now relies less on anatomical and developmental criteria. Indeed, the usefulness of morphology and ultrastructure in inferring phylogenetic relationships has been seriously challenged in recent years. “Lophophorates,” for example, appear to be deuterostomes based on morphological and developmental criteria, but group unambiguously with protostomes in most molecular analyses. Similarly, molecular data now align chaetognaths with protostomes, despite their many deuterostome developmental characteristics. The relationships between cephalochordates, chordates, and echinoderms are also uncertain: Some recent molecular data suggest that cephalochordates are more closely related to echinoderms than to other chordates, implying that some key chordate features were present in the ancestral deuterostome and later lost in the evolution of echinoderms and hemichordates. And molecular analyses, often in concert with careful ultrastructural studies, have mostly destroyed the idea that pseudopodia and flagella inform us about protozoan relationships.

Clearly, invertebrate systematics is a work in progress. Although the phylogenetic atmosphere is charged with excitement, beginning students typically view textbook discussion of such controversies as simply another set of facts to be memorized. For this reason, such issues are best treated in lecture, where they can be used to animate

class discussion. Indeed, the controversies surrounding phylogenetic speculation are what make phylogeny interesting, and can be used to make the animals themselves interesting. Chapter 2 introduces students to the range of approaches used in reconstructing phylogenies, and includes substantial discussion of cladistic analysis and the promise and potential pitfalls associated with the incorporation of molecular data. The book provides the foundation upon which instructors and students can build.

Whenever possible, I provide “Defining Characteristics” as each new animal group is introduced, to help students keep track of features separating each group of animals from other groups at the same taxonomic level. In essence, these defining characteristics are synapomorphies. For some groups there are no clear defining characteristics, or characteristics that have been proposed are too controversial to be included at the present time.

Most chapters conclude with a section entitled “Search the Web,” guiding students to particularly good websites associated with the group under discussion. I have listed only those sites that speak with verifiable authority and that are likely to be around and updated for a number of years.

Changes for the Seventh Edition

When I finished the second edition of this book in 1984, I thought that it might need to be revised perhaps once or twice in my lifetime. A series of careful developmental studies in concert with the increasing acceptance and use of cladistic methodology and molecular data in phylogenetic analyses have made the past 30 years far more exciting than I had imagined they would be, and the changes to this edition are substantial, despite the passage of only 4 years since I completed the previous edition.

Most chapters have been revised to reflect new discoveries and expanding research areas, including research of commercial importance and environmental relevance.

Remarkably, all of the rather dramatic organizational changes that I made for the previous editions have held up, and indeed have generally been bolstered by additional evidence. The pogonophorans, echiurans, and sipunculans, for example, for many years treated as 3 separate phyla, are all now widely accepted as modified annelids based upon morphological, developmental, and molecular data. Support has also generally increased for separating protostomes into at least two great groups—the Ecdysozoa and the Lophotrochozoa—although there is not yet complete agreement about exactly which animals each group contains or how the animals within each group are related to each other.

This edition contains some impressive new changes. For example, I now discuss the increasingly likely possibility that insects have evolved directly from crustacean ancestors, and that acoel and nemertodermatid flatworms may belong in a separate phylum, the Acoelomorpha, which may have little relationship with other flatworms. I have also updated phylogenetic relationships

for some other animals, including the tardigrades; indications of an association with nematodes seems to have resulted from a long-branch attraction problem which, once resolved, restores the tardigrades to the neighborhood of arthropods and onychophorans. In addition, the sponges now include 4 classes rather than 3—the Homoscleromorpha have been moved out of the Demospongiae to form a class of their own—*Veleva* and *Porpita* are no longer in separate hydrozoan orders, and the Class Polychaeta may no longer be a valid taxonomic category. The gnathostomulids have come to settle comfortably as close relatives of rotifers and acanthocephalans within the new clade Gnathifera, and the xenoturbellids seem to be deuterostomes, bringing the total number of extant deuterostome phyla to four.

Several chapters have been largely rewritten. In particular, I have reorganized the material on body cavities in Chapter 2 to better emphasize the protostome-deuterostome distinction. I also have updated the section “Inferring Evolutionary Relationships” in that chapter to incorporate more of the modern molecular approaches. In addition, I have updated the biological information about many of the animal groups discussed in this book. For example, I now discuss recent information about the role of sexual reproduction in the life cycle of cellular slime molds in Chapter 3. Moreover, it seems clear that the definitive host in the myxozoan life cycle is usually an invertebrate, with vertebrates usually serving as intermediate hosts—the opposite of what occurs in the trematode life cycle. In Chapter 6, I now draw more attention to the Staurozoa, given their possible basal position within the Medusozoa. Throughout the book, I have updated the General References sections and references listed in the “Topics for Further Discussion and Investigation” sections, and have added new topics to several chapters. I also have updated material in the “Taxonomic Detail” sections of many chapters. For example, students now can learn about a remarkable crustacean parasite that destroys the tongue of its fish host and then takes the tongue’s place with its own body.

The current edition deals somewhat more conspicuously with biomedical relevance, biological invasions, habitat degradation, and other contemporary issues. I have written several new Research Focus Boxes, added new “Topics for Further Discussion and Investigation” sections to some chapters, and included many new references to the recent primary literature, including many published as recently as 2013. I also have added some wonderful new websites to the Search the Web sections that close each chapter, and have written one new invertebrate riddle. In addition, since learning about invertebrates requires students to acquire a substantial new vocabulary, I have added a new online resource to give students some ideas for including that new vocabulary in their everyday conversation: Talking about Invertebrates (See left side of web page: <http://ase.tufts.edu/biology/labs/pechenik/publications/>); send your entries to me and I’ll post them for all to see.

The paradigm shifts that have occurred over the past 25 years or so have been truly remarkable, and there is no end in sight. If insects really evolved from crustacean ancestors, for example, as recent molecular and morphological studies indicate, that will require a substantial redefinition of what it means to be a crustacean. Similarly, there is now substantial molecular evidence that oligochaetes and leeches evolved from polychaete ancestors, which would essentially make the Polychaeta the equivalent of the Annelida, and a study in 2007 using expressed sequence tags has supported the inclusion of Ectoprocta and Entoprocta within a single phylum, the Bryozoa, bringing us back to a classification established over 100 years ago. Finally, although recent molecular studies using individual molecules continue to add support for the Ecdysozoa-Lophotrochozoa dichotomy, as noted earlier, a recently reported whole-genome study of nine eukaryotic species does not support that arrangement, but favors instead the older Articulata hypothesis in which arthropods are more closely related to annelids than to nematodes.

As more molecular data from more species and more genes from each species are collected, we should see increasing stability in the accepted arrangements. There is good reason to hope.

As always, I welcome constructive criticism from all readers, both instructors and students.

Jan.Pechenik@tufts.edu

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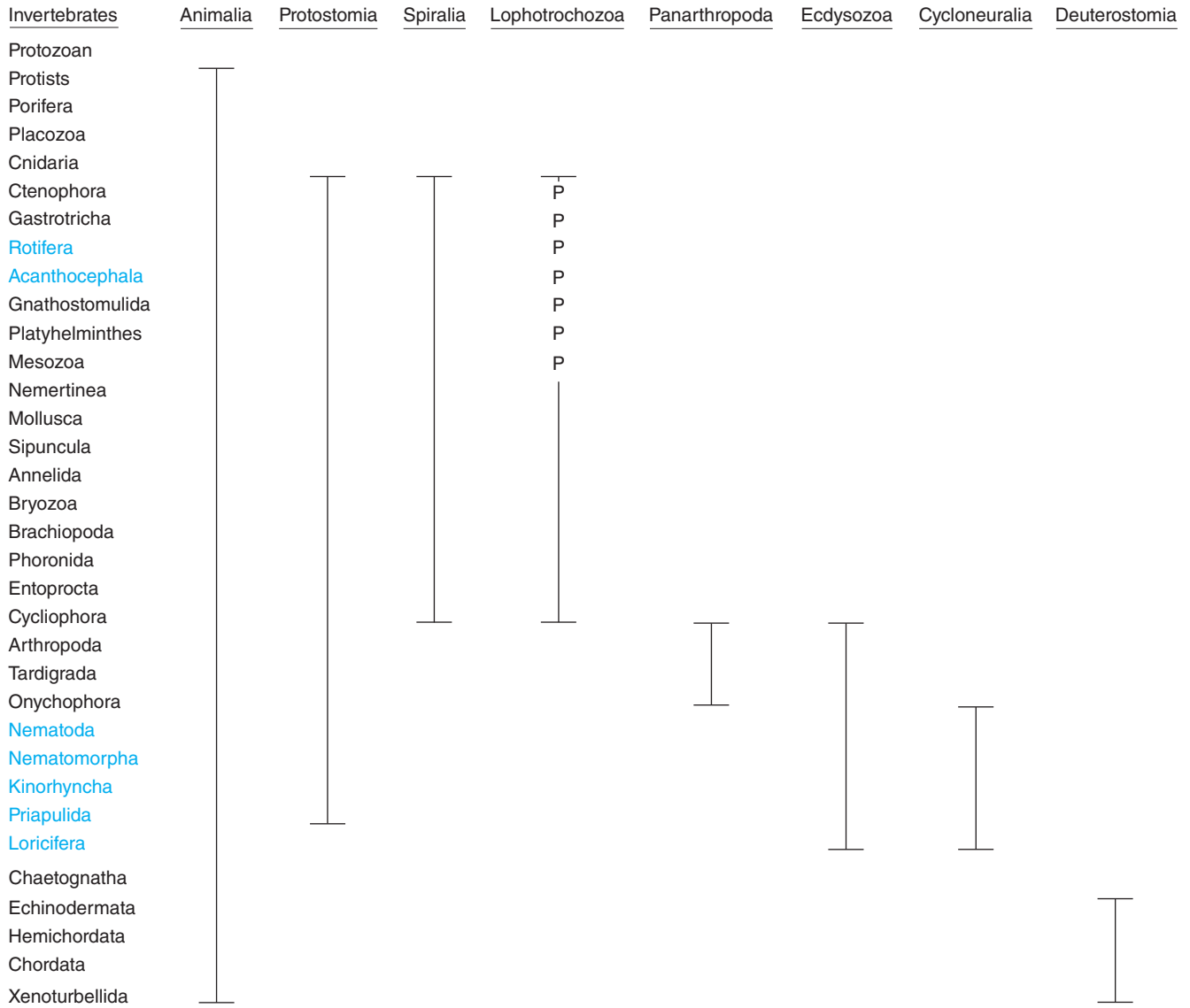
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2013 Guide to the Major Animal Groups
 (aschelminth groups are shaded blue)
 (P = Platyzoa)



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Introduction and Environmental Considerations



Introduction: The Importance of Research on Invertebrates

“We need invertebrates, but they don’t need us.”

E. O. Wilson. 1987. The little things that run the world (the importance and conservation of invertebrates).

Conservation Biology 1:344–346

It surprises me that people don’t want to learn more about invertebrates. For one thing, the diversity of invertebrate form and function is truly astounding. In addition, much fascinating and important research has been conducted and continues to be conducted using invertebrates.

Many diseases of humans and of the animals and plants upon which we depend are caused by invertebrates, either directly or indirectly, and invertebrates play critical roles in most food webs in all habitats. Studies on various invertebrate species have taught us much of what we presently know about the control of gene expression, mitosis, meiosis, and regeneration; the design of gene regulatory networks in embryonic development; aging, programmed cell death, wound repair, and regeneration; the mechanisms of pattern formation during embryonic development; the control and consequences of phenotypic plasticity, in which a single genotype can produce different phenotypes under different environmental conditions; the evolutionary history of hemoglobin and ecdysteroid function; fertilization and chemoreception; the transmission of nerve impulses; the biochemical basis of learning and memory; the biology of vision; and the biochemical and genetic basis for predisposition to some major diseases (e.g., type II diabetes). Much of what we know about the mechanisms by which genetic diversity originates, is maintained, and is transmitted to succeeding generations also comes through the study of invertebrates, as do many basic principles of animal behavior, development, physiology, ecology, and evolution. Similarly, molecular studies on various invertebrate species are rapidly increasing our

understanding of the genetic basis for evolutionary shifts in morphology and life history, including the possible role of horizontal gene transfer, in which sets of genes may be transferred intact from one species to another, and the role that such transfer may play in evolution. Certain invertebrate species recently have become key models for understanding the evolution of the vertebrate brain.

In addition, modern research on invertebrates is helping to unravel the story of how immune recognition systems evolved and how they work. Interest in certain invertebrates as biological agents for controlling various agricultural pests and as sources of unique chemicals of potential biomedical and commercial importance also is increasing. Some of the substances isolated from marine sponges, for example, promise to be potent antitumor agents, and others isolated from certain spiders and venomous snails are providing neurobiologists with highly specific chemical probes for studying key aspects of nerve and muscle function, such as how ion channels are opened and closed. Still other substances derived from invertebrates show considerable promise as instant adhesives (glues produced by onychophorans and barnacles and by some spider and bivalve species, for example) and anticorrosion agents (e.g., barnacle cements). Detailed studies of crustacean and insect navigation and locomotion, and how that locomotion is controlled and coordinated, may lead to the design of new robots, both flying and crawling, macro and micro; studies on the optical properties of certain sponge fibers may lead to the manufacture of more effective fiber optic cables; and detailed studies of how echinoderms form their remarkable calcite crystals may have similarly sophisticated engineering applications.

Invertebrates also have become widely used to evaluate and monitor pollutant stress in aquatic environments, and the rapid loss of invertebrate species from both terrestrial and aquatic habitats is gaining increasing attention in biodiversity studies.

The recently documented phenomenon Colony Collapse Disorder, in which hundreds of thousands of honeybees simply abandon their hives and disappear, is worrisome: apples, almonds, and approximately 90 other crops in the United States depend on honeybees for pollination, accounting for some \$15 billion in annual sales. Bumblebees, which pollinate some 15% of commercial crops in the U.S., are also in serious decline. Similarly ominous is the recently documented increase in the acidity of seawater in the world's oceans, as discussed in the next section.

Finally, there is a growing concern about the increased spread of various invertebrate species into nonnative habitats, and increasing attention is being paid to the mechanisms of transport and to the ecological impact of such biological invasions. Of course, nobody yet knows the consequences of continued pollution, biological invasions, and global climate change on food web function, in either aquatic or terrestrial food-webs; probably there is only one way to do the experiment, and we're all participating.

This book, together with lectures and laboratory sessions, opens the door to the great and growing literature of invertebrate biology.

Environmental Considerations

The organisms considered in this book are grouped into more than 30 phyla. The members of almost half of these phyla are entirely marine, and the members of the remaining phyla are found primarily in marine and, to a lesser extent, freshwater habitats. Excluding the arthropods, invertebrates generally have been far less successful in invading terrestrial environments. Even those invertebrate species that are terrestrial as adults often have aquatic developmental stages. It is worthwhile, therefore, to consider some of the physical properties of water—both fresh and salt—to discover why so many species are aquatic for all or part of their lives. The physical properties of salt water, freshwater, and air play major roles in determining the structural, physiological, and behavioral characteristics displayed by animals living in various habitats.

Air Is Dry, Water Is Wet

Air is dry, whereas water is wet. As trivial as this statement may seem, the repercussions with respect to morphology, respiratory physiology, nitrogen metabolism, and reproductive biology are tremendous, as seen in Table 1.1.

Because aquatic organisms are in no danger of drying out, gas exchange can be accomplished across the general body surface. Thus, the body walls of aquatic invertebrates are generally thin and water permeable, and any specialized respiratory structures that exist may be external and in direct contact with the surrounding medium. Gills, which can be structurally quite complex, are simply vascularized extensions of the outer body wall. These extensions increase the surface area available for gas exchange and, if they are especially thin walled, may also increase the efficiency of respiration (measured as the volume of gas exchanged per unit time per unit area).

In contrast to the minimal complexity required for aquatic respiratory systems, terrestrial organisms must cope with potential desiccation (dehydration). Terrestrial species relying on simple diffusion of gases through unspecialized body surfaces must have some means of maintaining a moist outer body surface, as by the secretion of mucus in earthworms. Truly terrestrial invertebrates generally have a water-impermeable outer body covering that prevents rapid dehydration. Gas exchange in such species must be accomplished through specialized, internal respiratory structures.

The union of sperm and egg, and the subsequent development of a zygote, can be achieved far more simply by aquatic invertebrates than by terrestrial species. Marine organisms, in particular, may shed sperm and eggs freely into the environment. Because the gametes, embryos, and larvae of marine species are not subject to dehydration or to osmotic stress, fertilization and development can

Table 1.1 Summary of the Different Lifestyles Possible in the Two Major Environments, Aquatic and Terrestrial, as They Reflect Differences in the Physical Properties of Water and Air

Property	Water	Air
Humidity	High: Exposed respiratory surfaces; external fertilization*; external development; excretion of ammonia	Low: Internalized respiratory surfaces; internal fertilization; protected development; excretion of urea and uric acid
Density	High: Rigid skeletal supports unnecessary; filter-feeding lifestyle possible; external fertilization; dispersing developmental stages*	Low: Rigid skeletal supports necessary; must move to find food; internal fertilization; sedentary developmental stages
Compressibility	Low: Transmits pressure changes uniformly and effectively	High: Less effective at transmitting pressure changes
Specific heat	High: Temperature stability	Low: Wide fluctuations in ambient temperature
Oxygen solubility	Low: 5–6 ml O ₂ /liter of water	High: 210 ml O ₂ /liter of air
Viscosity	High: Organisms sink slowly; greater frictional resistance to movement	Low: Faster rates of falling; less frictional resistance to movement
Rate of oxygen diffusion	Low: Animal must move (or must move water) for gas exchange	High: (about 10,000 times higher than in water)
Nutrient content	High: Salts and nutrients available through absorption directly from water for all life stages*; adults may make minimal nutrient investment per egg*	Low: No nutrients available via direct absorption from air; adults supply eggs with all nutrients and salts needed for development
Light-extinction coefficient	High: Animals may be far removed from sites of surface-water primary production	Low: Animals never far from sites of primary production

*Signifies features that are especially characteristic of marine invertebrates and uncommon among freshwater invertebrates.

be completed entirely in the water. Fertilization in the terrestrial environment, on the other hand, must be internal to avoid dehydration of gametes; terrestrial invertebrates, therefore, require more complex reproductive systems than do their marine counterparts. Successful fertilization of terrestrial eggs often involves complex reproductive behaviors as well.

Ammonia is the basic end product of amino acid metabolism in all organisms, regardless of habitat. Ammonia is usually very toxic, largely through its effects on cellular respiration. Even a small accumulation of ammonia in the tissues and blood is detrimental to individuals of most species. However, few terrestrial organisms can afford the luxury of constantly eliminating ammonia as it is produced because the water required to flush out the ammonia is in short supply. As an adaptation to life on land, terrestrial organisms usually incorporate ammonia into less toxic compounds (urea and uric acid), which then can be excreted in a smaller amount of water. This detoxification of ammonia requires additional biochemical pathways and an increased expenditure of energy.

Aquatic invertebrates, on the other hand, can simply use the surrounding water to dilute away metabolic ammonia as it is produced. Moreover, because water is wet, ammonia may be excreted by simple diffusion across the general body surface of many aquatic invertebrates. In contrast, all terrestrial animals require complex excretory systems.

Water Is the “Universal Solvent”

Water is a remarkably versatile solvent. The benefits to aquatic invertebrates are both direct and indirect. First of all, aquatic animals potentially can take up dissolved nutrients (including amino acids, carbohydrates, and salts) directly from the surrounding water by diffusion or by active uptake. In particular, dissolved salts and organic water-soluble nutrients may be taken up directly from water by developing embryos and larvae. Embryos of terrestrial organisms must be supplied (by their parents) with all food and salts needed for development and must be protected from desiccation as well. Second, as an indirect benefit to aquatic invertebrates, suspension in a nutrient-containing,

wet medium permits primary producers to take the form of small (typically less than 25 μm [micrometers]), suspended, single-celled organisms (**phytoplankton**); roots are not mandatory. Phytoplankton cells can attain high concentrations in water, and can easily be harvested and ingested by many suspension-feeding aquatic herbivores, including the developmental stages of many invertebrate species.

Water Absorbs Light

As light moves through water, it is absorbed and scattered by various pigments, molecules, and particles. Red light is absorbed most strongly, while blue light is absorbed the least. By a depth of about 200 m (meters), the ocean is completely dark. Thus, there can be no photosynthesis below this depth, and food-webs largely depend on what rains down from above. However, in some environments, a number of marine invertebrates from a number of different phyla have developed symbiotic associations with bacteria that can use chemical bond energy to drive carbon fixation, incorporating the carbon from CO_2 into carbohydrates just as plants do; i.e., some specialized aquatic food-webs are based on **chemosynthesis** rather than photosynthesis. The net result is the same, but the energy source that drives the carbon fixation is quite different.

Water Is Denser than Air

Water is far denser than air, a fact that has profound consequences for invertebrates. For example, a rigid skeletal support system is not required in water because the medium itself is supportive; water also supports delicate anatomical structures, such as gill filaments, that would collapse and cease to function properly in air. For the same reason, animals can often move with greater efficiency in water than in air, expending less energy to progress a given distance. Indeed, many aquatic invertebrate species expend virtually no energy at all for movement—they simply don't move. How do such animals feed without the ability to move? Because water is wet and dense, microscopic free-floating "plants" and animals (phytoplankton and **zooplankton**, respectively) live in suspension; this enables many other aquatic animals to make their living "sitting down," capturing food particles directly from the medium as it flows past the stationary animal. Often, some energy must be expended to move water past the animal's feeding structures, but the animal need not use energy in a search for food. Such a **suspension-feeding** existence, quite commonly encountered in aquatic environments, seems to have been exploited only by web-building spiders in the terrestrial habitat. Potential food particles simply do not occur in high concentrations in the dry, unresponsive air.

External fertilization and the external development of embryos and larvae, so commonly encountered among marine invertebrates, are made possible as much by

water's high density as by its wetness; the water supports both sperm and eggs and the embryo itself as it develops. In many groups of marine invertebrates, external fertilization and/or external larval development is the rule rather than the exception. Because little energy may be required to remain afloat in the aquatic medium, developmental stages (e.g., embryos and larvae) of aquatic invertebrates often serve as the dispersal stages for sedentary adults—exactly the opposite of the situation encountered among most terrestrial animals.

Water Has Thermal Stability

One additional advantage of water as a biological environment is its relatively high temperature stability with respect to air. Water has a high specific heat; that is, the number of calories required to heat 1 g (gram) of water 1°C is considerably greater than that required to raise the temperature of 1 g of most other substances by the same 1°C . Because of its high specific heat, water is slow to cool and slow to heat up; water temperature is relatively insensitive to short-term fluctuations in air temperature. Over a 24-hour period, air temperatures at midlatitudes may vary by 20°C or more. In contrast, for reasonably large volumes of water, local surface temperatures will probably not vary by more than 1°C to 2°C over the same time interval.

Differences in seasonal temperature fluctuations are even more striking. Near Cape Cod, Massachusetts, for example, local seawater temperature may vary between approximately 5°C during the winter and 20°C during the summer: a seasonal range of about 15°C . Air temperatures, on the other hand, fluctuate between approximately -25°C and 40°C : a seasonal range of 65°C . Even in small lakes and ponds, the annual range of water temperatures is much smaller than that of air temperatures in the same geographic area. Because the rates of all chemical reactions, including those associated with organismal metabolism, are altered by temperature, wide fluctuations in temperature (especially those occurring over short time intervals) are highly stressful to most invertebrates. Invertebrates living in thermally variable environments require biochemical, physiological, and/or behavioral adaptations not required by organisms living in more stable, aquatic habitats.

The Challenges of an Aquatic Life

Life in water does pose some problems. Light is extinguished over a much shorter distance in water than in air, so most aquatic **primary production** (fixation of carbon from carbon dioxide into carbohydrates, generally by photosynthesizing plants, algae, and phytoplankton) is limited to the upper 20 m to 50 m or so. Moreover, water's oxygen-carrying capacity, volume for volume, is only about 2.5% that of air. An additional problem for aquatic organisms is that the time required for a given molecule to diffuse across a given distance in water is

much, much greater than the time required for the same molecule to diffuse across the same distance in air: Indeed, oxygen moves more than 300,000 times faster in air than in water! An organism sitting completely still in motionless water would have a severe gas-exchange problem once the fluid immediately in contact with the respiratory surface had given up all available oxygen (and/or had become saturated with carbon dioxide). On the other hand, even the slightest movement of the water surrounding an animal's respiratory surface enhances gas exchange significantly. **Sessile** (nonmotile) organisms living in areas of significant water-current velocity thus benefit in terms of gas exchange as well as nutrient replenishment. Sessile animals living in still water invariably have some means of creating water flow over their respiratory surfaces.

Potential difficulties are also created by the greater density and viscosity of water. Water is about 800 times denser and about 50 times more viscous than air. **Viscosity** essentially measures the extent to which the molecules of a fluid stick to each other. In contrast, density, which was referred to earlier in discussing the benefits of life in water, is a measure of mass per unit volume. Because of water's greater density and viscosity, animals swimming through it or facing a current experience far more frictional resistance (called **drag**) than they would experience in air. For large animals moving quickly (or facing a fast-moving current), the greater drag is due primarily to the greater density of water, whereas small animals moving slowly (or facing a slow-moving current) are affected mainly by water's greater viscosity. Because viscosity increases much more dramatically in water than in air for any given decline in temperature, small, slow-moving aquatic organisms experience noticeably greater frictional resistance in swimming as temperature falls.

Indeed, small organisms—which really must swim slowly because of their small size—live in a world dominated by viscous forces, a world in which the **Reynolds numbers** (Re ; essentially a ratio of inertial to viscous forces) are very low. We live in a world of high Re , in which inertia plays a major role. In a world of low Re , in contrast, there is no such thing as “gliding” to a stop; instead, as soon as propulsion stops, the animal stops. It is difficult for us to imagine what life is like in such a world. Moreover, in a world of low Re , water tends to move primarily around rather than through bristly appendages; in such a world, rake-shaped objects behave much like solid paddles, so that they cannot readily filter food particles from the water. Clearly, animals operating at low Re are subjected to some physical selective pressures quite unlike those acting on larger, faster-moving organisms; even such basic biological functions as locomotion and suspension-feeding may require specialized physiological and behavioral adaptations, adaptations that often seem somewhat peculiar and counterintuitive to us.¹

The fact that water is the so-called universal solvent creates another problem that should be particularly acute for aquatic invertebrates. Many of our industrial and agricultural waste products are water soluble, and we insert fantastic amounts of such pollutants into aquatic ecosystems each year. Aquatic animals must live in particularly intimate contact with these pollutants. Consider, for example, that the gas exchange surfaces of aquatic invertebrates are always in direct contact with the surrounding fluid. Consider also that many aquatic invertebrates are small, so that the surface area across which pollutants can diffuse is high relative to the animal's body volume. Free-living embryonic and larval stages, so common in aquatic invertebrate life cycles, would seem especially vulnerable to pollutant insult, partly because of their high-surface-area:volume ratios and partly because they are undergoing such complex and critical developmental processes. Indeed, for any given toxicant, developmental stages typically suffer adverse effects at only one-tenth to one-hundredth the concentration required to affect adults of the same species to the same degree.

Carbon dioxide, like other gases, is also water soluble. Scientists estimate that the oceans have absorbed about a third of our excess CO_2 emissions over the past 50 years or so. Incredibly, this uptake of CO_2 has overwhelmed the bicarbonate buffering system of seawater—one of the most remarkable things to have occurred in my lifetime—and lowered ocean pH by about 0.1 pH unit. The pH of seawater is expected to continue declining (by up to 0.4 pH units) for the rest of the century. Rising acidity should eventually interfere with the ability of many marine organisms to calcify. Other consequences of continued acidification will probably be surprising, and could well be devastating: organisms like foraminiferans, corals, sea urchins, snails, clams, and the developmental stages of such creatures as sea urchins, snails, and clams—all of which secrete calcium carbonate supporting or protective structures—should be especially vulnerable. In addition, recent studies are showing that the ability of other animals to detect food and predators also may be affected, so the impact of reduced pH will not be limited to calcifying organisms.

Organisms living in freshwater face several difficulties unique to the freshwater environment. For one thing, most bodies of freshwater are ultimately ephemeral, with smaller ponds and lakes being subject to drying up at yearly or even more frequent intervals. Most marine invertebrates are not faced with such a high degree of habitat unreliability. Second, the internal body fluids of freshwater organisms are always higher in osmotic concentration than is the surrounding medium; that is, freshwater organisms are **hyperosmotic** to their surroundings, and water tends to diffuse inward along the osmotic concentration gradient. Some freshwater animals have reduced surface permeability to water, reducing the magnitude of this inflow. Complete impermeability to water is not possible, however, because respiratory surfaces must remain permeable for gas exchange to occur. Thus,

1. See *Topic for Further Discussion and Investigation* at the end of the chapter.

all freshwater animals must be capable of constantly expelling large volumes of incoming freshwater. In contrast, marine invertebrates are approximately in **osmotic equilibrium** with the medium in which they live; that is, the concentration of solutes in their body fluids matches that of the surrounding seawater.

Also, because salts are relatively rare in the freshwater medium (by definition of freshwater), most of the salts necessary for embryonic development must be supplied to the egg by the mother. By contrast, all salts required for the differentiation and growth of marine embryos are readily available in the surrounding medium.

The relative paucity of salts in freshwater has additional ramifications for animals living in it. Freshwater organisms, which must constantly expel incoming water, often possess sophisticated physiological mechanisms for reclaiming precious salts from the urine before the urine leaves the body; they also must possess mechanisms for replacing any salt loss that does occur.

Most freshwater environments lack the buffering capacity of seawater, so that, the pH of freshwater is far more sensitive to local, short-term fluctuation of acid and base content.

Origins and Diversity of Life

From such considerations of the properties of air, salt water, and freshwater, it is easy to understand why life must have originated in the ocean. The specialized physiological and/or morphological adaptations essential for existence on land or in freshwater are not required for the

relatively simple and generally less stressful existence possible in the marine environment. Once life arose, various **preadaptations** eventually evolved that made a transition from saltwater environments to other habitats possible. Such preadaptations for terrestrial and freshwater life apparently arose rarely in many groups of animals and not at all in others. Not surprisingly, most phyla are still best represented in the ocean, both in terms of species numbers and in terms of the diversity of body plans and lifestyles.

Topic for Further Discussion and Investigation

In what ways are small invertebrates adapted to life at low Re ?

Vogel, S. 1994. *Life in Moving Fluids*, 2d ed. Princeton, N.J.: Princeton University Press.

Vogel, S. 2003. *Comparative Biomechanics: Life's Physical World*. Princeton, N.J.: Princeton University Press.

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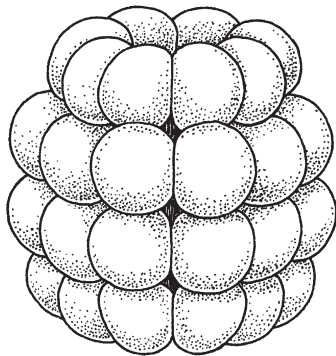
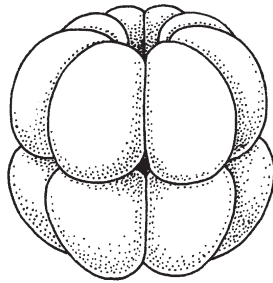
This is an excellent 15-minute introduction to the Re , how it is calculated, and its lifestyle implications.

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

At one time, presumably, there were no animals on Earth. 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. About 1.7 million animal species have now been described and named, but at least another 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 have evolved from single-celled ancestral forms: Fossils of the earliest known unicellular eukaryotes (see Chapter 3) are about 2 billion years old, but the oldest known fossils of multicellular animals (called **metazoans**) or their burrows are no more than 542 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.¹ The first sizable metazoans that are clearly related to modern animals appeared abruptly in the Cambrian period about 542 million years ago (mya). 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

¹ See *Topics for Further Discussion and Investigation*, no. 3, at the end of the chapter.

these 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.² For example, what may be cnidarian-like, echinoderm-like, and arthropod-like metazoan embryos were described in 1998 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.³ 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 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

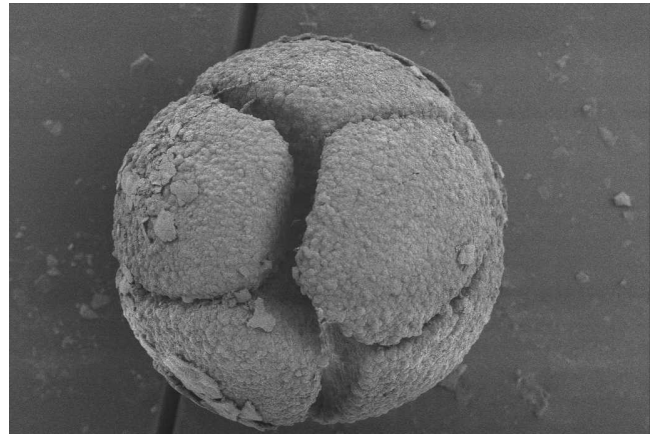


Figure 2.1

What appears to be a multicellular fossilized embryo (~ 500 μm diameter) from deposits in southern China formed about 580 million years ago. If this is truly the embryo of a bilaterally symmetrical, multicellular animal then a diversity of multicellular animal life undoubtedly existed long before the Burgess Shale record of the Cambrian explosion.

Based on Shuhai Xiao and Ed Seling, et al., 1998 in *Nature* 391:553–58. © and reprinted with permission of Shuhai Xiao. See also Yin et al., 2007. *Nature* 446: 661–663.

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 then to 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.

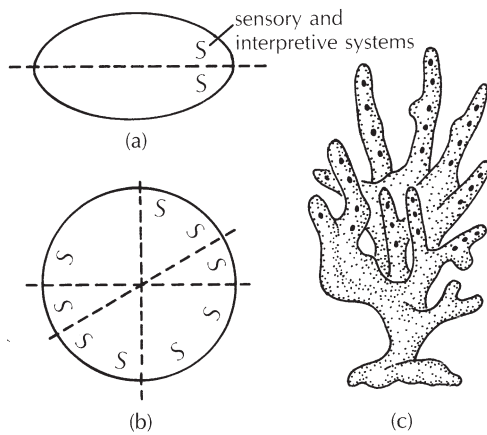


Figure 2.2

Various types of body symmetry. (a) Bilateral symmetry. (b) Radial symmetry. (c) Asymmetrical body plan of a marine sponge.

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 **unicellular** (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 metazoans 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.⁴ 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 creating classification schemes and deducing evolutionary relationships, as discussed in the next several sections. For many years, multicellular invertebrates have 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 adults. 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, a group that includes the jellyfish and corals) are generally considered to be diploblastic (Fig. 2.10). Most metazoans are instead **triploblastic** (*triplo* = 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. Key mesodermal derivatives include muscles and circulatory systems.

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. Diploblastic adults, for example, have musculature despite the absence of a morphologically or behaviorally distinct group of cells that can be termed a *mesoderm* in the early embryo.

4. Finnerty et al., 2004. *Science* 304:1335–37; Matus, D. Q. et al., 2006. *Proc. Natl. Acad. Sci.* 103:11195–200.