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 enormity 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 sixth 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 Too many people think of invertebrate zoology as an outdated field in which everything is already known. I hope that this book alters those perceptions, by presenting invertebrate zoology as a lively and modern area of ongoing and worthwhile biological inquiry.

Like previous editions, the sixth 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, 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 "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 they're learning useful skills in the process.

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 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 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 ancestral character in molluscs, the ancestral mollusc may have more closely resembled a bivalve than a gastropod, nematodes may be more closely related to arthropods than to rotifers, insects may have evolved from crustacean ancestors, and phoronids may be modified brachiopods. Similarly, opisthobranch molluscs and polychaete annelids may not be valid monophyletic groups, and nemertine worms, long considered acoelomates, may actually 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.

With increasing acceptance of the Phylocode, taxonomic rankings (e.g., class, subclass, order, family) are likely to be abandoned in the near future; nevertheless, I retain them here to make the hierarchical arrangements clearer to students, and easier to discuss. 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 Sixth Edition

When I finished the second edition of this book in 1984, I thought that it might need to be revised again in another 10–12 years. 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 25 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, and I now note the incipient emergence of The Phylocode, which, if widely accepted, will revolutionize systematics.

Remarkably, all of the rather dramatic organizational changes that I made for the fourth and fifth editions have held up, and indeed have generally been bolstered by additional evidence. The pogonophorans, for example, for many years treated as a separate phylum, are now widely accepted as modified annelids (members of the polychaete family Siboglinidae) based upon morphological, developmental, and molecular data; additional data also now support the inclusion of both sipunculans and echiurans among annelids. And support has generally increased for separating protostomes into at least 2 great groups—the Ecdysozoa and the Lophotrochozoa—although there is not yet complete agreement about exactly which animals each group contains.

Nevertheless, some impressive changes are new to this edition. A new order of insects has been added (the Mantophasmatodea), for example, the first new order of living insects to be established in nearly 100 years, and the medusa-lacking Staurozoa are now a separate class of cnidarians. The phyla Echiura and Sipuncula have been provisionally abandoned for this edition, since these animals—along with pogonophorans—now seem to be *bona fide* annelids. I have also updated phylogenetic relationships for some other animals, including the cladocerans and other branchiopods. Molecular data confirm that the collembolids, proturans, and diplurans are hexapods, but that they are not insects. The former grouping, Apterygota (=Thysanura), which contained all primitively wingless insects, has therefore been abandoned. The gnathostomulids have come to settle comfortably as close relatives of rotifers and acanthocephalans within the new clade Gnathifera, and a new deuterostome phylum, the Xenoturbellida, has been proposed for the ever-enigmatic worm *Xenoturbella bocki*, bringing the total number of extant deuterostome phyla to 4; as pointed out in another recent paper, however (Wallberg et al., 2007. *Zool. Scripta* 36: 509–23), the earlier (2006!) work did not include gene sequences from acoel or nemertodermatid flatworms, leaving the door open to potential changes in affiliation. Also new to this edition, molecular data now align chaetognaths with protostomes, despite their many deuterostome developmental characteristics, and the centipedes and millipedes (myriapods) have been unexpectedly linked with chelicerates, although through molecular rather than morphological analyses. And the myxozoans, long a most perplexing group of simple parasitic worms, have seemingly come to rest among the cnidarians, substantially increasing the diversity of cnidarian body plans.

Nematode systematics has undergone a thorough revolution in the past decade. For example, the old nematode orders Secernentea and Adenophorea are abandoned, as members of the Secernentea appear to have evolved from within the Adenophorea. Similarly, members of the former nematode order Strongylida (the strongylids) clearly evolved from rhabditid ancestors and so have been folded into the order Rhabditida.

I have updated the terminology used in discussing the siboglinids (formerly pogonophorans): Perviates are now called frenulates, and the Obturata is now the Vestimentifera.[1]

Chapter 3 has been seriously revised to incorporate the startling advances and uncertainties in our understanding of protist relationships, largely caused by recently published molecular data. The revision reflects the tentative consensus reached recently by the International Society of Protistologists (formerly the Society of Prozoologists). Among many other changes, the foraminiferans and radiolarians are now united in the Rhizaria, and the commercially important parasite *Perkinsus* is now classified with the Dinozoa rather than with the Apicomplexa.

1. Halanych, K. M. 2004. Molecular phylogeny of siboglinid annelids (a.k.a. pogonophorans): a review. *Hydriobiol.* 535–36 xvi (b): 297–307.

By popular request, I have moved the material on reproduction and development from the end of Chapter 14 (arthropods) into appropriate sections of the main presentation. I have also added the enigmatic subclass Facetotecta to the *Taxonomic Detail* at the end of that chapter. I also have a little more to say about insect flight, and about structure and function of compound eyes.

I have made such major changes only where they are supported by substantial argument and data, usually from at least several leading workers publishing in major journals, and have been careful in each chapter to indicate my sources.

Many new drawings and photographs have been added for this edition, largely taken from the recent research literature, and many older figures have been redrawn or otherwise improved. The current edition deals somewhat more conspicuously with biomedical relevance, biological invasions, habitat degradation, and other contemporary issues. I have written one new *Research Focus Box,* added new *Topics for Further Discussion and Investigation* to some chapters, and included many new references to the recent primary literature, including many published as recently as 2007 and 2008. I have also added some wonderful new websites to the Search the Web sections that close each chapter, and have written one new invertebrate riddle; readers are invited to submit their answers (and their own riddles) to me directly.

The paradigm shifts that have occurred over the past 20 years 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 recent study (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 9 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 some hope: Chapter 18, formerly Five Phyla of Uncertain Affiliation, is now Three Phyla of Uncertain Affiliation.

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