KINGDOMS & DOMAINS

An Illustrated Guide to the Phyla of Life on Earth

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Foreword by EDWARD O. WILSON

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An Illustrated Guide to the Phyla of Life on Earth

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COVER IMAGE — Classification schemes help us comprehend life on this blue and green planet. But classification schemes are an invention; the human hand attempting to sort, group, and rank the types of life that share Earth with us. Because no person witnessed the more than 3000 million years of the history of life, our domains, kingdoms, phyla, classes, and genera are approximations.

In the metaphor of the hand, the lines within the hand outline and separate the kingdoms. The thumb represents the earliest kingdom of bacteria (the Prokaryotae), which includes the Archaea (Archaebacteria & Eubacteria). The fingers, more like one another, represent the living forms composed of nucleated cells. The back of the hand and the baby finger are continuous; they form a loosely allied, ancient group of microbes and their descendants: members of kingdom Protoctista — amoebae, seaweeds, water molds, ciliates, slime nets, and myriad other water dwellers. The ring and middle fingers stand together: The molds, mushrooms, and yeast of kingdom Fungi and the green vegetation of kingdom Plantae made possible the habitation of the land. Members of kingdom Animalia, the most recent kingdom to venture onto dry land, are on the index finger.

No matter how we care to divide the phenomenon of life, regardless of the names that we choose to give to species or the topologies devised to show relationships, the multifarious forms of life envelop our planet and, over eons, gradually but profoundly change its surface. Life and Earth become a Gaian entity, intertwined where each alters the other. A graphic depiction of our taxonomic hypothesis, the hand and globe image, conveys the intricate mergers, fusions and anastomoses that comprise the web of life. [Illustration based on a design by Dorion Sagan.]

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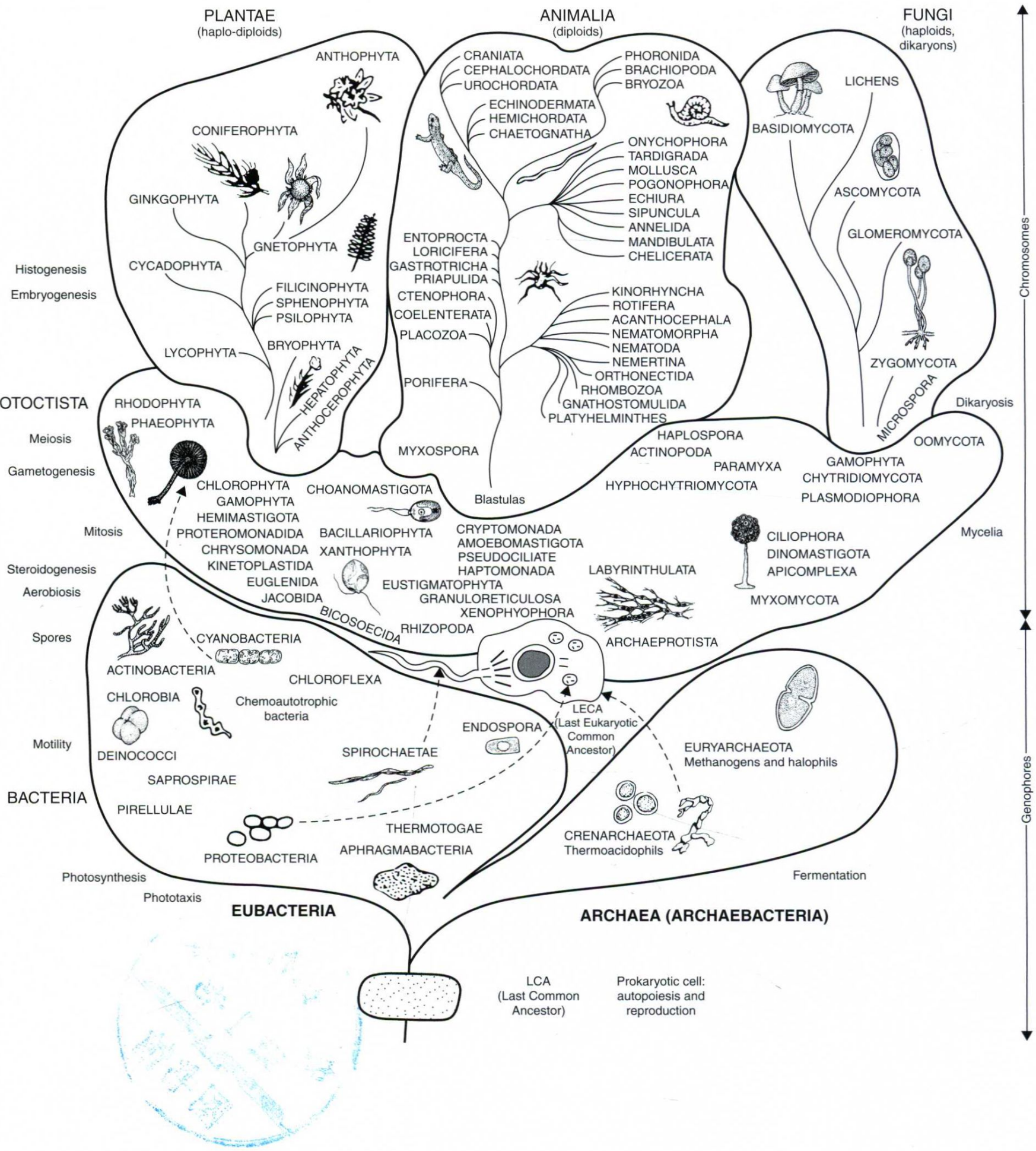
The phyla of life on Earth based on our modification of the Whittaker five-kingdom system and the symbiotic theory of the origin of eukaryotic cells.



This fourth edition is dedicated to Donald I. Williamson, Port Erin Marine Station, United Kingdom (who changed our view of the origins of animals and their larvae by recognition of the importance of evolutionary mergers) and to all other scientists, artists, teachers, and students who aided this labor of love of life on Earth (see Acknowledgments, page xxi*).*

FOREWORD

This lavishly illustrated book is an extravaganza. But then it is true that life, its subject, is also an extravaganza. It is further true that every species of organism that exists or ever existed is worthy of a book all its own, with striking art to illustrate it. The more we learn of the diversity of life, the more prodigious seem these products of over three thousand million years of evolution. Such is the "Creation," our living inheritance, to whose understanding and careful preservation we should feel uniquely committed. No one before the present era of biology could have imagined more than a small part of its true full efflorescence – not the scribes of Abrahamic sacred literature, not Aristotle who tried to encompass it all, not Linnaeus who devised the means to name and classify it systematically, and not even those biologists who have explored it so rigorously through the twentieth century.

About 1.8 million species, our rough estimates tell us (in 2009, serendipitously the bicentennial of Darwin's birth and the sesquicentennial of *The Origin of Species*), have been discovered and described. That includes perhaps three-fourths of the extant hundred thousand or so vertebrates, and, at a guess, ninety percent of the quarter million species of flowering plants thought to exist. But the sixty thousand known fungi are fewer than five percent of the estimated total, and the fewer than twenty thousand named nematode worms, the most abundant animals on Earth, are probably an even smaller fraction of the whole. Moreover, all this ignorance shrinks in the dismaying presence of the "dark matter" of the prokaryotic universe – or if you prefer, the Subkingdoms (Domains) of Archaea and Eubacteria. The exploration of what could turn out to be tens of millions or even hundreds of millions of well differentiated strains of these subvisible organisms has scarcely begun.

Kingdoms and Domains, this book, fearlessly enters the latter world and provides a guide through the rapidly shifting, most inclusive classification necessitated by new information pouring in about it. The technological breakthrough that is accelerating progress in this sector today is comparative genomics, more and more of it, learned faster and faster, and steadily falling in price per DNA base pair. Even so, the phenotypic traits must be added into the calculations as the reconstructed phylogeneticists push forward. It should be kept in mind that a small number of genes, or one step in symbiosis, can sometimes alter the structure and biochemistry of an organism in profound ways.

Meanwhile, the exploration of all of Earth's biodiversity, including the more familiar eukaryotic phyla, is about to be accelerated by the *Encyclopedia*

of Life, an online database launched in 2008 into which complete knowledge of all organisms down to the species level will be compiled, organized and made available to anyone, anywhere, and at any time.

Our fascination with the possibility of life on other worlds is entirely understandable. Yet it is passing strange that we pay so little attention to the largely unknown world all around us. The strange yet lovely biosphere is our only harbor in the vastness of space. Perhaps this attractive and comprehensive book will help us to redirect our gaze, closer to home.

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FOREWORD
To 1st–3rd editions

Like bureaucracy, knowledge has an inexorable tendency to ramify as it grows. In the early nineteenth century, the great French zoologist Georges Cuvier classified all "animals"—moving beings, both microscopic and visible—into just four great groups, or phyla. A century earlier, Linnaeus himself, the father of modern taxonomy, had lumped all "simple" animals into the single category "Vermes"—or worms.

Cuvier's four animal phyla have expanded to more than forty, distributed in two kingdoms, the Protoctista (for microscopic forms and their descendants) and the Animalia (for those that develop from embryos)—and remember, we have said nothing of plants, fungi, other protoctists, and bacteria as yet. The very names of these groups are imposing enough—kinorhynchs, priapulids, onychophorans, and gnathostomulids. Some biologists can spit out these names with a certain virtuosity, but most of us know rather few of the animals behind the names. This ignorance arises for two primary reasons: the names are simply now too many, and modern training in zoology is now so full of abstract theory that old-fashioned knowledge of organic diversity has, unfortunately, taken a backseat.

Margulis and Schwartz have generated here that rarest of intellectual treasures—something truly original and useful. If the originality comes before us partly as a "picture book," it should not be downgraded for that reason—for primates are visual animals, and the surest instruction in a myriad of unknown creatures must be a set of figures with concise instruction about their meaning—all done so admirably in this volume. It is remarkable that no one had previously thought of producing such a comprehensive, obvious, and valuable document.

My comments thus far have been disgracefully zoocentric. I have spoken only of animals, almost as if life were a ladder with animals on the top rungs and everything else inconspicuously and unimportantly below. The old taxonomies included two kingdoms (plants and animals, with unicells placed, in procrustean fashion, into one or the other camp), or at most three kingdoms

(animals, plants, and unicells). With this work, and its 96 phyla distributed among five kingdoms, we place animals (including ourselves) into proper perspective on the tree of life—we are a branch (albeit a large one) of a massive and ramifying tree. The greatest division is not even between plants and animals, but *within* the once-ignored microorganisms—the prokaryotic Bacteria and the eukaryotic Protoctista. The five kingdoms are arrayed as three great levels of life: the prokaryotes, the eukaryotic microorganisms and their derivatives (Protoctista), and the eukaryotic larger forms (Plantae, Animalia, and Fungi). These last three familiar kingdoms represent the three great ecological strategies for larger organisms: production (plants), absorption (fungi), and ingestion (animals).

Some people dismiss taxonomies and their revisions as mere exercises in abstract ordering—a kind of glorified stamp collecting of no scientific merit and fit only for small minds that need to categorize their results. No view could be more false and more inappropriately arrogant. Taxonomies are reflections of human thought; they express our most fundamental concepts about the objects of our universe. Each taxonomy is a theory about the creatures that it classifies.

The preceding material is a slightly shortened and lightly altered version of the preface that I wrote for the original edition of this book. As I reread my words and consider the remarkable changes in this field during the past 15 years—a growth of knowledge and development of thinking that, for once, justly deserves the overused designation of "revolutionary"—I am particularly struck by the wisdom and discernment of Margulis and Schwartz in their original, and now even more compelling, choice of the Five Kingdom system for ordering the diversity of life.

Molecular sequencing of nucleic acids has provoked the enormous gain in our understanding during the past 15 years. We can now obtain a much more accurate picture of the branching pattern on the tree of life through time by measuring the detailed similarities among organisms for the fine structure of genes held in common by all: as a general rule, the greater the differences between any two kinds of organisms, the longer they have been evolving on separate paths since their divergence from a common ancestor.

The system advocated here—five great kingdoms of life divided into two great domains (the Prokarya with their simple unicellular architecture lacking nuclei and other organelles and forming the kingdom of Bacteria, versus the Eukarya made of more complex cells and including the other four kingdoms of Protoctista, Animalia, Fungi, and Plantae)—might seem to be challenged by the discovery by Carl Woese and others that the genealogical tree of life has only three great branches, including two among the Prokarya (the Archaea and the Eubacteria), with all Eukarya on a third branch, and the three great

multicellular kingdoms of plants, animals, and fungi as twigs at the tips of this branch.

But classification must consider more than the timing of branching. Woese's surprising discovery makes excellent sense when we realize that life is at least 3.5 billion years old on Earth, and that only Prokarya lived during the first 2 billion years or so. Since Eukarya arose so much later, they are confined to a single branch on a system that records time of branching alone.

Classification must also record degree and amount of diversity and complexity (while never violating the primary signal of phylogeny, or order of branching), as well as the timing of branch points. When these criteria are added, the breaking of the enormous eukaryote branch into four kingdoms, and the compression of the two prokaryote branches into one kingdom of Bacteria seems fully justified, if only for our legitimately parochial interest in the astonishing diversity of organisms in our visible range of size and complexity.

Still, as the authors duly and happily note, and from an enlarged and less human-centered perspective, bacteria really are the dominant form of life on Earth—and always have been and probably always will be. They are more abundant, more indestructible, more diverse in biochemistry (if not in complexity and outward form), and inhabit a greater range of environments than all the other four kingdoms combined. But we cannot grasp this fundamental fact, and so much else about evolution, until we abandon our biased view of life as a linear chain leading to human complexity at a pinnacle, and focus instead upon the rich range of diversity itself as the primary phenomenon of life's spread and meaning. And we cannot grasp life's full diversity without such excellent works as this book, dedicated to presenting the full story of life's vastness—from the "humble" and invisible (to us!) bacteria that really dominate life's history to the arrogant, fragile single species, *Homo sapiens*—a true upstart and weakling, but the Earth's first creature endowed with the great evolutionary invention of language, a device that may only lead to our self-destruction, but that also yields all our distinctive glories, including our ability to understand by classifying.

Foreword to 1st–3rd editions

Stephen Jay Gould (1943–2002)
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PREFACE

This book provides an illustrated guide to the diversity of life on Earth. As a comprehensive reference to both microbes and their larger descendants, it serves as a guidebook to living organisms based on their evolution. What do they look like, where do they dwell, how are they related to one another, how best do scientists group them? We try to answer such questions by photographs, simplified text and drawings. Brief essays introduce the broad outlines of the "higher" (largest, most inclusive) taxa. If curiosity leads, references and further reading are included. NASA scientists opened our eyes to the need for an illustrated guide to the diversity of life on Earth to inform their search for extraterrestrial life. *Kingdoms and Domains* includes diagrams and photographs of whole organisms that should enable recognition of lifeforms even in outer space. We write for all students of biology at any level of expertise—whether participants in biology, biodiversity, zoology, botany, mycology, systematics, evolution, ecology, genetics, and geomicrobiology—or curious naturalists, geologists, park rangers, space scientists, and armchair explorers. What characteristics distinguish the members of one taxon? What broad view of evolutionary relationships is most valid?

The reader is encouraged to seek evidence of the history of life by firsthand visits to fossil sites, prehistoric dioramas, and museum exhibits. The extraordinary history of life, documented in fossils including the molecular fossil record, inspires us to look appreciatively at present-day life.

Tips for reading this book include major habitats illustrated for each phylum (the seven ecostrips are explained on page 25). Colophons (page 28) indicate how the organism is viewed in the photographs. A chronology of the past four thousand million years of Earth history is summarized in Figure I-4, and Table I-1 summarizes the classification scheme.

Our frontispiece illustrates differences between the archaebacteria and the eubacteria as well as distinctions among the eukaryotes—animals, plants, fungi, and protoctists. These differences and distinctions are summarized in the Introduction and fleshed out in the introductory essays for each kingdom. Concepts of kingdoms and phyla originate in the classification proposals of

scientists of the twentieth century—including Robert Whittaker and Herbert Copeland—built on earlier attempts of Linnaeus, Jussieu, Cuvier, and Haeckel to order the biota. We have extended these proposals and present a five-kingdom system consistent with both the fossil record and the most recent molecular data.

The molecular data have perhaps most profoundly affected our view of bacteria and protoctists. In accord with changes in bacterial classification that recognize differences in ribosomal RNA molecules, we have classified 16 phyla in superkingdom Prokarya (Prokaryotae, Monera): 2 phyla in subkingdom Archaea and 14 phyla in subkingdom Eubacteria. We have incorporated protoctist reclassification based on the *Handbook of Protoctista* second edition with up-to-date ultrastructural, ecological, and molecular information for more than 30 protoctist phyla.

In kingdom Fungi, the three phyla of our earlier edition have been expanded to six. We incorporate both phycobiont and mycobiont into the symbiogenetic unity phylum Lichenes (≡phylum Mycophycophyta). Like all other eukaryotic taxa, only more conspicuously, lichens evolved by symbiogenesis. We now include the deuteromycotes—fungi that have lost differentiated asci or basidia—in phylum Ascomycota; some of these fungi will be moved to Basidiomycota and when their sexual (meiotic spore-forming) tissue is discovered.

Plant classification has changed in accord with recognition of the morphological and biochemical differences between the nonvascular plants and mosses, liverworts, and hornworts. These bryophytes probably evolved independent of one another from algal ancestors. Each—formerly a class in phylum Bryophyta—is now afforded phylum status: Bryophyta (mosses), Hepatophyta (liverworts), and Anthocerophyta (hornworts). Research from the frontiers of botany that has enlightened our understanding of plant relationships includes the discovery by ethnobotanists of diverse drugs, details of nitrogen gas and nitrogenous compounds in forests, elucidation of the evolutionary origin of the seed plants, and advances in understanding frequency and modes of plant hybridization.

Concepts of animal taxa also change rapidly. Relationships within and among the phyla continue to be modified as phylogenetic information from ultrastructural, developmental, morphological, and molecular sources continues to abound. Ribosomal RNA sequences and evidence from proteins tell us that the closest relatives of animals are fungi; plants are more distant relatives. As Haeckel observed in 1874, animals and choanomastigotes (unicellular protoctists) share common ancestry. Molecular data support his inference. Sponges and comb jellies form a lineage within the animal kingdom; the placozoan *Trichoplax* and Cnidaria share common ancestry. The more complex bilaterally

symmetrical animal phyla (A-23 to craniates like us A-37) as well as mandibulates (insects and crustaceans, A-21) and mollusks (A-26), probably evolved by merges of phyletic lineages as Donald I. Williamson argues. Adult rotifers (A-14) and onychophora (A-28) became larvae of holometabolous (metamorphosing) animals through anatomosis of phylogenies, probably by "forbidden fertilizations" (hybridogenesis), see Box A-i, p. 238 on larval transfer).

The rhombozoans and orthonectids, formerly together in phylum Mesozoa, are now separate phyla because of their unique characteristics. The five hooked-mouthed worms (pentastomes), now a class within Crustacea, led us to abandon phylum Pentastomida. We have moved arthropods into two phyla: Chelicerata and Mandibulata. Because some recent Burgess shale fossil evidence suggests arthropods are monophyletic, these two arthropod taxa may eventually be reunited. As fragmentary molecular data become more complete, all animal phylogenetic relationships will be refined.

Why do classification schemes change? Every taxon—class, order, phylum, domain, kingdom—based on the study of relationship—is artificial. We recognize only eukaryotic species as natural taxa. A case in point is the phylum Loricifera—a group of minute marine organisms first described by R. P. Higgins in 1983. Because loriciferans could not be placed in any previously known inclusive taxon without stretching the phylum concept, he established a new phylum just for them. Phylum Loricifera was a hypothesis to be tested, as are all new taxa. After more than two dozen years of evidence gathering on the biology of loriciferans, Loricifera persists as a phylum. Priapulids appear to be closest to them, and the kinorhynchs are more distant relatives. In 1995, a new species, *Symbion pandora*, was reported and a new phylum, Cycliophora, was proposed to accommodate this single species. As is the case for loriciferans, the relationships of *Symbion* to other phyla will be tested—possible relatives are entoprocts and bryozoans (ectoprocts). All newly suggested hypothetical life cycles and morphologies, and metabolic pathways require rigorous scrutiny with the goal of more accurate classification. We do not yet accept much new taxonomy, especially claims based on molecular data but rather we await firsthand biological confirmations of evidence.

As in the earlier editions, a handy reference Appendix expanded in a list of c. 4000 genera includes all those mentioned in this book and many others. The vernacular or common names by which these genera are known are given, as is the phylum for each genus. The glossary provides definitions of terms. So that readers may move easily from glossary to chapter essays, we frequently indicate the phylum and kingdom to which a term applies. Again an Appendix lists all kingdoms and phyla.

Six sets of 35-mm color transparencies of the five kingdoms including phylogenetic drawings are available from Ward's Natural Science Establishment,

Inc., 5100 West Henrietta Road, P.O. Box 92912, Rochester NY 14692-9012 (1-800-962-2660). Five of these transparency sets depict a member of each phylum of bacteria, protoctists, fungi, plants, and animals; the sixth set introduces the general features of each kingdom and prokaryote–eukaryote distinctions. A printed teacher's guide describes each slide.

Five Kingdoms is available in translation from the following publishers: Spanish: 2008, Tusquets, Barcelona; Japanese: Nikeii Science, Tokyo; German: Spektrum der Wissenschaft, Heidelberg; Portuguese: 2004, Guanabara Koogan, SA Rio de Janeiro, Brazil.

Our colleagues generously continue to provide photographs, drawings, manuscripts, publications, and constructive criticism for the complete rewriting of this fourth edition. We thank them for their great kindness and invite them to continue their contributions. We welcome additional relevant new material. Please send corrections, critical comment, new illustration possibilities, etc. to either coauthor at University of Massachusetts-Amherst.

This book grew out of our own need and that of our students for a single-volume reference to the diversity of life on Earth. Your response tells us that our passion for our astonishing planetmates is shared.

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