

Preface

Some ten years ago we began the adventure of preparing a book on the tree of life that would gather current knowledge on the phylogenetic relationships of the main clades of living organisms. We wanted to achieve the most homogeneous and updated work possible, and were aware that a book of more than 40 chapters representing the principal branches of the tree would require the fluid coordination of its many (75) prestigious authors as well as close assistance from the publisher. We are indebted for everyone's restless efforts and support. We have to acknowledge that the work of coordinating this book has proven much more complex and challenging than we could have ever expected. Our idea of publishing the book in 2009 (the International Year of Darwin) or 2010 (the International Year of Biodiversity) turned out to be unachievable; finally, it was published in Spanish (*El Árbol de la Vida*) in 2012. The book we present now in English is more than a mere translation; updated results on the tree of life are included, together with more branches (and therefore, chapters) of hyperdiverse groups of organisms not previously included in the Spanish version.

The modern concept of a tree of life goes back to the nineteenth century (see the Introduction for a historical overview), when Charles Darwin (1859) and especially Ernst Haeckel (1866) interpreted the relationships among living organisms and illustrated them in the form of a tree. Both understood that Earth's biodiversity had arisen according to the principle of descent with modification, and expressed kinship relationships between living organisms in the form of trees (tree thinking). The idea that a phylogenetic framework is a necessary requirement to best understand and classify biodiversity was firmly established in the twentieth century. The evolutionary principles proposed by Willi Hennig (1950) were decisive for understanding that classification of living organisms must follow direct ancestor–descendant relationships (principle of monophyly), thereby providing solid ground for a classification (systematics) that would integrate morphological diversity (taxonomy) and evolution (phylogeny).

Monophyletic groups (i.e., those related by a single origin) are defined based on character states derived from and shared by all the descendants of a common ancestor. In phylogenetic terms, monophyletic groups share morphological characters, or morphological synapomorphies, unique to the considered group. In con-

cert with the principle of monophyly, morphological synapomorphies have been used to structure the tree of life precisely and to choose suitable names for the groupings defined within phylogenies. For example, the most conspicuous and evident morphological synapomorphies of angiosperms (Chapter 12) are seeds enclosed in a fruit and the presence of flowers; of chelicerates (Chapter 27), the presence of chelicerae, four pairs of legs, and a body divided into prosoma and opisthosoma. The morphological synapomorphies of different groups are explained in Box 1 of each chapter, showing the unique (derived) morphological characters of each group.

Any phylogenetic reconstruction based on accumulated divergence in DNA sequences represents a great advance in knowledge of the evolutionary history of the tree of life, reflecting the separation of two clades coming from a common ancestor. With the refinement of DNA techniques and phylogenetic methodologies, and the greater understanding of the fossil record, which is used to date divergence events in trees, this body of knowledge has been steadily increasing since the 1960s. It is clear today that there are more extinct than extant species and clades, and that most diverse groups exhibiting many living clades and species have arisen paradoxically from previously small branches that escaped extinction in earlier times. After more than 20 years of international research efforts to elucidate phylogenetic relationships based on DNA sequence data, the tree of life has been found to have, in phylogenetic terms, an imbalanced, stepwise structure (a ladderized tree, see opening trees of the different chapters), as opposed to the balanced, bifurcated structure that was traditionally assumed. This is probably the most unexpected and fascinating result for the tree of life as a whole, and now we realize that there was previously an artificial tendency to show classifications in a bifurcated manner, that is, with one-to-one comparisons of the major taxonomic groups (prokaryotes–eukaryotes, monocotyledons–dicotyledons, protists–metazoans, radiates–bilaterians, among others). Now, phylogenetic relationships have been found to be dichotomous only in some historically paired major groups (protostomes–deuterostomes, ascomycetes–basidiomycetes) that definitely diverged from a most recent common ancestor. It is precisely this ladderized structure that was used to organize this book.

The revolution in classifying living organisms based on DNA sequences has profound consequences for understanding their true relationships. The principle of monophyly—specifically, identification of each evolutionary group based on both the most recent common ancestor and all its descending species (and only those species)—has not always provided groupings compatible with previous classifications based on Linnaean taxonomy. Researchers today are making great efforts to reconcile the new phylogenetic results with earlier classifications. Integrating major groups, identified by means of molecular phylogenies, into the biological system of classification requires creating new names—which cannot always be directly assimilated into scientific names (e.g., the informal name *eudicotyledons*)—and an exhaustive reevaluation and reconception of traditionally accepted taxa. Since some decisions on the circumscription of taxonomic groups are not final, in this book we have attempted to use the names most widely agreed upon in the scientific community.

We have opted to use quotation marks on organism names throughout this book to refer to traditional taxonomic groups that have been found not to be monophyletic. Some significant examples are: “prokaryotes,” “protists,” “algae,” “bryophytes,” “pteridophytes,” “fungi,” “crustaceans,” “fishes,” and “reptiles.” In many cases, the discrepancy is due to certain traditional groups having been defined by the absence of a morphological character that is present in another related derived group. Now, scientific efforts are made to find character presence in phylogenetics. In other cases, the morphological character used to define the group is indeed present, but it is plesiomorphic, i.e., it does not appear in all the descendants of a most recent common ancestor. An extreme case of discrepancy affects the former circumscription of “fungi.” It is now acknowledged that the morphological characters that originally defined “fungi” have recurrently appeared in independent groups due to evolutionary convergence, a phenomenon that has occurred markedly across the tree of life. It should be noted that for certain nonmonophyletic groups in this book, we have been able to avoid the use of quotation marks by adding an adjective used to specify the monophyletic groups. For example, the group “algae” had multiple origins, as revealed by phylogenetic results, but *red* algae (rhodophytes), *glaucophytes* (glaucophytes), and *green* algae (chlorophytes) taken together do form three monophyletic groups. Quotation marks were also circumvented by using a broadly used name that included the majority of organisms in a monophyletic group, such as fungi and ferns, and leaving small groups out.

When we began this project, we were aware of its magnitude and difficulty because others had previously published books on the tree of life after years of preparation. In our case, we wanted not only to provide

a resource for college students and professionals in biology and other disciplines, but also to give the book a solid structure and homogeneous content nonexistent in other books. Specifically, all 44 chapters dealing with the main branches of the tree of life have the same structure. Each chapter begins with the group’s phylogenetic tree, in which the branches usually end in taxonomic names or, sometimes, informal lineage names. In all cases, thick lines in the trees represent branches of well-supported subgroups whereas thin lines represent groups with moderate phylogenetic support, and instable groups are shown unresolved (polytomies). The structure of each chapter is as follows:

- Summary
- What is a (chapter subject)?
- Introduction
- Box 1: Morphological characters unique to (the subject)
- Box 2: (Subject) by the numbers
- Basic Terms
- Characteristics of (the subject’s) Genomes
- Phylogenetic Results Compared with Previous Classifications
- Evolution of Characters
- Evolutionary Tendencies
- Biogeography and Biodiversity
- Differentiation and Speciation
- Principal Questions Remaining

Additional boxes with evolutionary topics of special interest for each group of organisms complete the different chapters. Note, however, that all groups of organisms have not been investigated to the same extent, so some natural and unavoidable inequalities exist among chapters.

Inference of evolutionary (monophyletic) groups and kinship relationships make phylogenies an essential tool to provide the evolutionary framework on which to interpret the results of comparative biology. To that end, the book concludes with 11 chapters: eight chapters on aspects of evolution to which phylogenies are especially indispensable, and three chapters briefly explaining current techniques and methods of phylogenetic reconstruction.

Our aim with this book is to help the reader understand and interpret the major groups of the tree of life. We hope we provide a useful publication tracing the evolution of living organisms from their origin more than 3 billion years ago to the astonishing diversity we enjoy today.

From the editors on behalf of our superior author team,
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