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BIOLOGY



the **TIMETREE** *of* **LIFE**

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Preface

This book addresses one of the most basic of biological questions: the Tree of Life and its timescale. Our goal was to bring together experts on all of the major groups of organisms to produce a state-of-the-art synthesis of the molecular timescales of life. At the same time, we wanted to make this information on phylogenetic trees scaled to time—timetrees—accessible to everyone, including students and scientists of all disciplines, to facilitate interdisciplinary research and discovery. The result is essentially an encyclopedia of The Tree of Life. On the one hand it has a uniform style and minimum of jargon to make it useful for nonspecialists, while on the other hand it contains the data and literature references needed by active researchers.

Early in the project, we made two decisions to ensure that a single, manageable volume was produced. First, we decided to include only divergence times estimated by molecular clocks. The integration of fossil and molecular timetrees is complex and the number of fossil taxa is quite large. Second, we limited coverage of taxa to the family level and above, because any finer resolution below the family level (e.g., genus or species) would have required multiple volumes. In the future, we look forward to relaxing both of those limitations.

Chapters in this book correspond to evolutionary groups (taxa) and as such are arranged in a hierarchy. For example, the chapter on placental mammals covers only the orders whereas chapters on individual orders of placental mammals cover the families. Beyond this, our decisions as to the scope of each chapter were largely based on the published literature on molecular timescales, which is uneven in its taxonomic coverage. For example, there are more chapters on plants and tetrapods than on protists and invertebrates, reflecting the imbalance in the number of studies reporting time estimates pertaining to those groups. Also, if a group (e.g., class or order) was covered in a single published study we were more likely to treat that taxon as a single chapter rather than splitting or merging it with other taxa. We took great efforts to include all evolutionary groups—prokaryotes and eukaryotes—with published times estimates, but additionally needed to include new data and analyses to fill in taxonomic gaps in 13 chapters. The current gaps in coverage are certain to disappear in the near future as more timetrees become available.

Each chapter begins by summarizing aspects of the diversity and distribution of the group in question, showing a color image of one or more representatives as the first figure. If fossils exist, highlights of the fossil record are mentioned. The remainder of the chapter then discusses the phylogenetic relationships of the included taxa

and their times of divergence based on molecular data. The time estimates, whether published or new, are presented in a table with measures of statistical confidence. The first two columns of every table pertain to the nodes and times in the timetree, which is the second figure of each chapter. We asked the authors to be precise in discussing divergence times, referring to the split of two lineages rather than the “age” of a taxon. Authors were encouraged to conclude their chapters by relating the timetree to other aspects of evolutionary history and Earth history such as plate tectonics, climate change, and biogeography. Therefore, even in chapters that do not contain new data, this section may contain a new synthesis and new ideas.

One of the most difficult tasks of each author was to construct a single summary timetree for their group. Multiple timetrees were not permitted, because of space limitations. As guidance, we urged authors to average time estimates across studies, for each node, and use those mean time estimates in the timetree. For groups in which multiple studies exist, and each study has estimates for every node (i.e., a complete table), this averaging approach usually worked well. However, in cases where one published study included all taxa and other studies estimated times for only one or two nodes (i.e., a sparse table), the averaging approach was often impractical, in which case the most complete study was used for the summary timetree by some authors. A few authors also preferred not to average time estimates if the outcome was inconsistent with currently accepted tree topology or if they disagreed with the conclusions of a particular study. In this sense, contributing authors made the best possible choices in coming up with the final timetrees. All timetree chapters received rigorous peer review. In the case of those authored or coauthored by one of the editors (S.B.H.), the other editor (S.K.) handled the review process independently. All reviewers were kept anonymous, even when they asked to be identified to the authors. We owe a great debt to this large body of reviewers who significantly improved the overall quality of the book.

All of the timetrees in this book are drawn in the same format. Higher taxa names, if present, are shown in vertical text on the right. Nodes are numbered from oldest to youngest, and there is a timescale at the bottom showing two levels of geologic periods. The geologic timescale, colors, and names of periods follow a recent, widely used system (*A Geologic Timescale 2004*, edited by F. M. Gradstein *et al.*, Cambridge University Press, 2004). Node numbers were used on the tree specifically so that users of the book will be able to determine the exact time estimates for each node from the table. This system also permits users to find confidence intervals for each node from different published studies. It was not practical to place confidence intervals directly on the timetrees because the timetree summarizes multiple studies, each with different confidence intervals.

Although we contemplated this book for some years, a catalyst for going forward was the great enthusiasm of the participants in a symposium that we organized in 2006, “Discovering the Timetree of Life,” at the annual meeting of the Society for Molecular Biology and Evolution at the Biodesign Institute in Tempe, Arizona. The Astrobiology Institute of the U.S. National Aeronautics and Space Administration (NASA) provided funding for that symposium, and the speakers were John C. Avise, Fabia U. Battistuzzi, Debashish Bhattacharya, Michael J. Benton, Jaime E. Blair, Franky Bossuyt, Linda E. Graham, S. Blair Hedges, Sudhir Kumar, William J. Murphy, Juan

C. Opazo, Michael J. Sanderson, Jeffrey L. Thorne, Marcel Van Tuinen, and Shuhai Xiao. Melissa Kirven-Brooks (NASA) assisted with the logistics.

A majority of our work on this book took place while both of us were on sabbatical, and therefore we thank our institutions (Pennsylvania State University and Arizona State University) for providing time away from other duties. Staff and students in our laboratories (Solny Adalsteinsson, Matthew P. Heinicke, Wayne Parkhurst, Omy Keyes, Jana McAlpin, and Michael Suleski) provided technical assistance. We especially thank Michael Suleski for redrawing all of the timetrees in the book—for consistency—based on originals submitted by the authors. We also thank the funding agencies supporting our laboratories and research on molecular clocks: the National Science Foundation (S.B.H. and S.K.), NASA Astrobiology Institute (S.B.H.), the National Institutes of Health (S.K.), Japan Society for the Promotion of Science (S.K.), and the Science Foundation of Arizona (S.K.). We are grateful to Ian Sherman and the staff of Oxford University Press (especially Helen Eaton) for supporting this project. Finally, we thank all the authors for their excellent contributions and for tolerating numerous text and graphical edits that enabled us to maintain a uniformity of style.

S. Blair Hedges and Sudhir Kumar