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Is It Time for Timetrees?

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Short Heading/Review Title: Is It Time for Timetrees?

The Timetree of Life edited by S. Blair Hedges and Sudhir Kumar, Oxford University Press, 2009. £100.00, hbk (576 pages) ISBN: 978 0 19 953503 3

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Anchoring phylogenies to absolute time has been a major goal of systematists since Darwin, and efforts to do so have exploded with the rise of molecular phylogenetics. Unfortunately, numerous factors complicate these efforts, including how to model changes in the rate of molecular evolution [1,2] and how to incorporate fossil data [3], which constitute the primary bases of rate calibrations. Substantial progress has been made on these fronts recently, and the development of "relaxed clock" methods has been particularly important. However, the flexibility provided by these new methods comes at a cost—a wide range of date estimates can be generated from the same data by using different methods [4,5].

Into this tumult comes *The Timetree of Life*, a volume edited by S. Blair Hedges and Sudhir Kumar. Hedges and Kumar have been major players in this field for nearly two decades, publishing divergence time estimates for a wide array of taxa [6] and generating some controversy in the process [7,8]. The book is split into two sections—an introductory section comprising overviews of the history, methodology and utility of divergence time estimation and a "Timetrees" section comprising taxon-specific chapters, each featuring an overview of the focal taxon and a dated phylogeny (a "timetree").

Some of the introductory chapters are valuable reviews of the uses of timetrees and of the methods used to produce them. For example, Benton *et al*. summarize the use of fossils to calibrate timetrees. This is a central issue in timetree estimation, but there has been substantial confusion regarding how fossil data should be used in this context. Fossils can certainly be used to provide upper bounds for divergence times—the divergence between the chimp and human lineages, for example, cannot have occurred more recently than the earliest hominid fossil. Lower bounds for divergence times can also be estimated using fossils, but this is not straightforward. Benton et al. address these issues, and also present minimum and maximum dates (and supporting fossil evidence) for 65 nodes across animal phylogeny. This chapter is a superb resource for zoologists, but it should also be useful to anyone interested in learning a paleontological perspective on timetree construction.

Unfortunately, other introductory chapters are not so informative. Avise presents a brief synopsis of the potential uses of timetrees, but many of these uses will be obvious to most readers. By contrast, Gradstein and Ogg describe the methods used to develop the geological time scale, a process that is anything *but* obvious to most biologists. As such, this chapter could have been a fantastic primer, but instead I found it to be rather abstruse.

The timetree chapters, written by experts on each taxon, make up the bulk of the book. The taxonomic coverage of these chapters is understandably scattershot—vertebrates, plants and arthropods are well represented; fungi, microbes and most invertebrates less so. Some uniformity has been imposed (e.g., the timetrees are all in the same graphic format), but any edited volume covering so much ground will show some variation in depth and quality across chapters. For example, the amount of information on divergence times varies widely across taxa, so some chapters synthesize results from several studies, while others represent the first divergence time estimates for particular groups. Furthermore, some chapters include detailed explanations of the methods and the fossil evidence used, while others do not.

Is the time right for a compendium of timetrees? The editors argue that "the time *has* come, and that it is now". However, they also acknowledge the spotty taxonomic coverage, and note that advances in paleontology and molecular phylogenetics will have significant impacts on timetree development. All healthy

scientific disciplines are in a similar state of flux, but "chronophylogenetics" is so vast and so rapidly developing that it will be a long time before a full Timetree of Life could be published. The editors are well aware of this challenge, and have initiated an online database (www.timetree.org) that can be updated in light of new data. In my opinion, this is a better way to present a continually evolving set of timetrees.

In short, I think the introductory section of this book will be a useful reference for many readers, and many of the taxon-specific timetree chapters are excellent syntheses of the relevant literature. I believe this book will be viewed as a landmark compendium in the history of timetree estimation. I must admit, though, that I await continued development of the online database more than I do a future, more complete volume of *The Timetree of Life*.

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