

Book Review

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The Timetree of Life.—S. Blair Hedges and Sudhir Kumar, editors. New York: Oxford University Press, 2009. xxi+551 pp. ISBN 978-0-19-953503-3. \$US200, £100 (hardback).

Historically, phylogenetic analysis in systematics has focused on the branching order of the taxa, with less attention being given to branch lengths. Evolutionists and palaeontologists have more frequently had the opposite bias, with a specific interest in the timescale of the bifurcations, which requires at least estimates of relative branch lengths. If the phylogenetic tree can be calibrated in some way, such as by the use of fossils, then the tree can also be scaled to absolute times. A phylogenetic tree scaled to absolute time is, in this new book, referred to as a “timetree.”

The objective of the book is an ambitious one: to produce a state-of-the-art synthesis of the absolute timescales of all of life based on molecular data. To this end, a large collection of authors has been assembled to construct timetrees for as many taxonomic groups as possible. The bulk of the book consists of brief chapters for each of the groups, summarizing the molecular data at hand, the methods used to produce the trees, and the calibration data available. The analysis methods have been standardized as much as possible, and the results are presented in a uniform manner. For example, the trees are all in the same presentational style, and a single geological timescale has been used. All divergence times are presented as tabled numerical estimates, as well as in the trees. The level of detail differs between taxonomic groups, depending on the amount of extant molecular and calibration data, although each treatment uses a family as the operational taxonomic unit.

The book is thus not really one for reading, but is instead more in the nature of an encyclopedia with a narrow focus. It is a timely compilation of the data currently available and is therefore a unique resource for anyone interested in evolutionary biology in the broad sense. I suspect that it will be heavily consulted by experts and nonexperts alike, although the price may prevent it from appearing in too many personal libraries. There is an associated web page, which contains most of the quantitative information: www.timetree.org.

There are four introductory chapters preceding the detailed data, which in themselves make interesting reading. Hedges and Kumar provide an outline of their views on the tree of life and its timescale, recapitulating a viewpoint that is well known to anyone familiar with the literature on time-scaled trees over the past 20 years. John Avise then summarizes the optimistic point of view inherent in the book, discussing some of the advances that will (hopefully) flow from the acquisition of time-

trees. Gradstein and Ogg provide a readable introduction to the geological timescale used, as this is the sole source of calibration data applied throughout the book.

Finally, Benton and colleagues present a discussion of the analytical approach to producing timetrees from a combination of molecular and fossil data. This is not meant to be a critical survey of the available methods but is nevertheless a clear explication of the decisions necessary for calibrating and constraining phylogenetic trees. They conclude with a detailed consideration of the estimates for various dates that are commonly used throughout the book.

The remaining 400+ pages detail the timetrees themselves. Each timetree chapter has a summary of both the calibration and the molecular data and also of the various published studies containing time estimates. The times from the latter are tabulated for easy comparison. The timetree in each chapter is based on either an original analysis of the available data or a combination of the published time estimates. Where there were multiple time estimates for any one divergence, these estimates have usually been averaged.

There is some coverage of each of bacteria, protists, plants, fungi, and animals, although the coverage is very uneven. This unevenness potentially limits the usefulness of the book. To make myself as an example reader, my parasitological work variously involves apicomplexans, mites, and nematodes. Neither apicomplexans nor mites make an appearance in the book, and nematodes are only briefly covered, so that my direct personal interest in the book is thereby limited.

The unevenness stems from lack of data for either the phylogenetic trees or the calibrations. The timetrees are based on the published literature in almost all cases for both types of data (i.e., there are few original data in the book). The lack of molecular data means that for many of the groups only a limited subset of taxa have been included in the trees (e.g., only animal parasites within the nematodes), and many of the timetrees are very unresolved. The lack of resolution may also stem from conflicts in the data rather than lack of data, of course. The taxonomic scheme used for each group is not always clear, unfortunately.

The lack of fossil data prevents phylogenetic trees from becoming timetrees. We all know that the fossil record is limited, but it is important to remember that many groups are unlikely ever to be found as fossils, at least in large enough quantities to be useful for calibration. This includes endoparasites as the most taxonomically widespread example. There is little reason to be optimistic about being able to resolve the issues involved for any soft-bodied taxa (contrary to the editors' optimistic claim on p. xi). Only relative dates

are usually provided for such groups, although it may be possible to use indirect dates, such as cospeciation events, as the calibration times.

I am sure that many people will disagree with (at least some of) the timetrees produced in this book based on issues with either the molecular data or the fossil data. To counter this, some of the authors have provided multiple estimates of dates based on different computer programs or different calibrations, although the editors have limited them to presenting only a single time-tree for their group. Perhaps, the required consistency between treatments has also produced an unfortunate "painting by numbers" approach, where the presentational constraints have had an undue influence on the analyses.

Tucked away on p. 6 is the seemingly innocent statement: "[this book] summarizes the current state of knowledge . . . , with some caveats." These caveats loom much larger in my mind than they apparently do in the minds of the editors, as their list is rather short and not focused on data analysis. Unfortunately, the methodological caveats are not really discussed in the book, although they are incidentally referred to on various occasions. I will therefore present some of the more obviously important assumptions here in order to give an idea of the limitations of the approach used to construct the timetrees.

The foremost limitation is that "only divergence times estimated by molecular clocks" (p. xi) have been included. I seriously doubt that anyone actually believes in the molecular clock: it is simply a convenient methodological tool to bypass what is an insurmountable problem. The mathematical justification for the clock is one of averages: our estimates are assumed to be scattered around some average value that represents the long-term pattern. The assumption of stochastic variation is thus substituted for other likely sources of variation in evolutionary rates. Relaxed clocks are one attempt to deal with this issue, although we have no idea how successful they ultimately might be.

The editors have taken this assumption one step further, however, by encouraging the authors to average all conflicting estimates of time, whatever their source. This ignores the fact that the estimates may not be directly comparable, in which case their average is unlikely to have much biological meaning (e.g., the mean of a bimodal distribution is a nonsensical average). The philosophy here is apparently that any estimate is better than no estimate at all, which is unlikely to be a route to high-quality science.

There is also the issue of compounding sources of error. There are errors in the molecular data, in the data analyses, and in the calibration dates. The final time estimate may very well have a confidence interval (although I doubt very much that there is any serious biological basis for their estimation), but there is no way that such a thing can estimate the accumulated error. This is perhaps the biggest unaddressed problem of timetrees.

There are also technical issues associated with the use of fossil dates, which are well documented in the primary literature, as well as issues with the estimation of divergence times based on a calibration, which appear never to have been critically reviewed. Every research group seems to have their own favorite methodology, so I doubt that there is much consistency of time estimates across the taxonomic groups in this book.

To a systematist, perhaps the most uncomfortable aspect of the book is likely to be the use of families as the operational taxonomic unit across all of life. Even the editors state that the "biological meaning [of families] is unclear" (p. 8), which is simply one way of saying that a family of plants is not the same as a family of insects or a family of bacteria; and yet they then blithely proceed to a detailed comparison of families and their diversity. John Avise goes even further by suggesting that "when secure timetrees become widely available, opportunities will arise to develop the first ever universally standardized scheme of biological classification" (p. 23). I seem to recall Charles Darwin making, a similar sort of claim in his most famous book, and that suggestion is no closer to reality now that it was 150 years ago.

Overall, I am impressed by the editors' decades-long dedication to their subject and what they are trying to achieve. However, given that so many questionable assumptions have been used in the analyses, I cannot help wondering whether this book is not so much "long overdue" as "somewhat premature." Perhaps, the most relevant way to evaluate the book is to ask the question: "do I think that any of the data will still be considered correct in 10 years' time?" My answer is: "given the past 10 years, probably not." I am sure that the editors and authors see this publication as a stimulus to correcting the past and present misestimates of time, and in this view they are probably correct. It is, however, a very expensive stimulus, and the web page is certainly much better value for money.

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