

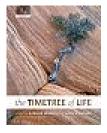
Journal of Sedimentary Research

An International Journal of SEPM

Paul McCarthy and Gene Rankey, Editors A.J. (Tom) van Loon, Associate Editor for Book Reviews



The Timetree of Life, edited by S. Blair Hedges and Sudhir Kumar, 2009. Oxford University Press, Oxford, UK. Hardcover, xxi + 551 pages. Price EUR 115.00; GBP 100.00. ISBN 978-0-19-953503-3.



The 200th birthday of Darwin was reason for Oxford University Press (OUP) to publish a monumental work dealing with the evolution of life, considered in the context of geological time. The highly appropriate cover indicates that the book forms part of OUP's works in biology, but this book contains also essential information for earth scientists, in particular paleontologists. However, fossils have become so important for sedimentologists (for both dating and environmental interpretation), that this book is of great importance for sedimentologists as well. But some (quite elementary) knowledge of biological taxonomy and of genetics is required, as the book is, for a major part, arranged taxonomically, and as the key to evolutionary relationships is genetics.

Some of the numerous pitfalls regarding fossils that sedimentologists and paleontologists are confronted with in practice may be avoided in the future, thanks to the state-of-the-art tools that the genetic information in this book provides. In addition, the book is convincing proof that tracing the evolution back from living organisms to their ancestors has already become a reality. This proof is based on the results obtained with the molecular-clock approach, which itself is based on an evaluation of the moment of divergence from earlier forms with DNA and protein-sequence analysis of living organisms. The book comprises results from a wide variety of applications of this approach, and thus sketches a significant new picture of the biological evolution. That is important not only for biologists: "The immense value of having a robust Timetree of Life—for all fields of science—cannot be overstated" (p.16), as expressed by the editors in their introductory chapter (Discovering the timetree of life).

Many scientists are still sceptical about the molecular-clock approach. That is, obviously, their good right, but much of this scepticism is based on the fact that the molecular clock often brings unexpected results, which do not match paradigms. One should realise, however, that the unexpected character of the results does not automatically imply that these results are wrong. But the reverse does not hold either. Neglecting that fundamental changes of our long-cherished insights may be required, is a wrong way of doing science, just as overestimation of the achievements of new methods. The authors did, indeed, their very best to convince everybody regarding the efficacy of the new method. So, if you are sceptical with respect to DNA-based paleontology, don't be in a hurry to put this book aside: better try in-depth reading.

Some theoretical background information can't be missed when reading this book. The first part therefore provides a theoretical background. Hedges & Kumar review the state and importance of available timetrees, but also point at the incompleteness of the fossil record: "If we were to know the total number of species that existed at all times in the past, we would have a complete view of the rate of evolutionary diversification (speciation) through time. This information would be valuable for understanding not only how diversification in some groups (e.g., predators) was affected by diversification in other groups (e.g., prey), but also the relationship between biological diversification and Earth history" (p. 9-10). The curves calculated on the basis of 1610 family-level lineages indicate a significant radiation of life during the past 300 Ma (and they confirm the occurrence of a Permian/Triassic catastrophic event), but they indicate neither the Cambrian explosion nor the Cretaceous/Paleogene extinction. The authors explain the Cambrian explosion as an artefact, but this contrasts with known facts from

paleontology (e.g., Brasier, 2009). Their conclusion might, in our opinion, well be changed by an account of already extinct lineages.

Avise speculates, still in this first part of the book, about the usefulness of timetrees for the development of universal biological classifications. He also mentions that some controversies can be solved about how species enlarged their distribution areas: "Interest has long been centered on whether ancient vicariant events (related to plate tectonic movements) or subsequent over-water dispersals (e.g., by rafting) account for the presence of various terrestrial vertebrates in the West Indies. Geological evidence indicates that the Greater Antilles formed in a close proximity to North and South America during the mid-Cretaceous and that these islands began drifting from their continental partners at least 80 million years ago (Ma). The vicariance scenario thus predicts that sister clades on the islands vs. mainlands separated more than 80 Ma, whereas dispersal scenarios predict that the separations were more recent and probably variable in time. From molecular phylogenetic appraisals of nodal dates for more than 35 relevant pairs of vertebrate taxa, Hedges [...] effectively falsified the ancient vicariance hypothesis for these faunas" (p. 22-23). Such findings are truly important for many earth scientists!

A chapter on modern chronostratigraphy is authored by Gradstein & Ogg. No new aspects are found here for those earth scientists who are aware of the latest progress in chronostratigraphy, but this chapter must be most valuable for biologists dealing with fossil material or with evolution.

Benton et al. discuss the age of dozens of divergence events that were found on the basis of the paleontological record. The caniform-feliform (dog-shape/cat-shape) split, for instance, occurred—according to paleontological finds—at least 39.68 Ma ago, and 65.8 Ma ago maximally. Look at the relevant page in the second part of this volume and learn that the molecular clock suggests that this happened 52.9 Ma ago! But 'pure' paleontologists are not always wrong and they appeared able to predict the presence of 'missing links' on the basis of interpretation of evolutionary developments on the basis of earlier finds, in spite of the incomplete fossil record that was already noted by Darwin as these authors admit (p. 36-37): "Darwin did, however, predict that intense efforts by palaeontologists would fill many of the gaps in the record and allow the deeper parts of the tree of life to be disentangled. In many cases (e.g., basal tetrapods, synapsids, and dinapsids) his prediction has been fantastically confirmed ..."

Unfortunately, this first part of the book lacks, in our opinion, some important subjects. We tend to agree, for instance, that a detailed comparison of molecular-clock data with the fossil record may be out of scope, but a special chapter that reviews the evolution of life as suggested by paleontological finds would, in our opinion, have been a must. Fortunately, references to the fossil record exist in many particular chapters, including that by Benton et al. Geologists would certainly also appreciate some attention for living fossils. It is, in our opinion, also remarkable that this book, with its second part that is structured on a taxonomical basis, nowhere refers to the strange fact that mammals form a taxon that should not exist as a separate taxon: each taxon includes all other taxa that have originated as evolutionary descendants. For instance, a bird like a crow is a species (a taxon) that belongs to the birds (Aves, a higher-rank taxon that split off from one of the already existing banches of the tree of life earlier), which belong to the vertebrates (Vertebrata, a still higher taxon split off from an older branch still earlier), etc. However, mammals evolved from the fishes (Pisces)—with lung fishes as the intermediate step—but mammals are not included in the taxon of the fishes! As far as we are aware, only mammals form such an exception (probably a result of human-centred thinking). In this context, it is also remarkable that most information about the descent of Man is not provided in the systematic second part, where human ancestors are discussed briefly together with other primates, but in the chapter by Benton et al. (p. 46-49) about calibrating and constraining molecular clocks.

The book's second part is a 'classical' encyclopedia. It starts with a chapter (by Bledges) about life, dealing with the earliest developments of life forms on Earth. A truly interesting chapter! This is followed by three chapters (dealing with the Archaebacteria, the Eubacteria and the Eukaryota, resp.) about the tree superkingdoms distinguished nowadays.

Similarly-designed pieces of text follow, dealing with taxonomically high-ranked groups of organisms. Each piece contains a figure of the relevant part of the timetree and a table with divergence times. The text is somewhat supplementary, but it provides the basic biological and evolutionary knowledge of each group. Of course, molecular-clock data are always discussed in the text. Each of the pieces also contains a little, but nice and characteristic picture of a

representative of the taxon dealt with. According to the data presented in this second part, the molecular clock suggests that the first divergence of life occurred somewhere in the Hadean, about 4.2 Ga ago. And even the timetree of Archaebacteria is analyzed with an indicated precision!

Reviewing the various groups dealt with in this second part, seems beyond the scope of the present review because it would become too detailed. Let it suffice to mention that this second part itself is subdivided into twelve groups: protists, plants, fungi, animals, invertebrates, vertebrates, fishes, amphibians, amniotes, reptiles, birds, and mammals. These twelve groups thus do not all have a similar taxonomic rank; the choice made was obviously based on practical arguments. This results in some differences in dealing with the various topics, but these are commonly subdivided again, sometimes several times. For instance, the mammals are subdivided into monotremes, marsupials and placental mammals. The placental mammals are again subdivided into several groups. The lowest-level contributions each take only a few pages, so that relatively little information is given in writing (but, as mentioned before, the contributions all contain a nice picture and a uniformly designed part of the timetree of life). But one would certainly expect to learn more about Man's ancestors more than actually written in the section about primates.

The book does not only present data, but interpretations as well. Blair, as an example, states that Neoproterozoic environmental changes evidently influenced the evolution of the metazoans. This echoes earlier hypotheses linking the Neoproterozoic glaciations with the rise of metazoans.

We both enjoyed reading this book. It is obvious, from the very beginning of the book till the end that UOP, the book editors and the numerous authors have delivered a magnificent piece of work. This does not imply, however, that—apart from the few omissions that we mentioned earlier—we found no mistakes, but none of these concern the biological aspects. Geologists, however, will find, for instance, that chrono- and lithostratigraphic terminology are sometimes mixed up. Worse, in our opinion, is that ages are not written in a consistent way. The official abbreviation for "million" year is Ma (mega annum), which should be distinguished from myr. Datings with accuracy indications are, remarkably enough, commonly written in two different ways, for example as $542.5 \text{ Ma} \pm 1.0 \text{ myr}$! This should certainly be corrected in the next edition.

We should emphasize, however, that the volume under review in its entity is impressive by both its comprehensive contents and its presentation. The text is always clear for non-specialists in the taxon under discussion, but it avoids undue simplifications and major caveats. We are convinced that this well-thought-over book will still be valuable when its information will have become partly outdated. Undoubtedly, this volume is an exciting gift to Darwin's 200th anniversary.

Dmitry A. Ruban Southern Federal University Rostov na Donu, Russia e-mail: ruban-d@mail.ru A.J. (Tom) van Loon Adam Mickiewicz University Poznan, Poland email: tvanloon@amu.edu.pl



SEPM—The Society for Sedimentary Geology

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