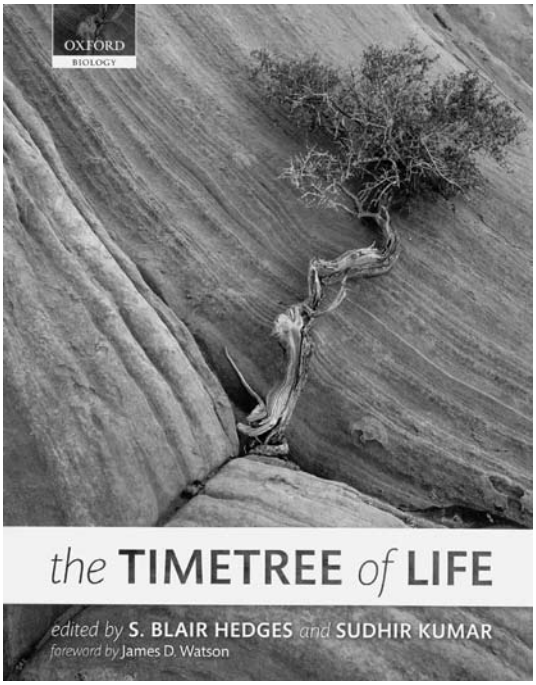
The timetree of life, edited by S. Blair Hedges & Sudhir Kumar, 2009. Oxford University Press, Oxford, UK. Hardcover, xxi + 551 pages. Price EUR 115.00; GBP 100.00. ISBN 978-0-19-953503-3.



In the framework of the 200th birthday of Darwin, Oxford University Press (OUP) has published 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 palaeontologists. Some (quite elementary) knowledge of biological taxonomy and of genetics is, however, required, as the book is, for a major part, arranged taxonomically, and as genetics form the key to evolutionary relationships.

Genetics provides state-of-the-art tools that may help to avoid some of the numerous palaeontological pitfalls. 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, as expressed by the editors in their introductory chapter (Discovering the timetree of life): "*The immense value of having a robust Timetree of Life – for all fields of science – cannot be overstated*" (p.16).

We are well aware that many scientists are 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. So, if you are sceptical with respect to DNA-based palaeontology, don't be in a hurry to put this book aside: better try in-depth reading. The authors did their very best to convince everybody regarding the efficacy of the new method.

The first part of the book 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/Palaeogene extinction. The authors explain the Cambrian explosion as an artefact,

but this contrasts with known facts from palaeontology (e.g., Brasier, 2009). We are curious whether an account of already extinct lineages would change this conclusion.

Also in this first part of the book, Avise speculates 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). How important for many earth scientists such findings are!

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

Benton et al. discuss the age of dozens of divergence events that were found on the basis of the palaeontological record. The caniform-feliform (dog-shape/cat-shape) split, for instance, occurred – according to palaeontological 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' palaeontologists 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: "*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 ...*" admit these authors (p. 36–37).

Some important subjects are, in our opinion, lacking in this first part of the book. 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 palaeontological 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 branches 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 (Pisces)! 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 provided (p. 46–49) in the chapter by Benton et al. about calibrating and constraining molecular clocks, and not in the systematic second part, where human ancestors are discussed briefly together with other primates.

The second part of this volume is a 'classical' encyclopaedia. 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 that deal with each of the three superkingdoms dis-

tinguished nowadays: the Archaebacteria, the Eubacteria and the Eukaryota.

Then follow similarly-designed pieces of text 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!

It is beyond the scope of the present review to address the various groups dealt with in this second part, which in itself is subdivided into twelve parts: protists, plants, fungi, animals, invertebrates, vertebrates, fishes, amphibians, amniotes, reptiles, birds, and mammals. These twelve parts 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). In the section about primates, one would expect to learn about Man's ancestors more than actually written here.

It should be noticed here that 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 (Ruban, 2007; Brasier, 2009).

It should be clear that 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. But geologists 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 (see rules in Ogg et al., 2008). Datings with accuracy indications are, remarkably enough, commonly written as, for example, 542.5 Ma ± 1.0 myr: two different ways of using an abbreviation in one dating!

The volume under review is nevertheless 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. Read and enjoy it!

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