

Technical / minor comments and suggestions

- **Formal description.** The revisions to this section brought much clarification. I believe that that the second equation numbered (1) has an error: in this equation for the likelihood, the term $P(\Psi_s|\Psi_t, \theta)$ should be omitted, because Ψ_s is conditioned upon in the left-hand side. Instead, this term should be used in an additional equation (3) I believe, to describe the term on the right-hand side of the first equation (1) for the clock model: $P(\Psi_t, \Psi_s, \theta) = P(\Psi_s|\Psi_t, \theta) \times P(\Psi_t, \theta)$. In the same section, more clarification could avoid confusion over notations:
 - define “timetree” (second line of the “formal description” section), and clarify that branches are measured in years (or other time units) in Ψ_t
 - clarify what “rate modifiers” mean (line 5). I first interpreted this as a set of rates, one per branch, that modify ages into substitutions per site, and then the rest of the section didn’t make sense. Did you mean “parameters of the prior distribution for branch rates”? I suggest avoiding “rates” and using this alternate “parameter” wording: line 5, 2 lines after the equations, perhaps later.
- **Branch-length tree:** I found this terminology confusing. Both trees Ψ_t and Ψ_s have branch lengths. Naming Ψ_s the “branch-length” tree could cause confusion for many readers. I suggest modifying this terminology to something that mentions substitutions to refer to the units of branch lengths; possibly “substitution tree”, which would mirror the term “time tree”. Please check for all instances (p.7, p.10 in the main text, and 7+ instances in the SM: protocol section, variance section)
- The Methods section is still unclear about the number of simulated alignments. On page 9, section “Alignment simulation”, change “simulate alignments” to “simulate one alignment”. In section “Inference based on simulated data”, change “the simulated alignments” to “the simulated alignment”.
- **Numbering.** Please fix the numbering of equations: both are numbered (1) on page 5. In the first sentence of section “two-step inference of timetrees”, I believe that the reference should be to equation (2), not equation (1), but please check equation references if the numbering is modified. Also, supplementary figures should be renumbered: the second figure S2 should be relabelled S3, figure Sk should be re-labelled Sk+1 for k=3-8, and all references to these supplementary figures need to be adjusted: pages 10, 11, 26 in the main text, and in the SM text of the two-step section, informativeness section, and verification section.
- Figures 3 and 4: Could “n” and “y” be changed to “no” and “yes” to improve the legend? Or better, change to “balanced” and “unbalanced” to match the terminology in figure 2.
- Figure 5 legend: at the end, should “constraints” be replaced by “calibrations”?
- Figure 6 legend: add “144” in front of “relative age constraints”, to read: “(c) 144 relative age constraints...”. This number of constraints is easily forgotten by the time the reader gets to this figure. The Results section that we read with this figure actually has all the “methods” information (e.g. which analyses were performed, what the fossil calibrations were etc.) except for the number of constraints. I don’t mind the unusual structure as it makes the results section easy to read. But it would be good to recall the number of constraints here to be consistent.
- Results on Archaea (page 17): below are some wording suggestions to alleviate confusion I had about

which constraints were used. The section can be misunderstood to mean that only 2 constraints were used: precisely those that were not used (unless I misunderstood!). Also this results section again contains all the methods except for the number of constraints.

- To address both: change the sentence starting with “Note that, in the following analyses” to “Note that, in the following analyses, we did not use the two transfers listed above. Instead, we used 431 relative constraints derived from...”
- next paragraph, start with: “As the age of the root of Archaea is uncertain, ...”
- The **citation format** should be modified throughout the manuscript, to move the opening parenthesis when the authors’ names are part of a sentence, and to remove an extra pair of parentheses when a citation is already inside parentheses. The current formatting is hindering the flow of reading. As examples of the first formatting issue: The discussion starts with a parenthesis; change “We used an empirical sequence alignment ... from (dos Reis et al. 2012)” to “We used an empirical sequence alignment ... from dos Reis et al. (2012)”. Examples of the second formatting issue: remove the inside pair of parentheses in “(e.g., the HKY mode, (Hasegawa, Kishino, and Yano 1985))” and in “(see (Lepage et al. 2007) for a presentation of both)”. I counted 17 instances in the main text, and 9 instances in the Supplementary Material.
- Typos I spotted:
 - p.1: “11fossil” -> “11 fossil”
 - p.18: “on simulation” -> “in simulations”
 - p.19: “And a tutorial” -> “A tutorial” SM, simulation protocol: “and 1-15 constraints” -> “and 0-15 constraints” in the bottom red box