



Reply to: Modelling hominin evolution requires accurate hominin data

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REPLYING TO C. S. Mongle et al. *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-022-01791-2> (2022).

In their recent communication, Mongle et al.¹ argue that there are several problems with our recent analysis²: a problematic character matrix, a problematic geochronology and questionable body mass estimates. For the sake of brevity, we only focus on these main criticisms and refer to Supplementary Table 1 for further details but note that even if one considers their analysis to be correct and ours wrong, the discrepancies in divergence-time estimates for the nodes between the two analyses are a minimal 2.9% mean percentage difference and a 1.1% median percentage difference (Supplementary Table 2). In our view, dismissing our results and conclusions on the basis of such negligible differences is unmerited, especially when considering that almost all their mean divergence-time estimates are within our 95% highest posterior density intervals (HPD) (Fig. 1). Additionally, using point estimates (for example, mean values) is inappropriate in Bayesian analyses comparing divergence-time estimates, as the uncertainty around these values is not considered. Instead, posterior distributions should have been compared using the 95% HPD^{3,4}.

Mongle et al. criticize the apparent redundancy of some of the morphological characters used by Dembo et al.^{5,6}. However, they do not provide an empirical assessment showing how the exclusion of these characters affects our divergence-time estimates. An empirical assessment is the only way of testing their claim that redundancy would influence the estimation of divergence times and/or the evolutionary rates. Hence, we re-ran our analysis excluding the characters considered redundant by Mongle et al. The obtained results unequivocally show that a “redundant” character matrix is not an issue² for our analyses, as there is considerable overlap in the 95% HPDs of divergence times obtained in both analyses (Fig. 1) and the mean percentage difference for the node mean ages is ~2% (2.02%; Supplementary Table 2 and Fig. 1). In addition, when following Mongle et al.'s own list, we were able to remove only 25% of the characters, which means that the 40% value mentioned by Mongle et al.⁷ is unfounded. Furthermore, many of the characters considered redundant by Mongle et al. are questionable, as evident from their own list (depending on the applied criteria they can or cannot be considered redundant; see, for example, characters 22 and 23, among many others). Mongle et al. seem also to ignore the modifications made to the Dembo et al.⁵ matrix in Dembo et al.⁶. To give one example, Mongle et al. consider redundant a character that was already removed in the matrix of Dembo et al.⁶ (that is, character 63: alveolar clivus shape).

It seems that Mongle et al. misinterpreted our Methods section², as they claim that we made a gross error by not using the “correct” first and last appearance datums (FADs and LADs) of the analysed hominins. We did not use species' FADs or LADs as suggested by Mongle et al. but rather explicitly mentioned that the age of the fossil specimens used to score morphology (the Dembo et al.⁶ hypodigm) was used for the taxa without mitochondrial DNA available². Therefore, the comparisons made by Mongle et al. are inadequate, as the criteria used in both cases are different. Our criterion was based on the fact that when performing total evidence dating (TED) the rate of morphological evolution is estimated⁸. Therefore, including the FAD of a specimen that is not part of the hypodigm entails the assumption that the morphology of this early representative is identical to specimens from younger ages (a morphological stasis assumption) and this can affect TED divergence-time estimates^{3,4}. To avoid this issue, each taxon should be ideally scored using only one relatively complete specimen or several specimens belonging to the same fossiliferous horizon (same radiometric age). In this context, the data of Dembo et al.⁶ pose a particular challenge because the hypodigms that were morphologically scored are, in many cases, from different fossil localities and horizons. Simulations have shown that in cases of morphological stasis, more accurate and precise results are obtained by using the oldest stratigraphic occurrence of a lineage³. Consequently, instead of using the whole temporal range that encompasses the entire hypodigm for each taxon, we decided to base our calibration bounds on the radiometric uncertainty of the oldest specimen listed.

In relation to the taxa with mtDNA available, our approach was again explicitly stated: “In taxa with mtDNA sequences available, the sequences were selected from individuals aged equally, or as close as possible, to the morphologically scored fossils and the age associated with these sequences was used to calibrate the fossil tips.” Mongle et al. have not accounted for this methodological approach in their criticism of our analyses. Ideally, to be completely consistent, we should have used mtDNA from the oldest member of the hypodigm for each taxon but unfortunately this is not possible. For example, the oldest *Homo sapiens* in Dembo et al.⁶ is Jebel Irhoud with a direct estimate of 286 ± 32 thousand years ago (ka) (ref. ⁹) and no mtDNA available. Therefore, we chose one of the oldest *H. sapiens* specimens with mtDNA available (Tianyuan 1 dated at 39.475 ± 0.645 ka (ref. ¹⁰)). Mongle et al. criticized this choice as this specimen is not listed in the hypodigm of Dembo et al.⁶.

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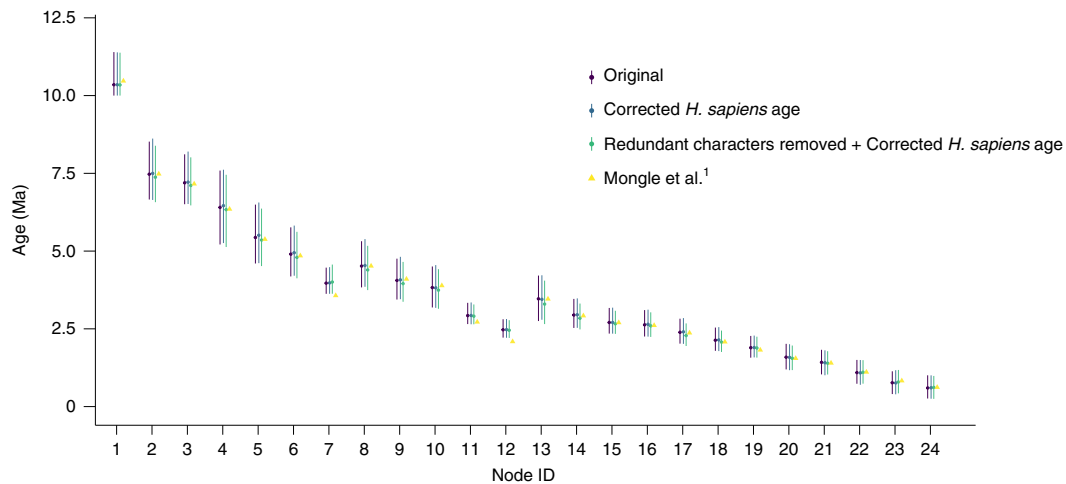


Fig. 1 | The effect of different calibration approaches in divergence-time estimates in TED analyses of the hominin phylogeny. The dots indicate the mean and the lines correspond to the associated 95% HPD of the divergence-time estimations for each node. Different colours indicate different calibration approaches. 'Original' indicates the analysis in Püschel et al.² using the Dembo et al.⁶ topological hypothesis. 'Corrected *H. sapiens* age' is the same treatment as Original but changing the age to 39.475 ± 0.645 ka, which is the correct age for the Tianyuan1 specimen used in the analyses for *H. sapiens*¹⁰. 'Redundant characters removed + Corrected *H. sapiens* age', is the same treatment as the latter but with 25% of the redundant characters (according to Mongle et al.) removed. Mongle et al.¹ corresponds to the Mongle et al. analysis. It is important to note that Mongle et al. did not include the 95% HPDs for their estimated node mean ages but it is likely that, if present, these intervals would considerably overlap with the three other calibration approaches.

However, this hypodigm⁶ consists of a wide range of hominins from different stratigraphic ages (286 ± 32 ka to the present) and from different locations, including Africa, the Middle East, Europe and Asia. Hence, it is reasonable to consider the anatomy of Tianyuan 1 within that wide range of morphological variation. We also used the age associated with this specimen to calibrate the *H. sapiens* tip because we also estimated the evolutionary rate of the mtDNA⁸. As such, adding the whole temporal range that comprises the hypodigm of Dembo et al.⁶ (286 ± 32 ka to the present) would have added an unnecessary level of uncertainty, considering that the age of the mtDNA sequence is known¹⁰. Finally, Mongle et al. claim that their FAD and LAD dates were based on the hypodigm of Dembo et al.⁶, which we can show is not always true. Furthermore, on occasion they chose questionable dates (Supplementary Table 1).

Mongle et al. argue that body mass estimates should not be provided for some taxa that lack any postcranial skeletal elements. However, there is a long tradition in vertebrate palaeontology and palaeoanthropology that applies regression equations based on craniodental elements to estimate body mass^{11–16}. Additionally, in the absence of any other body mass data we considered it reasonable to include estimates derived from cranial equations. Furthermore, we only used cranial estimates for two specimens belonging to two species (*Sahelanthropus tchadensis* and *Paranthropus aethiopicus*) which means that Mongle et al.'s criticism is overstated. In the case of *S. tchadensis*, we used a body mass estimate (58 kg) obtained for the TM266 cranium, as it is to our knowledge the only body mass estimate available for this species based on an actual method rather than mere opinions¹⁷. Furthermore, this value is consistent with the preliminary assessment of the TM266-01-063 femur (attributed to *S. tchadensis*) that suggests that the body mass of this individual exceeded 47 kg (ref.¹⁸). In the case of *P. aethiopicus*, we used a body mass value (38 kg) computed for the KNM-WT17000 cranium, which is consistent with the only postcranial estimates available for this species (31–37.7 kg) obtained for the possible *P. aethiopicus* EP1000/98 tibia^{19–21}. Mongle et al. criticized the body mass estimate we used for *H. rudolfensis* (55.2 kg). This value can be found in Table 2 of McHenry²² and is based on estimates from McHenry²³ (the cited reference in Püschel et al.²) that were obtained from several

specimens attributed to *H. rudolfensis*^{24,25}. Contrary to what is claimed by Mongle et al., there are several postcranial specimens that have been attributed to *H. rudolfensis*. For instance, KNM-ER 1472 along with KNM-ER 1481 were found geographically close to the cranium KNM-ER 1470 (*H. rudolfensis* lectotype) and are about the same geological age. Hence, it has been argued that on the basis of their sympatry and approximate synchronicity with KNM-ER 1470, they should be attributed to *H. rudolfensis*²⁴. KNM-ER 813 exhibits clear morphological differences with respect to OH8, which suggests that these two fossil tali do not belong to the same species^{26,27}. If OH 8 is considered to belong to *H. habilis*, then KNM-ER 813 may belong to *H. rudolfensis*²⁴. Finally, if we accept that the KNM-ER 1472 and KNM-ER 1481 femora belong to *H. rudolfensis*, then it becomes likely that the KNM-ER 3228 pelvic bone also belongs to this species as it is morphologically compatible with the femora²⁵.

More important than what Mongle et al. criticize about our paper is what they choose to omit. None of our divergence-time estimates are contrary to the current palaeoanthropological evidence. The conclusions reached by Mongle et al. are not supported, as their results are almost identical to ours (Fig. 1 and Supplementary Table 2), thus showing the robustness of our analyses to minor date differences (which are bound to emerge as the fossil record improves). Furthermore, we also show that some of their criticisms are based on either incorrect information and/or flawed interpretations of the available evidence.

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Author contributions

H.P.P. and T.A.P. conceived and designed the reply. H.P.P. carried out all the mentioned analyses. H.P.P. and T.A.P. wrote an initial draft. H.P.P., O.C.B., J.E.O., R.B. and T.A.P. interpreted the obtained results and contributed to the writing of the submitted version of this work.

Competing interests

The authors declare no competing interests.

Additional information

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