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Reply to: Modelling hominin evolution requires accurate hominin data

Citation for published version:

Püschel, HP, Bertrand, OC, Reilly, JEO, Bobe, R & Püschel, TA 2022, 'Reply to: Modelling hominin evolution requires accurate hominin data', *Nature Ecology & Evolution*. <https://doi.org/10.1038/s41559-022-01792-1>

Digital Object Identifier (DOI):

[10.1038/s41559-022-01792-1](https://doi.org/10.1038/s41559-022-01792-1)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Nature Ecology & Evolution

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1 **Response to “Modeling hominin evolution requires accurate hominin data”**

2

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22 Mongle et al. (MPSG hereafter) criticize our paper¹ by questioning the quality of the analysed
23 data and concluding that, since they believed it to be flawed, then our conclusions would also
24 be wrong. Before considering this claim in detail, we must first look at the results provided by
25 MPSG to support their conclusion. Even if one considers their analysis to be correct and ours
26 wrong, the discrepancies in divergence-time estimates for the nodes between the two analyses
27 are a minimal 2.9% mean percentage difference and a 1.1% median percentage difference
28 (Table 1). In our view, dismissing our results and conclusions based on such negligible
29 differences is unmerited, especially when considering that almost all their mean divergence-
30 time estimates are within our 95% highest posterior density intervals (HPD) (Fig. 1).
31 Additionally, using point estimates (e.g., mean values) is inappropriate in Bayesian analyses
32 comparing divergence-time estimates, as the uncertainty around these values is not considered.
33 Instead, posterior distributions should have been compared using the 95% HPD^{2,3}.

34

35 Considering the abovementioned issues, we can now respond to the problems MPSG claim to
36 have identified: (a) a problematic character matrix, (b) a problematic geochronology, and (c)
37 questionable body mass estimates. Although we think all their response's sections show serious
38 problems, for the sake of brevity we only focus on the main criticisms and refer to S1 for further
39 details.

40

41 **(a) Problematic character matrix**

42 MPSG criticise the apparent redundancy of some of Dembo et al.^{4,5} morphological characters.
43 However, they do not provide an empirical assessment showing how the exclusion of these
44 characters affects our divergence-time estimates. An empirical assessment is the only way of
45 testing their claim that redundancy would influence the estimation of divergence times and/or
46 the evolutionary rates. Hence, we re-ran our analysis excluding the characters considered
47 redundant by MPSG. The obtained results unequivocally show that a “redundant” character
48 matrix is not an issue¹ for our analyses, as there is considerable overlap in the 95% HPDs of
49 divergence-times obtained in both analyses (Figure 1), and the mean percentage difference for
50 the node mean ages is ~ 2% (2.02%; Table 1; Fig. 1). In addition, when following MPSG's
51 own list, we were able to remove only 25% of the characters, which means that the 40% value
52 mentioned by MPSG⁶ is an unfounded overstatement. Furthermore, many of the characters
53 considered redundant by MPSG are questionable as evident from their own list (depending on
54 the applied criteria they can or cannot be considered redundant; see for e.g., characters 22 and
55 23, among many others). MPSG seem to also ignore the modifications done to the Dembo et

56 al. (2015) matrix in Dembo et al. (2016). To give one blatant example, MPSG consider
57 redundant a character that was already removed in Dembo's et al. (2016) matrix (i.e., Character
58 63: Alveolar clivus shape).

59

60 **(b) Problematic geochronology**

61 It seems that MPSG misinterpreted our Methods section¹, as they claim that we made a gross
62 error by not using the 'correct' First and Last Appearance Datums (i.e., FADs and LADs) of
63 the analysed hominins. We did not use species' FADs or LADs as suggested by MPSG¹ but
64 rather explicitly mentioned that the age of the fossil specimens used to score morphology (i.e.,
65 Dembo's et al.⁵ hypodigm) was used for the taxa without mtDNA available. Therefore, the
66 comparisons made by MPSG are inadequate as the criteria used in both cases are different. Our
67 criterion was based on the fact that when performing Total Evidence Dating (TED) the rate of
68 morphological evolution is estimated⁷. Therefore, including the FAD of a specimen which is
69 not part of the hypodigm entails the assumption that the morphology of this early representative
70 is identical to specimens from younger ages (i.e., a morphological stasis assumption) and this
71 can have an impact on TED divergence-time estimates^{2,3}. To avoid this issue, each taxon should
72 be ideally scored using only one relatively complete specimen or several specimens belonging
73 to the same fossiliferous horizon (i.e., same radiometric age). In this context, Dembo et al.⁵
74 data poses a particular challenge because the hypodigms that were morphologically scored are
75 in many cases from different fossil localities and horizons. Simulations have shown that in
76 cases of morphological stasis, more accurate and precise results are obtained by using the oldest
77 stratigraphic occurrence of a lineage². Consequently, instead of using the whole temporal range
78 that encompasses the entire hypodigm for each taxon, we decided to base our calibration
79 bounds on the radiometric uncertainty of the oldest specimen listed.

80

81 In relation to the taxa with mtDNA available, our approach was again explicitly stated: "*In taxa*
82 *with mtDNA sequences available, the sequences were selected from individuals aged equally,*
83 *or as close as possible, to the morphologically scored fossils and the age associated with these*
84 *sequences was used to calibrate the fossil tips.*" Yet again, MPSG have not accounted for this
85 methodological approach in their criticism of our analyses. Ideally, to be completely consistent,
86 we should have used mtDNA from the oldest member of the hypodigm for of each taxon, but
87 unfortunately this is not possible. For example, the oldest *Homo sapiens* in Dembo's et al⁵ is
88 Jebel Irhoud with a direct estimate of 286 ± 32 ka⁸ and no mtDNA available. Therefore, we
89 chose one of the oldest *H. sapiens* specimens with mtDNA available (i.e., Tianyuan 1 dated at

90 39.475 ± 0.645 ka⁹). MPSG criticised this choice as this specimen is not listed in Dembo's et.
91 al⁵ hypodigm. However, this hypodigm⁵ consists of a wide range of hominins from different
92 stratigraphic ages (from 286 ± 32 ka to the present) and from different locations, including
93 Africa, the Middle East, Europe and Asia. Hence, it is only reasonable to consider Tianyuan's
94 1 anatomy within that wide range of morphological variation. We also used the age associated
95 to this specimen to calibrate the *H. sapiens* tip because we also estimated mtDNA's evolution
96 rate⁷. Hence, adding the whole temporal range that comprises Dembo's et al⁵ hypodigm (from
97 286 ± 32 ka to the present) would have added an unnecessary level of uncertainty, considering
98 that the age of the mtDNA sequence is known⁹.

99

100 Finally, MPSG claim that their FAD and LAD dates were based on Dembo's et al.⁵ hypodigm,
101 which we can show is not always true. Furthermore, on many occasions they chose
102 questionable dates (see S1).

103

104 **c) Body mass estimates**

105 MPSG argue that body mass estimates are provided for some taxa that lack any postcranial
106 skeletal elements. MPSG seem to disregard the long tradition in vertebrate palaeontology and
107 palaeoanthropology that applies regression equations based on craniodental elements to
108 estimate body mass¹⁰⁻¹⁵. Additionally, in the absence of any other body mass data we
109 considered that it is only reasonable to include estimates derived from cranial equations.
110 Furthermore, we only used cranial estimates for two specimens belonging to two species (i.e.,
111 *S. tchadensis* and *P. aethiopicus*) which means that MPSG's criticism is mostly unfounded. In
112 the case of *S. tchadensis*, we used a body mass estimate (58 kg) obtained for the TM 266
113 cranium, as it is to our knowledge the only body mass estimate available for this species based
114 on an actual method rather than mere opinions¹⁶. Furthermore, this value is consistent with the
115 preliminary assessment of the TM 266-01-063 femur (attributed to *S. tchadensis*) that suggests
116 that the body mass of this individual exceeded 47 kg¹⁷. In the case of *P. aethiopicus*, we used
117 a body mass value (38 kg) computed for the KNM-WT 17000 cranium, which is consistent
118 with the only postcranial estimates available for this species (31-37.7 kg) obtained for the
119 possible *P. aethiopicus* EP1000/98 tibia¹⁸⁻²⁰. MPSG criticised the body mass estimate we used
120 for *H. rudolfensis* (55.2 kg). This value can be found in Table 2 of McHenry²¹ and is based on
121 estimates from McHenry²² (the cited reference in Püschel et al.¹) that were obtained from
122 several specimens attributed to *H. rudolfensis*^{23,24}. Contrary to what is claimed by MPSG, there
123 are several postcranial specimens that have been attributed to *H. rudolfensis*. For instance,

124 KNM-ER 1472 along with KNM-ER 1481 were found geographically close to the cranium
125 KNM-ER 1470 (i.e., *H. rudolfensis* lectotype) and are about the same geological age. Hence,
126 it has been argued that based on their sympatry and approximate synchronicity with KNM-ER
127 1470, that they should be attributed to *H. rudolfensis*²³. KNM-ER 813 exhibits clear
128 morphological differences with respect to OH 8, which suggests that these two fossil tali do
129 not belong to the same species^{25,26}. If OH 8 is considered to belong to *H. habilis*, then KNM-
130 ER 813 may belong to *H. rudolfensis*²³. Finally, if we accept that the KNM-ER 1472 and KNM-
131 ER1481 femora belong to *H. rudolfensis*, then it becomes likely that the KNM-ER 3228 pelvic
132 bone also belongs to this species as it is morphologically compatible with the femora²⁴.

133

134 **Conclusions**

135

136 More important than what MPSG say about our paper, is what they choose to omit. None of
137 our divergence-time estimates are contrary to the current palaeoanthropological evidence. The
138 conclusions reached by MPSG are not supported, as their results are almost identical to ours
139 (Fig 1. and Table 1), hence showing the robustness of our analyses to minor date differences
140 (which are bound to happen as the fossil record improves). Furthermore, we also show that
141 some of their criticisms are based on either incorrect information and/or flawed interpretations
142 of the available evidence.

143

144

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206

207 **Figure caption**

208

209 **Figure 1.** The effect of different calibration approaches in divergence-time estimates in TED
210 analyses of the hominin phylogeny. The dots indicate the mean, and the lines correspond to the
211 associated 95% highest posterior density interval (HPD) of the divergence-time estimations for
212 each node. Different colours indicate different calibration approaches. Original indicates the
213 analysis in Püschel et al.¹ using the Dembo et al.⁵ topological hypothesis. Corr. *Homo sapiens*
214 age is the same treatment as Original but changing the age to 39.475 ± 0.645 ka, which is the
215 correct age for the Tianyuan 1 specimen used in the analyses for *H. sapiens*⁹. Redun. char.
216 removed + Corr. *H. sapiens* age, is the same treatment as the latter but with 25% of the
217 redundant characters (i.e., according to MPSG) removed. MPSG corresponds to the Mongle et
218 al. analysis. It is important to note that MPSG did not included the 95% HPDs for their
219 estimated node mean ages, but it is likely that if present, these intervals would considerably
220 overlap with the three other calibration approaches. Abbreviations: char., character; corr.,
221 corrected; redun., redundant.