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## Reply to: Modelling hominin evolution requires accurate hominin data

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

2

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21

22 Mongle et al. (MPSG hereafter) criticize our paper<sup>1</sup> 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<sup>2,3</sup>.

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.<sup>4,5</sup> 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 issue<sup>1</sup> 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 MPSG<sup>6</sup> 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 section<sup>1</sup>, 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 MPSG<sup>1</sup> but  
64 rather explicitly mentioned that the age of the fossil specimens used to score morphology (i.e.,  
65 Dembo's et al.<sup>5</sup> 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 estimated<sup>7</sup>. 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<sup>2,3</sup>. 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.<sup>5</sup>  
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 lineage<sup>2</sup>. 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 al<sup>5</sup> is  
88 Jebel Irhoud with a direct estimate of  $286 \pm 32$  ka<sup>8</sup> 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 ka<sup>9</sup>). MPSG criticised this choice as this specimen is not listed in Dembo's et.  
91 al<sup>5</sup> hypodigm. However, this hypodigm<sup>5</sup> 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 rate<sup>7</sup>. Hence, adding the whole temporal range that comprises Dembo's et al<sup>5</sup> 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 known<sup>9</sup>.

99

100 Finally, MPSG claim that their FAD and LAD dates were based on Dembo's et al.<sup>5</sup> 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 mass<sup>10-15</sup>. 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 opinions<sup>16</sup>. 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 kg<sup>17</sup>. 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 tibia<sup>18-20</sup>. MPSG criticised the body mass estimate we used  
120 for *H. rudolfensis* (55.2 kg). This value can be found in Table 2 of McHenry<sup>21</sup> and is based on  
121 estimates from McHenry<sup>22</sup> (the cited reference in Püschel et al.<sup>1</sup>) that were obtained from  
122 several specimens attributed to *H. rudolfensis*<sup>23,24</sup>. 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*<sup>23</sup>. 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<sup>25,26</sup>. If OH 8 is considered to belong to *H. habilis*, then KNM-  
130 ER 813 may belong to *H. rudolfensis*<sup>23</sup>. 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 femora<sup>24</sup>.

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.<sup>1</sup> using the Dembo et al.<sup>5</sup> topological hypothesis. Corr. *Homo sapiens*  
214 age is the same treatment as Original but changing the age to  $39.475 \pm 0.645$  ka, which is the  
215 correct age for the Tianyuan 1 specimen used in the analyses for *H. sapiens*<sup>9</sup>. 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.