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# Evidence for increased hominid diversity in the Early-Middle Pleistocene of Indonesia

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Since the first discovery of *Pithecanthropus (Homo) erectus* by E. Dubois at Trinil in 1891, over 200 hominid dentognathic remains have been collected from the Early-Middle Pleistocene deposits of Java, Indonesia, forming the largest palaeoanthropological collection in Southeast Asia. Most of these fossils are currently attributed to *H. erectus*. However, because of the substantial morphological and metric variation in the Indonesian assemblage, some robust specimens, such as the partial mandibles Sangiran 5 and Sangiran 6a, were formerly variably allocated to other taxa (*Meganthropus palaeojavanicus*, *Pithecanthropus dubius*, *Pongo* sp.). To resolve the taxonomic uncertainty surrounding these and other contentious Indonesian hominid specimens, we used Occlusal Fingerprint Analysis to reconstruct their chewing kinematics, and also used various morphometric approaches based on microtomography to examine internal dental structures. Our results confirm the presence of *Meganthropus* as a Pleistocene Indonesian hominid distinct from *Pongo*, *Gigantopithecus* and *Homo*, and further reveal that

**Eugene Dubois' *Homo erectus* paratype molars from 1891 are not hominin (human lineage), but instead are more likely to belong to *Meganthropus*.**

During the Quaternary, episodes of glacial eustasy combined with tectonic uplift and volcanoclastic deposition periodically altered the palaeobiogeography of the Sunda region. These physical and resultant environmental changes facilitated or inhibited intermittent faunal exchanges with the Asian mainland<sup>1</sup> and influenced the evolutionary dynamics of the local faunas, including hominids<sup>2</sup>. The presence of hominids (great apes and humans) in Southeast Asia during the Early and Middle Pleistocene is well documented in the fossil record, with at least three firmly established genera: *Gigantopithecus*, *Pongo* and *Homo*<sup>3-6</sup>. The existence of a putative “mystery ape” has also been evoked<sup>7</sup>. Due to the implied vicariance and relict survivorship accompanying these geomorphological events, the appraisal of palaeobiodiversity at a regional scale is difficult. The presence of *Homo* in insular Southeast Asia since the Early Pleistocene has been amply documented by cranial, dental and postcranial remains<sup>3</sup>. Conversely, apart from four isolated teeth recently discovered in Peninsular Malaysia<sup>8</sup>, only a few dental specimens representing *Pongo* sp. have been reported from the Early and Middle Pleistocene deposits of Indonesia<sup>9</sup>. Because of the convergence in molar crown size and overall morphology between fossil *Homo* and *Pongo*, the taxonomic diagnosis of many Asian Early Pleistocene hominid dentognathic specimens has been debated for over a century, especially concerning isolated teeth and occlusally worn specimens<sup>10,11</sup> (Supplementary Figure 1 and Supplementary Material). The resulting taxonomic confusion has affected the historical debate on the evolution of the genus *Homo* in Southeast Asia and, more generally, the assessment of Pleistocene hominid palaeobiodiversity<sup>7</sup>.

Using three-dimensional virtual imaging, we reassess the taxonomic assignment of two isolated maxillary molars from Trinil (Trinil 11620 and Trinil 11621)<sup>10,11</sup>, paratypes of *H. erectus*<sup>12</sup>, and of the partial mandibles Sangiran 5, the holotype of *Pithecanthropus dubius*<sup>13</sup>, and Sangiran 6a, the holotype of *Meganthropus paleojavanicus*<sup>14,15</sup>, all currently considered to be *H. erectus*<sup>16-18</sup>. We also re-examine the mandibular specimen Arjuna 9, regarded as a robust *H. erectus* similar to Sangiran 6a<sup>19</sup>, and seven isolated upper and lower permanent molar crowns from the Early-Middle Pleistocene Sangiran Dome formations (FS-77, SMF-8855, SMF-8864, SMF-8865, SMF-8879, SMF-8898 and SMF-10055), provisionally labelled as *Pongo* sp., but whose taxonomic identity remains problematic (Figure 1, Supplementary Figure 2 and Supplementary Material). The analyses and/or examined features include Occlusal Fingerprint Analysis, enamel distribution and relative enamel thickness, crown-root surface area proportions, enamel-dentine junction topography, and pulp chamber morphology. We compare the results from this Indonesian assemblage with similar data from extant and fossil *Homo* and *Pongo*, as well as the fossil hominids *Sivapithecus* (Late Miocene, South Asia),

82 *Lufengpithecus* (Late Miocene, southern China), and *Gigantopithecus* (Pleistocene, China and  
83 Southeast Asia)<sup>20</sup> (Supplementary Tables 1-4).

84  
85 **Results**

86 One important distinction between humans and non-human apes concerns their dietary ecology and  
87 feeding behaviours, reflected in their masticatory apparatus by different morphological adaptations  
88 and structural characteristics<sup>21,22</sup>. Occlusal Fingerprint Analysis<sup>23</sup> of crown wear patterns reveals that  
89 all robust Indonesian hominid molars suitable for this investigation (9 of 13) exhibit an ape-like  
90 functional macrowear pattern that differs significantly ( $p<0.05$ ) from that of extant and extinct  
91 hominin samples, including Javanese *H. erectus* (Figure 2 and Supplementary Table 5). This pattern  
92 is characterised by a high dominance of power stroke Phase II over Phase I, evidenced by enlarged  
93 Phase II wear facets (Supplementary Table 6). In contrast, humans and extinct hominins, including  
94 Chinese and Indonesian *H. erectus*, display proportionately larger buccal Phase I wear facets,  
95 indicative of distinct masticatory behaviour (Figure 2).

96 Patterns of enamel distribution are sensitive indicators of dietary adaptations and taxonomic  
97 affinities in anthropoids<sup>22</sup>. Morphometric cartographies distinguish between hominin and ape  
98 patterns: in the former, the thickest enamel is deposited on the “functional cusps” rather than on the  
99 “guiding” cusps<sup>22</sup>, while in apes, and notably in *Pongo*, it lies at the periphery of the occlusal basin<sup>24-</sup>  
100 <sup>26</sup>. Our analyses reveal that all but one of the modestly worn hominid molars from Java (n=8) show  
101 an ape pattern. The maxillary molar Trinil 11620 displays even relatively thicker enamel at the  
102 periphery of the occlusal basin than is typically found in *Pongo*, more closely approximating the  
103 Miocene apes *Sivapithecus* and *Lufengpithecus* (Figure 3). Conversely, the lower molar specimen  
104 SMF-8865 closely resembles the condition characterising African and Indonesian *H. erectus*, showing  
105 the thickest enamel localized on the buccal cusps, while Arjuna 9, FS-77, SMF8855, SMF-8864 and  
106 SMF-8879 have the thickest enamel distributed along the marginal ridges around the occlusal basin.  
107 Crown tissue proportions, including the commonly used Relative Enamel Thickness index<sup>24,26,27</sup>,  
108 overlap across all extinct and extant samples and do not discriminate the Javanese robust specimens  
109 (Supplementary Figure 3 and Supplementary Tables 7-8).

110 Crown-root surface area proportions have also been demonstrated to show a strong phylogenetic  
111 signal, independent of feeding adaptations in tooth morphology<sup>28</sup>. Both upper molars from Trinil and  
112 the lower post-canine teeth of Sangiran 6a and Arjuna 9 exhibit proportionally large root surfaces  
113 compared to the lateral (non-occlusal) crown area, resembling pongines and *Lufengpithecus* and  
114 differing substantially from *Homo* (Figure 4, Supplementary Figure 4 and Supplementary Table 9).

115 The topography of the enamel-dentine junction (EDJ), which reliably distinguishes fossil and  
116 extant hominid taxa<sup>24,26,29</sup>, approximates the inner enamel epithelium of the developing tooth and

117 provides useful information about taxon-specific processes underlying crown growth<sup>29</sup>. Six of the  
118 Javanese lower molars show a cingulum-like, mesiodistally extended buccal protostylid at the EDJ,  
119 which is distinct from the morphology commonly found in *Homo* and *Pongo* but similar to the  
120 condition expressed by the Miocene Chinese ape *Lufengpithecus* (Supplementary Figure 5; see also  
121 Supplementary Figure 6 for the lower P4 EDJ morphology). The specimen SMF-8865 does not show  
122 the same coarse wrinkling pattern at the EDJ as the other robust Indonesian hominids, or the dense  
123 crenulation pattern typical of *Pongo*, but rather resembles the *H. erectus* condition (Supplementary  
124 Figure 5).

125 We also performed geometric morphometric (GM) analyses of the molar EDJ to compare the  
126 Indonesian fossil specimens to an assemblage of fossil and extant hominids (Figure 5). The results  
127 show statistical discrimination between *Pongo* and *Homo* and unambiguously classify the robust  
128 Javanese specimens as non-human apes, again with the exception of SMF-8865 (Supplementary  
129 Table 10). Indeed, except for the latter specimen, the EDJ shape of this Javanese sample of robust  
130 teeth is distinguished from *Homo* and overlaps those of *Pongo* and *Lufengpithecus*, even if some  
131 specimens like the holotype of *Meganthropus*<sup>14,15</sup>, Sangiran 6a, are outside the variation of *Pongo*  
132 (Figure 5, Supplementary Figure 7). As in fossil *Pongo*<sup>24</sup>, *Gigantopithecus*<sup>24</sup>, *Sivapithecus* and  
133 *Lufengpithecus*, the EDJ of these teeth consistently exhibits a low topography with higher mesial than  
134 distal dentine horns. Interestingly, comparable results are obtained when the same analysis is  
135 performed on the lower P4 of Sangiran 6a (Supplementary Figures 8-9 and Supplementary Table 11).  
136 Conversely, in *Homo*<sup>26,29</sup> and in SMF-8865 as well, the EDJ typically shows higher relief, with  
137 dentine horns of sub-equal height and more distally-set buccal cusps (Figure 5). In light of this, it is  
138 noteworthy that a pongine-like endostructural signature (but different from that typical of *Pongo*) was  
139 recently identified in an isolated deciduous mandibular molar from the Early Pleistocene of Sangiran  
140 that was originally labelled as *Meganthropus*<sup>14</sup>, but later allocated to early *Homo* (rev. in ref. 26).

141 While the taxonomic significance of the EDJ is supported by previous studies<sup>29</sup>, that of pulp  
142 chamber shape has not been systematically evaluated. However, marked morphological differences  
143 are notable in the height, thickness and shape of the pulp chamber between fossil and extant hominid  
144 taxa (Supplementary Figures 10-11). Accordingly, we performed a preliminarily GM analysis limited  
145 to the four extant hominid genera. Our results demonstrate that *Homo* and *Pongo* are statistically  
146 distinguished by pulp chamber morphology (Supplementary Material and Supplementary Figure 12).  
147 Based on these results, three-dimensional landmark-based analyses of the shape of the pulp chamber  
148 (not possible for SMF-8865) were thus extended to the fossil specimens. Similar to the analyses of  
149 the EDJ, they clearly discriminate the robust Javanese specimens from *Homo* (Supplementary Table  
150 10). However, in contrast to the results of EDJ shape, the shape of the pulp chamber also distinguishes  
151 most of the fossil specimens forming the Javanese assemblage from *Pongo* (except for SMF-8879)

152 and approximates *Lufengpithecus* (Figure 5 and Supplementary Figure 13).

153 When only non-hominin taxa are considered in the GM analyses of the EDJ and pulp chamber, the  
154 robust Indonesian molars are generally distinguished from *Pongo* (except for SMF-8879, which falls  
155 close to or within the *Pongo* range of variation) and approximate the Miocene representatives,  
156 especially *Lufengpithecus* (Figure 6 and Supplementary Figures 14-15).

157

## 158 Discussion

159 Previous attempts to sort the Indonesian hominid dentognathic remains into morphs primarily based  
160 on their external morphology provided different, sometimes contradictory, results<sup>7,18,19,30</sup>. This is  
161 because the fossil assemblage shows variable preservation conditions and most dental remains are  
162 affected by extensive occlusal wear (Supplementary Figure 1). Based on multiple aspects of dental  
163 morphology, our re-analysis of this long-controversial sample of robust Pleistocene dentognathic  
164 specimens from Java demonstrates that, with the exception of the isolated crown SMF-8865, which  
165 we attribute to *H. erectus*, all the specimens investigated here most likely represent non-hominin  
166 species. Moreover, Trinil 11620, Trinil 11621, Sangiran 5, Sangiran 6a, Arjuna 9, FS-77 and SMF-  
167 8864 are dentally distinct from *Pongo* and represent a third ape lineage in addition to *Pongo* and  
168 *Gigantopithecus* that survived beyond the Miocene in South-eastern Asia. We propose to allocate this  
169 material to the resurrected species *Meganthropus palaeojavanicus* von Koenigswald, 1950<sup>14,15</sup>, but  
170 as a non-hominin. The holotype is Sangiran 6a and the other specimens are paratypes. Consequently,  
171 *Pithecanthropus dubius*<sup>15</sup> becomes a junior synonym of *Meganthropus palaeojavanicus*.

172 Unlike most apes, Sangiran 6a and Sangiran 9<sup>14-17</sup> lack the canine/P3 honing complex and the P3  
173 is non-sectorial, being more similar to the P4 with reduced crown height, a relatively prominent  
174 metaconid (thus being clearly bicuspid) and a more buccolingually oriented crown major axis. In all  
175 these features, *Meganthropus* is similar to Plio-Pleistocene hominins, which might argue for  
176 *Meganthropus* being a hominin rather than a non-hominin hominid as we conclude from our analysis  
177 of internal dental structure. However, there are other fossil apes in which the P3 is non-sectorial and  
178 converges on a hominin-like morphology, most strikingly among megadont species that have  
179 undergone marked canine reduction, such as the Late Miocene *Indopithecus*<sup>31</sup>, and especially the  
180 Pleistocene *Gigantopithecus*<sup>6,32</sup>, in which the P3 is typically bicuspid. A relatively low-crowned and  
181 more transversely oriented P3 associated with some degree of canine reduction (at least with respect  
182 to its cervical dimensions) also characterises the Late Miocene megadont *Ouranopithecus*<sup>33</sup>. While  
183 having a sectorial P3, *Lufengpithecus* also shows strong expression of the metaconid, in some cases  
184 bordering on a bicuspid morphology<sup>34</sup>.

185 Concerning Trinil 11620, this tooth was among those in another recent attempt to sort out the  
186 identities of Pleistocene dental remains, mostly from China but including several teeth from Southeast

187 Asia as well<sup>11</sup>. Other than 2D enamel thickness and EDJ topography, that study examined different  
188 aspects of dental morphology than those examined here, and, with the exception of Trinil 11620, on  
189 an entirely different sample. While Trinil 11620 is identified *a priori* as a hominin in that study and  
190 another previous study<sup>11,35</sup>, this is based on a prior analysis<sup>10</sup> to decide only whether it should be  
191 assigned to *Homo* or *Pongo*, without considering the possible presence of an additional Pleistocene  
192 ape lineage in Southeast Asia in addition to *Pongo* and *Gigantopithecus*. Also, no results or  
193 conclusions are reported for it other than a long-period (Retzius) developmental line periodicity of  
194 either 6 or 7<sup>10</sup>. These values are well below the reported range of periodicities for fossil or extant  
195 *Pongo* and a value of 6 would be an unusually low value for fossil or extant *Homo*<sup>11,35,36</sup>. While  
196 *Gigantopithecus* and *Sivapithecus* typically show values of 8-11 days<sup>11,37</sup>, we note that in a small  
197 sample of *Lufengpithecus*, the Retzius line periodicity is 7-9 days<sup>38</sup>. Although we did not examine  
198 long-period line periodicity, and there is substantial variation in long-period line periodicities in  
199 hominid taxa<sup>35,36</sup>, the low value for Trinil 11620 could perhaps be considered as additional support  
200 for the assignment of this tooth to *Meganthropus*.

201 In keeping with its prior definition, *Meganthropus* is distinguished from *Homo* by having  
202 absolutely large teeth<sup>14,15</sup>, a mandibular corpus with a thick and rounded inferior border, a large  
203 extramolar sulcus and strong lateral prominence<sup>15-17</sup>, molarised premolars, and low molar crowns  
204 with coarse wrinkling converging toward the centre of the occlusal surface<sup>14,15</sup>. Our results  
205 demonstrate that *Meganthropus* is further distinguished from *Homo* by an ape-like molar occlusal  
206 macrowear pattern, peripherally-distributed thicker molar enamel, a low crowned EDJ with relatively  
207 short dentine horns, a particularly slender pulp shape with high horns, and lower crown/root surface  
208 area proportions. It further differs from penecontemporaneous *H. erectus* by the presence of a  
209 cingulum-like protostylid in both the enamel and the underlying EDJ. This feature is commonly found  
210 in *Australopithecus* and *Paranthropus*, but *Meganthropus* differs from these two hominins by its ape-  
211 like occlusal wear pattern (Supplementary Figure 16), thicker peripheral enamel (whereas thicker  
212 enamel is found at the cusp tip in australopiths<sup>39</sup>), the lower EDJ topography, and more slender pulp  
213 chamber with vertically elongated pulp horns (Supplementary Figure 17). As a further consequence  
214 of recognising *Meganthropus* as non-hominin, certain features commonly regarded as characteristic  
215 of hominins, such as the loss of the canine/P3 honing complex, lack of a marked mandibular simian  
216 shelf, moderately mesiodistally elongated premolars with a double root and premolar/molar size  
217 proportions<sup>12,14-17</sup>, more likely represent homoplastic traits in *Meganthropus*. From our results, it is  
218 also evident that, aside from marked differences in mandibular morphology and proportions,  
219 *Meganthropus* differs from *Pongo* by having laterally-positioned molar dentine horns, a slender pulp  
220 chamber, and a cingulum-like expression of the protostylid (Figure 6 and Supplementary Figures 5  
221 and 10). *Meganthropus* is also clearly distinct from *Gigantopithecus*, the latter displaying higher-

crowned and narrower molars with low bulbous cusps and rounded crests, a large cuspule formed by a lobe between the protoconid and metaconid giving the lower molars a distinctive cusp pattern comprised of two pairs of main cusps arranged peripherally, a line of smaller midline cusps that includes the talonid cuspule and the hypoconulid, the lack or faint expression of the protostylid, strong buccolingual mid-crown waisting<sup>6</sup>, thicker occlusal enamel, and higher EDJ topography<sup>24</sup> (for a detailed differential diagnosis of *Meganthropus*, see Supplementary Material section 3, Supplementary Figure 18 and Supplementary Table 12).

We provisionally assign SMF-8879 to *Pongo* sp. Future analyses should clarify the taxonomic status of the specimens SMF-8855, SMF-8898 and SMF-10055, currently regarded as pongines, but which also share some features with the Asian Miocene apes, as well as other specimens from Early Pleistocene Java whose status continues to be debated (e.g., Sangiran 8, Sangiran 9, Sangiran 27)<sup>16,17</sup>.

Across most of Eurasia, apes became extinct prior to the end of the Miocene. They survived into the Pleistocene only in South-eastern Asia, represented by *Gigantopithecus* and *Pongo*, both known from southern-most China into Southeast Asia<sup>5,40</sup>. To these can be added *Meganthropus* from Java, formerly suggested to be an ape by some<sup>12,14,15</sup> but only confidently demonstrated to be so by the comparative analyses presented here. As demonstrated by paleobotanical, paleontological and geochemical proxies<sup>2,41-43</sup>, the Early to Middle Pleistocene palaeoenvironments of Sangiran and Trinil included a variety of mixed and temporally shifting habitats, ranging from open woodland areas to dense forests capable of supporting the presence of multiple large-bodied hominid species in addition to at least two arboreal monkeys, *Macaca fascicularis* and *Trachypithecus cristatus*<sup>2</sup>. Of the other apes present during the late Miocene in South and Southeast Asia - *Sivapithecus*, *Khoratpithecus*, and *Lufengpithecus* - *Meganthropus* appears to be dentally most similar to the last, evidenced by the presence in both of low-cusped and wrinkled molar crowns<sup>21,44,45</sup> with a squat EDJ, an extended protostylid and a slender pulp chamber (Figure 5, Supplementary Figures 5 and 10). In contrast, *Sivapithecus* and *Khoratpithecus* have higher, more bunodont molars with marked mid-crown buccolingual constriction<sup>21,22</sup> and *Sivapithecus* has proportionally higher dentine horns (Figure 5). In sum, when combining evidence from the occlusal wear pattern, internal tooth structure, and aspects related to dental development<sup>10</sup>, *Meganthropus* shows greatest affinity to *Lufengpithecus*, and we hypothesize that these taxa are phylogenetically closely related. Substantiating this will require fuller knowledge than currently available of character polarity and homology versus homoplasy in features of tooth internal structure and dental development as a whole.

## Conclusion

During the Early-Middle Pleistocene, at least three and perhaps four hominid genera inhabited what is now Indonesia: *Homo*, *Pongo* and *Meganthropus*, with the possible presence of *Gigantopithecus*<sup>40</sup>.



257 This is a higher level of diversity than previously recognised and, with the newly resurrected genus  
258 *Meganthropus* now recognized as an ape, is particularly noteworthy for the late survival of two to  
259 three large ape lineages. Whether related to the expansion of *H. erectus*, palaeoenvironmental  
260 changes, competition with *Pongo* or *Gigantopithecus*, or some combination of these factors,  
261 *Meganthropus* did not persist beyond the Middle Pleistocene, leaving only three species of the genus  
262 *Pongo* (*P. pygmaeus*, *P. abelii* and *P. tapanuliensis*) subsisting today in remote and protected  
263 Indonesian localities<sup>46</sup>.

264

## 265 **Methods**

266 **X-ray and neutron microtomography.** Except for the Trinil molars and Sangiran 5 (see below), all  
267 Javanese hominid specimens studied here (Sangiran 6a, Arjuna 9, FS-77, SMF-8855, SMF-8864,  
268 SMF-8865, SMF-8879, SMF-8898 and SMF-10055) were scanned using the X-ray microfocus  
269 sources (X- $\mu$ CT) at: the Helmholtz-Zentrum Berlin (equipment CONRAD II instrument), the  
270 Department of Human Evolution of the Max Plank Institute of Leipzig (equipment BIR ACTIS  
271 225/300), the University of Poitiers (equipment X8050-16 Viscom AG), and the Seckenberg  
272 Research Institute (Phoenix Nanotom s 180). Acquisitions were performed according to the  
273 following parameters: 100-160 kV, 0.11-90  $\mu$ A, 0.14-0.36° of angular step. The final volumes were  
274 reconstructed with voxel sizes ranging from 20.8 to 40.7  $\mu$ m. The two Trinil molars (11620 and  
275 11621) were scanned by SR- $\mu$ CT on beamline ID 19 of the European Synchrotron Radiation  
276 Facility at Grenoble using absorption mode with an isotropic voxel size of 31.12  $\mu$ m<sup>3</sup> at an energy  
277 of 60 keV<sup>10</sup>. The dataset of 632 images is available in 8 bits .tif format at the ESRF Paleontological  
278 Database (<http://paleo.esrf.eu>). The X- $\mu$ CT acquisitions of the comparative fossil and extant  
279 hominid specimens were performed using various equipment with the following parameters: 95-145  
280 kV, 0.04-0.40  $\mu$ A, 0.17-0.36° of angular step. The final volumes were reconstructed with voxel  
281 sizes ranging from 8.3 to 60.0  $\mu$ m.

282 The specimens Sangiran 5 and Sangiran 6a were scanned by neutron microtomography (n-  
283  $\mu$ CT)<sup>47-51</sup> at the ANTARES Imaging facility (SR4a beamline) of the Heinz Maier-Leibnitz Center  
284 (FRM II) of Technische Universität München. The neutron beam originated from the cold source of  
285 the FRM II reactor, with an energy range mostly from 3 to 20 meV, a collimation ratio of L/D=500  
286 (ratio between sample-detector distance and collimator aperture) and an intensity of 6.4 x 10<sup>7</sup>  
287 n/cm<sup>2</sup>s. A 20  $\mu$ m Gadox screen was used to detect neutrons. Both a cooled scientific CCD camera  
288 (Andor ikon-L) and cooled scientific CMOS camera (Andor NEO) were used as detectors. The final  
289 virtual volume of these specimens was reconstructed with an isotropic voxel size of 20.45  $\mu$ m.

290

291 **Data processing.** Some specimens showed low contrast between the enamel and dentine in some

parts of the dataset, precluding automatic segmentation. In such cases, enamel and dentine were segmented using the magic wand tool in Avizo 8.0 (FEI Visualization Sciences Group) and manual corrections were locally applied. Use of the interpolation tool was limited to areas where the distinction between enamel and dentine could not be precisely demarcated. A volumetric reconstruction was then generated for each specimen. In most cases, the contrast resolution enabled carrying out a semi-automatic threshold-based segmentation following the half-maximum height method (HMH<sup>52</sup>) and the region of interest thresholding protocol (ROI-Tb<sup>53</sup>) taking repeated measurements on different slices of the virtual stack<sup>54</sup>. Because the detection of the tissue interfaces is based on attenuation at the boundary of a structure in both X-ray and neutron-based microtomography, we performed a threshold-based segmentation with manual corrections, as usually applied for X-ray acquisitions<sup>55,56</sup>. We quantified the degree of morphological and dimensional coherence between the X-ray microtomography (X- $\mu$ CT) and n- $\mu$ CT datasets of Sangiran 6a. The superimposed EDJ based on the X- $\mu$ CT and n- $\mu$ CT records show maximum 240  $\mu$ m differences and an average of 65.7  $\mu$ m variation (Supplementary Figure 19). Considering the difference in voxel size of the two original datasets (39.33  $\mu$ m and 20.45  $\mu$ m for the X-ray and neutron data, respectively), the differences in LM1 enamel volume (349.26  $\mu$ m<sup>3</sup> and 346.61  $\mu$ m<sup>3</sup>), dentine-pulp volume (529.1  $\mu$ m<sup>3</sup> and 526.7  $\mu$ m<sup>3</sup>) and crown volume (878.4  $\mu$ m<sup>3</sup> and 873.3  $\mu$ m<sup>3</sup>) are less than 1% and can be regarded as negligible.

**Occlusal Fingerprint Analyses.** The analysis of dental wear facets enables the reconstruction of occlusal behaviour<sup>23</sup>. Qualitative wear facet analysis performed by Mills<sup>57</sup> already led to the conclusion that in primates and insectivores the occlusal power stroke of the chewing cycle consists of two phases (buccal Phase and lingual Phase), which were later determined as Phase I and Phase II<sup>58,59</sup>. The chewing cycle starts with the preparatory (closing) stroke where three-body contact (tooth-food-tooth) leads to puncture-crushing activity with rare contacts of antagonistic crowns. Real chewing starts with Phase I<sup>59</sup>, in which during stereotypic cycles tooth-tooth contacts may occur more commonly, producing guiding buccal and lingual Phase I facets through shearing activity along the buccal slopes of the buccal and lingual cusps of the lowers and complementary facets on the lingual cusp slopes of the upper molars. Phase I ends in maximum intercuspation (centric occlusion) leading into Phase II with a more or less lateral shift of the lower jaw leading to grinding activity until the last antagonistic contacts. During the recovery stroke the jaws open with no dental contacts<sup>23,25,59</sup>. The Phase I and Phase II pathway of the power stroke is recorded in the wear facet pattern on the occluding molars<sup>23,60-63</sup>. To assess the occlusal motion pattern(s) characteristic of the Early Pleistocene robust Javanese hominid teeth considered here, we applied Occlusal Fingerprint Analysis (OFA) to attribute proportions of wear facet areas to power stroke

327 phases in order to compare occlusal motion patterns in a sample of extant and fossil Asian great  
328 apes and *Homo*. Occlusal macrowear areas, including wear facets following Maier and Schneck<sup>60</sup>,  
329 were identified on virtual surface models of upper and lower molar crowns following the OFA  
330 method described in Kullmer et al.<sup>23</sup> and Fiorenza et al.<sup>64</sup>. The 3D surface data acquisition derived  
331 either from  $\mu$ CT datasets or from 3D surface scanning with a smartSCAN-HE (Breuckmann  
332 GmbH). Scans were taken either from originals or from high resolution casts that provide  
333 reasonable resolution of macrowear for mapping wear facet areas<sup>61</sup>. We used the modular software  
334 package PolyWorks® 2016 (InnovMetric Inc.) to edit the surface models. The polyline tool in the  
335 software module IMEdit was applied to interactively mark and fit closed polylines onto the model  
336 surfaces along the perimeter of wear facets in each tooth crown. By re-triangulation of the crown  
337 surfaces, the polylines became integrated into the surface models. To measure each wear facet area,  
338 triangles were selected up to each polyline curve, grouped and color-coded following the occlusal  
339 compass<sup>23,62</sup>. The area measurement tool in IMEdit was used to compute area in mm<sup>2</sup> for each wear  
340 facet. Wear facet areas were summed for chewing cycle power stroke phases<sup>59,65</sup>. Buccal Phase 1  
341 (BPh I), lingual Phase 1 (LPh I) and Phase 2 (Ph II) facet area data were grouped for comparing  
342 percentage distribution of wear. To compare power stroke movements only, flat worn areas on cusp  
343 tips, identified as tip crushing areas<sup>64</sup>, were excluded because this type of tissue loss usually results  
344 from puncture-crushing activity<sup>59,65</sup> and is not attributable with certainty to one of the two power  
345 stroke phases. Percentage results are illustrated in ternary plots. Each corner of the triangle  
346 represents 100% of one variable. Accordingly, a sample with an equal distribution of wear facet  
347 areas will be placed in the centre of the triangle. The plots were generated using the ggtern package  
348 v.2.2.2<sup>66</sup> in R v.3.4<sup>67</sup>. The R package RVAideMemoire 0.9-66<sup>68</sup> was used to perform one-way  
349 permutational multivariate analysis of variance (PERMANOVA) on the three variables (BPh I, LPh  
350 I and Ph II) separately for the maxillary and mandibular molar samples. A Bray-Curtis similarity  
351 matrix was calculated based on a 9999 permutations parameter. For both upper and lower molars  
352 the test was significant ( $p < 0.05$ ), with values for the pseudo-F model of 18.78 and 13.98 and R<sup>2</sup>  
353 coefficients of 0.53 and 0.57, respectively. Post-hoc PERMANOVA pairwise comparisons were run  
354 with a false discovery rate (FDR) correction (Supplementary Table 5).

355  
356 **3D tooth tissue proportions.** Premolar and molar crowns and roots were digitally isolated at the  
357 cervix along the best-fit plane and surface rendering was performed using unconstrained smoothing  
358 for visualization, while constrained smoothing was applied for the quantitative analyses. For the  
359 molar teeth, seven linear, surface, and volumetric variables describing tooth tissue proportions were  
360 digitally measured or calculated on the molars: Ve, the volume of the enamel cap (mm<sup>3</sup>); Vcdp; the  
361 volume of the crown dentine+pulp (mm<sup>3</sup>); Vc, the total crown volume; SEDJ, the surface area of

the enamel-dentine junction ( $\text{mm}^2$ );  $V_{\text{cdp}}/V_{\text{c}}$ , the percent of the crown volume that is dentine and pulp (%); 3D AET ( $=V_{\text{e}}/\text{SEDJ}$ ), the three-dimensional average enamel thickness (mm); 3D RET ( $=3\text{D AET}/V_{\text{cdp}}^{1/3} \times 100$ ), the scale-free three-dimensional relative enamel thickness (see methodological details in refs. 24,36,69). For both premolars and molars, the following parameters were also calculated: LEA, the lateral enamel surface area ( $\text{mm}^2$ )<sup>70</sup>; RA, the total root surface area ( $\text{mm}^2$ )<sup>70</sup>; CRR ( $=\text{LEA}/\text{RA} \times 100$ ), the crown-root ratio (%) (see Figure 4, Supplementary Figures 3-4 and Supplementary Tables 3,4,7,8). Because of the advanced degree of occlusal wear in Sangiran 6a, only crown-root proportions were assessed for the mandibular fourth premolar.

Intra- and interobserver accuracy tests of the measures run by two observers provided differences  $<5\%$ . Adjusted Z-score analyses<sup>71,72</sup> were performed on three tooth crown tissue proportions parameters ( $V_{\text{cdp}}/V_{\text{c}}$ , 3D AET and 3D RET) for the robust Indonesian hominid maxillary (Trinil 11620, Trinil 11621 and SMF-8898) and mandibular molars (Arjuna 9, FS-77, SMF-8855, SMF-8864, SMF-8865, SMF-8879 and SMF-10055) and were compared with extant and fossil hominid samples (Supplementary Figure 20 and Supplementary Table 8). This statistical test was also applied for the CRR parameter on the maxillary molars Trinil 11620 and Trinil 11621, on the mandibular fourth premolar of Sangiran 6a and on the molars of Sangiran 6a and Arjuna 9 preserving complete roots (Figure 4, Supplementary Figure 4 and Supplementary Table 9). This statistical method allows the comparison of unbalanced samples, which is often the case when dealing with the fossil record, using the Student's t inverse distribution following the formula:  $[(x-m)/(s \times \sqrt{1+1/n})]/(\text{Student.t.inverse}(0.05;n-1))$ , where x is the value of the variable; m is the mean of the same variable for a comparative sample; n is the size of the comparative sample; and s is the standard deviation of the comparative sample.

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**Enamel thickness distribution cartographies.** The 3D topographic mapping of site-specific enamel thickness variation was generated from the segmented enamel and crown dentine components of unworn to only slightly worn teeth and rendered using chromatic scales<sup>73-77</sup>. A rainbow chromatic scale was also used to illustrate gradual variation of enamel thickness, ranging from the thickest (in red) to the thinnest (in blue) (Figure 3).

390

**Geometric morphometric analyses.** 3D geometric morphometric (GM) analyses were conducted on the virtual surfaces of the EDJ of the maxillary molars and mandibular fourth premolar and molars. The landmarks were set along the marginal outline of the EDJ occlusal basin<sup>77</sup>. For the maxillary molars, six landmarks were set: three at the apex of the paracone, protocone and metacone dentine horns, and three at each intermediate lowest point between two horns along the dentine marginal ridges and oblique crest. For the lower fourth premolar, eight landmarks were

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placed on the EDJ surface: four at the apex of the protoconid, metaconid, entoconid and hypoconid dentine horns and four at each intermediate lowest point between two horns along the dentine marginal ridge. For the mandibular molars, seven landmarks were placed: four at the apex of the protoconid, metaconid, entoconid and hypoconid dentine horns and three at each intermediate lowest point between two horns along the dentine marginal ridge (located by translating the cervical plane occlusally), except between the two distal horns (because of the variable presence of the hypoconulid, notably in modern humans, this cusp and the distal marginal ridge were not considered). While the specimen Trinil 11620 is virtually unworn, the protocone dentine horn apex of Trinil 11621 is affected by wear. It was thus reconstructed based on the intact height and morphology of the paracone, as well as on those of the mesial dentine horns of Trinil 11620. A similar procedure was applied to reconstruct the buccal dentine horns of Sangiran 5 and Sangiran 6a (Figure 1). We also conducted GM analyses on pulp chamber shape, setting similarly located landmarks on the cavity roof of the maxillary and mandibular molars, but not on that of the lower premolar because of a lack of expression of the distal cusps on its pulp chamber. We performed generalized Procrustes analyses, principal component analyses (PCA) and between-group principal component analyses (bgPCA) based on the Procrustes shape coordinates<sup>78</sup> and using genera as groups (Figures 5-6 and Supplementary Figures 9-11 and 13-15). The robust Indonesian hominid specimens were included a posteriori in the bgPCA. The analyses were performed using the package ade4 v.1.7-6<sup>79</sup> for R v.3.4<sup>67</sup>. Allometry was tested using multiple regressions<sup>80</sup> in which the explanatory variable is the centroid size and the dependent variables are the PC and bgPC scores. In all PCA and bgPCA, the first components only show a weak allometric signal ( $0.00 < R^2 < 0.30$ ), the differences between specimens thus mostly representing shape-variation. In order to statistically assess the taxonomic affinities of the robust Indonesian hominid molars, we used a supervised classification method by Support Vector Machine (SVM). Compared with linear discriminant analyses (LDA) and quadratic discriminant analyses (QDA), SVM makes no assumptions about the data, meaning it is a very flexible and powerful method<sup>81</sup>. SVM tests were performed on the PC scores from each GM analysis on the number of PCs needed to achieve more than 95% of the total variability (i.e., 6 to 11 PCs) (Supplementary Tables 5 and 11). Leave-2-out cross-validations were run in order to validate the model (predictive accuracy) of classification for the groups including hominins (*Homo*) on the one hand and apes (*Ponginae-Lufengpithecus*) on the other. We then tested the attribution of the Indonesian fossil hominid specimens included in the GM analyses (Arjuna 9, Sangiran 5, Sangiran 6a, FS-77, SMF-8855, SMF-8864, SMF-8865, SMF-8879, SMF-8898, SMF-10055, Trinil 11620, Trinil 11621) with respect to the model.

**Data availability.** The authors declare that all data supporting the findings of this study are

432 available within the paper [and its Supplementary information files].

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## Author Contributions

The study was initiated by C.Z. during his PhD research project under the supervision of R.M. Microtomographic-based data were collected and elaborated by C.Z., A.M.B., F.D., J.K., O.K., A.T.N., K.T.N., B.S., J.-J.H., M.M.S., J.X. and R.M. Quantitative data were compiled and analysed by C.Z., J.D., O.K., L.P., M.M.S and R.M. C.Z, R.M, O.K. and J.K. wrote the manuscript with contributions from all other authors.

## Competing interests

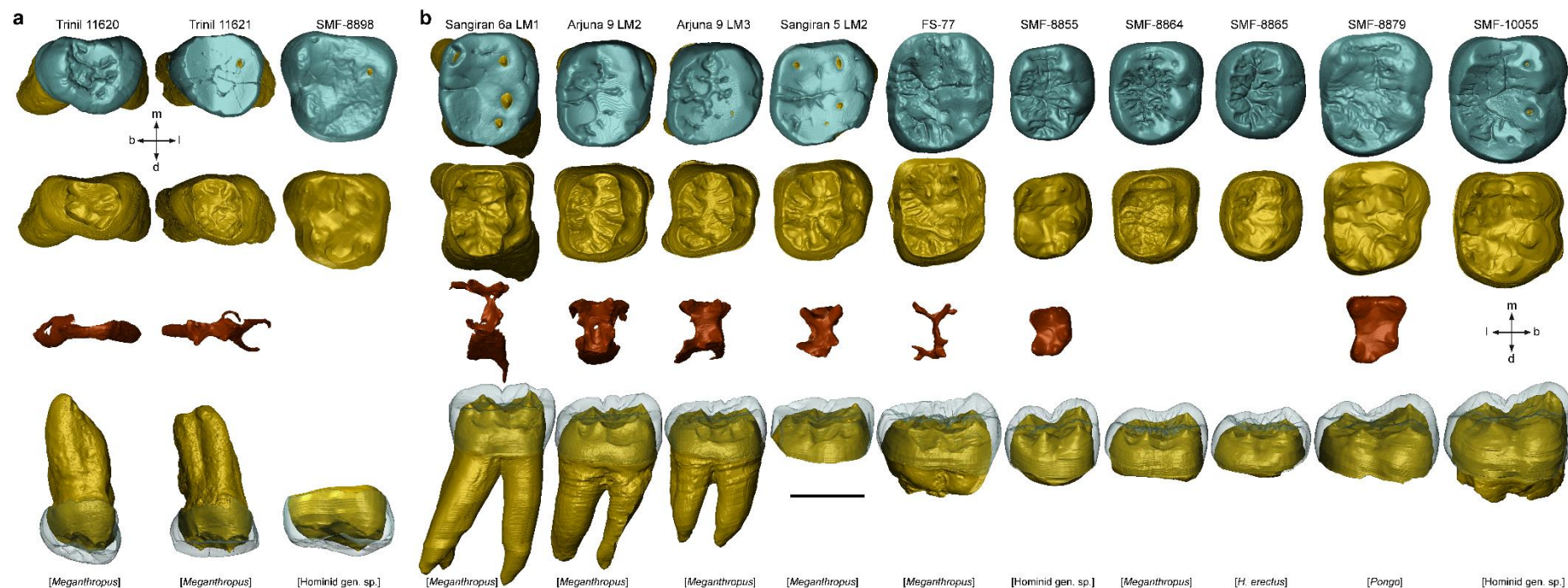
The authors declare no competing interests.

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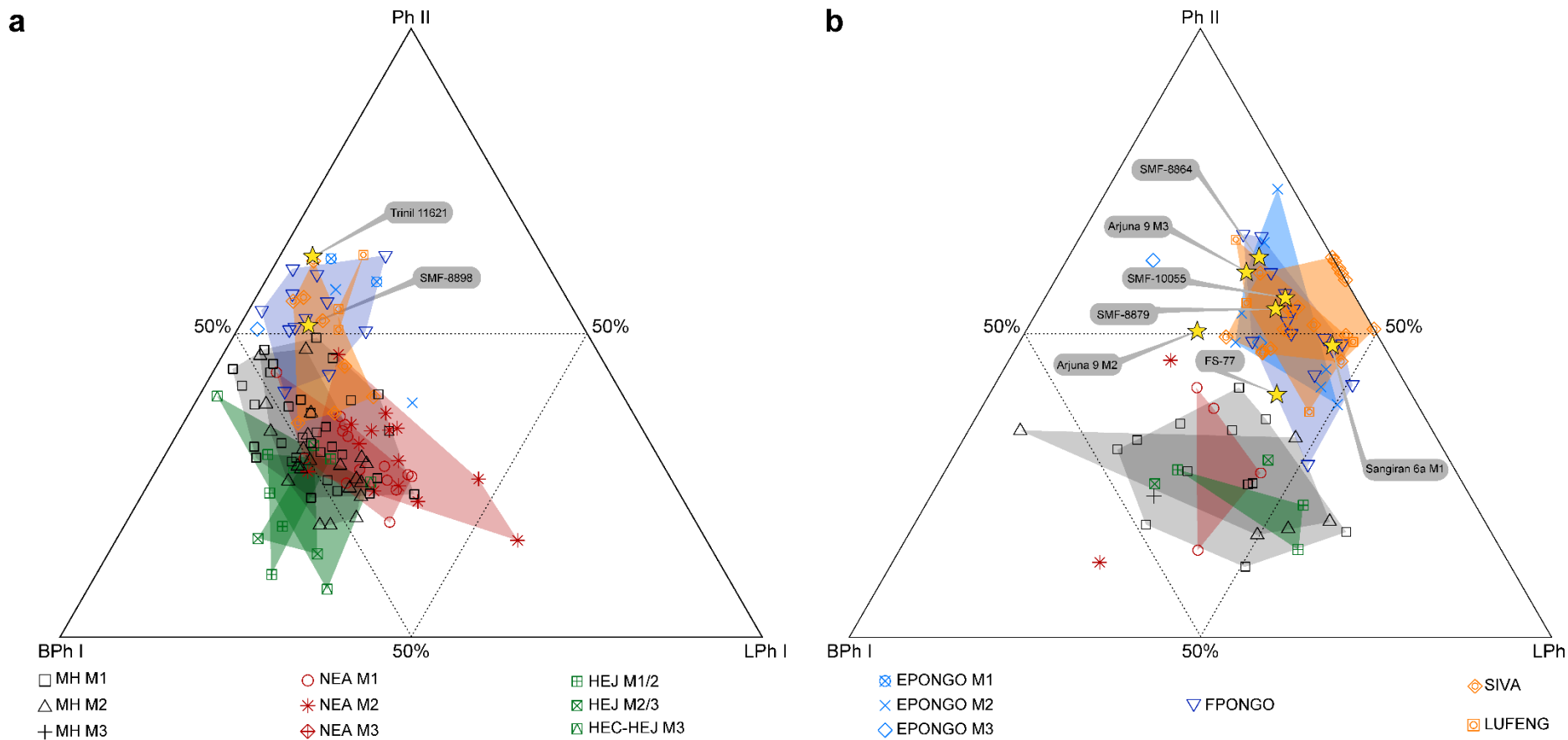
**Additional Information**

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(clement.zanolli@gmail.com).

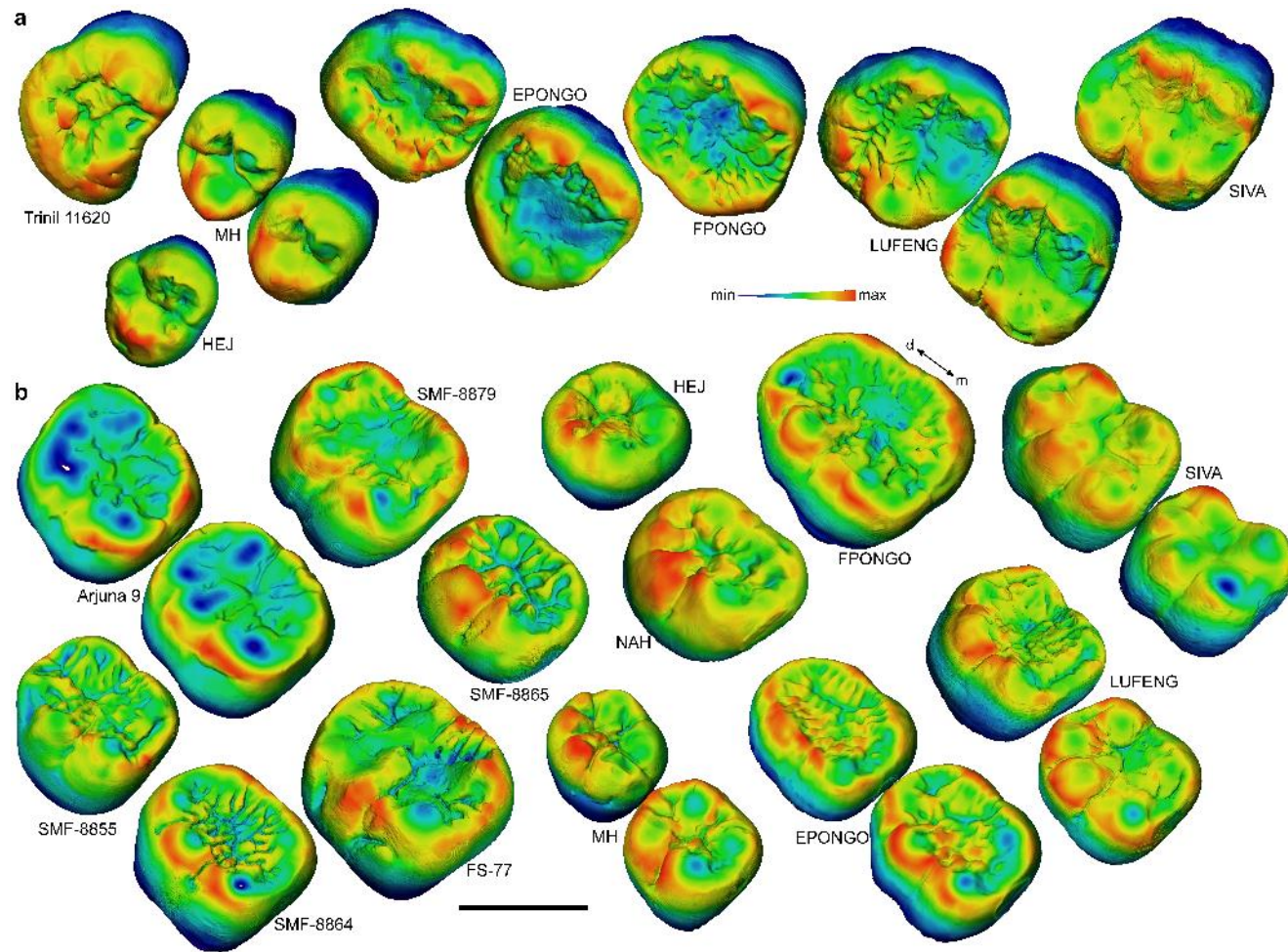




**Figure 1 | Virtual rendering of the Indonesian hominid teeth examined for taxonomic reassessment. a**, Maxillary molars. **b**, Mandibular molars (Supplementary Table 1). From the top, the rows show: the external occlusal morphology, the occlusal dentine, the occlusal pulp cavity and the EDJ with the overlain semi-transparent enamel cap in buccal view. For SMF-8879, only the crown is imaged. For Trinil 11621, Sangiran 5 and 6a, the worn dentine horn apices were reconstructed following the morphology of the other well-preserved cusps (see Methods). b, buccal; d, distal; l, lingual; m, mesial. Scale bar, 10 mm.



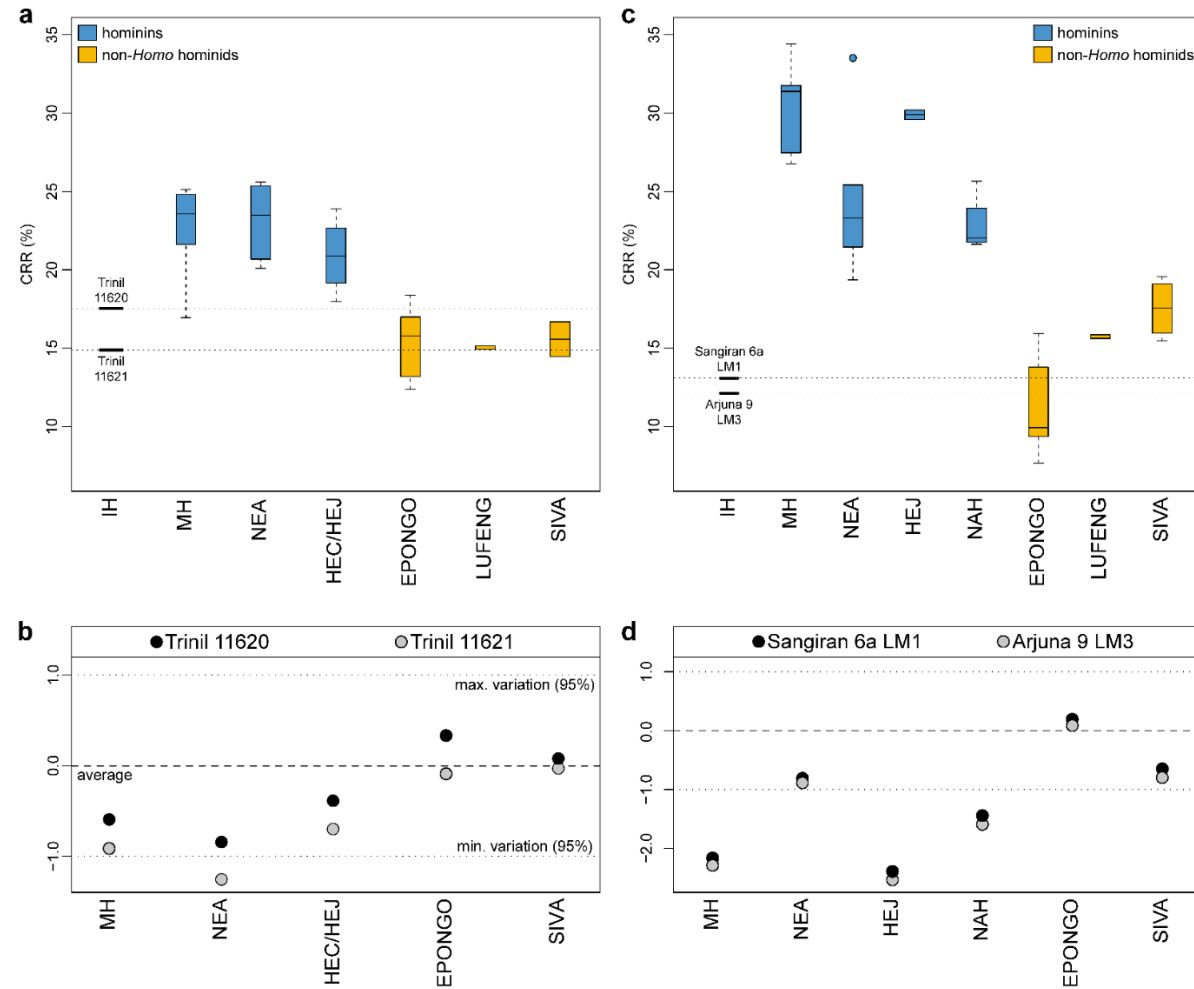
**Figure 2 | Occlusal Fingerprint Analyses. a, b**, Ternary diagram showing the proportions (in %) of relative wear areas of buccal phase I (BPh I), lingual phase I (LPh I), and phase II (Ph II) facets for the Indonesian fossil hominid maxillary (**a**) and mandibular (**b**) molars (Supplementary Table 1) compared with fossil and extant hominid specimens/samples. Each base of the triangle represents a ratio of 0% while the vertices correspond to a percentage of 100%. EPONGO, extant *Pongo*; FPONGO, fossil *Pongo*; HEC, *H. erectus* from China; HEJ, *H. erectus* from Java; LUFENG, *Lufengpithecus*; MH, modern humans; NEA, Neanderthals; SIVA, *Sivapithecus* (Supplementary Table 2).



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662 **Figure 3 | Enamel thickness cartographies.** **a**, Maxillary molars, **b**, Mandibular molars. The Indonesian hominid teeth (Supplementary Table 1)  
663 are compared with fossil and extant hominid specimens. EPONGO, extant *Pongo*; FPONGO, fossil *Pongo*; HEJ, *H. erectus* from Java;  
664 LUFENG, *Lufengpithecus*; MH, modern humans; NAH, North African late Early Pleistocene *Homo*; SIVA, *Sivapithecus* (Supplementary Table  
665 2). Irrespective of their original side, all specimens are displayed as right antimeres in a slightly oblique occlusal perspective. Scale bar, 10 mm.



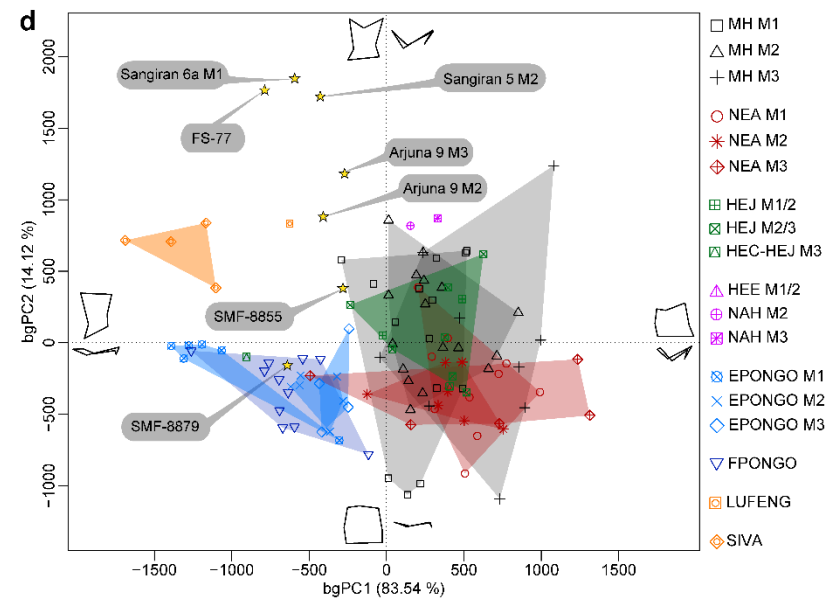
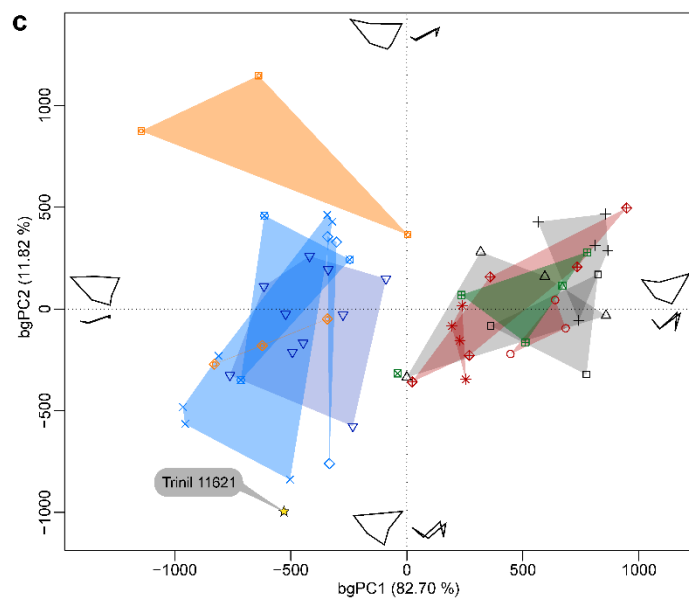
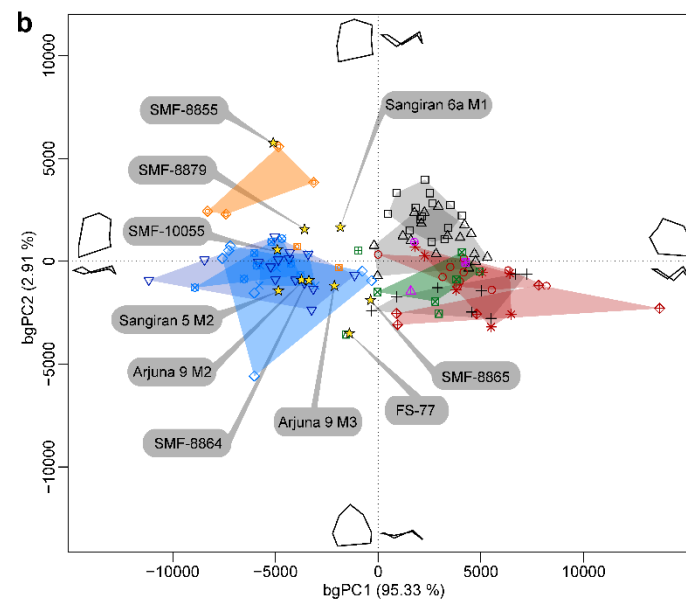
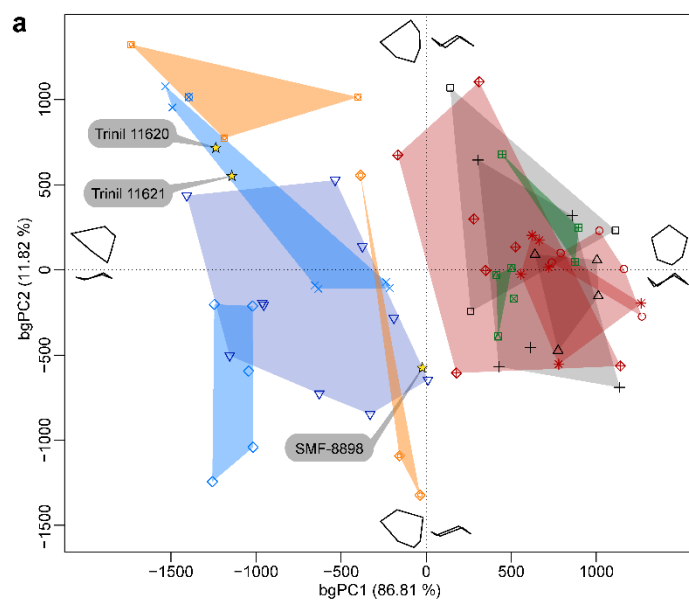


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668 **Figure 4 | Molar crown-root proportions.** **a, b,** The crown-root ratio (CRR, in %) and its adjusted Z-score statistics for the Indonesian hominid  
669 (IH) maxillary molars from Trinil compared with fossil and extant hominid specimens/samples. **c, d,** Similar comparative analyses for the  
670 mandibular molars of Sangiran 6a and Arjuna 9 (Supplementary Table 1). The boxplots show the median, the 25<sup>th</sup> and 75<sup>th</sup> percentiles (upper and  
671 lower hinges), and the range (lower and upper whiskers). EPONGO, extant *Pongo*; HEC, *H. erectus* from China; HEJ, *H. erectus* from Java;  
672 LUFENG, *Lufengpithecus*; MH, modern humans; NAH; North African late Early *Homo*; NEA, Neanderthals; SIVA, *Sivapithecus*

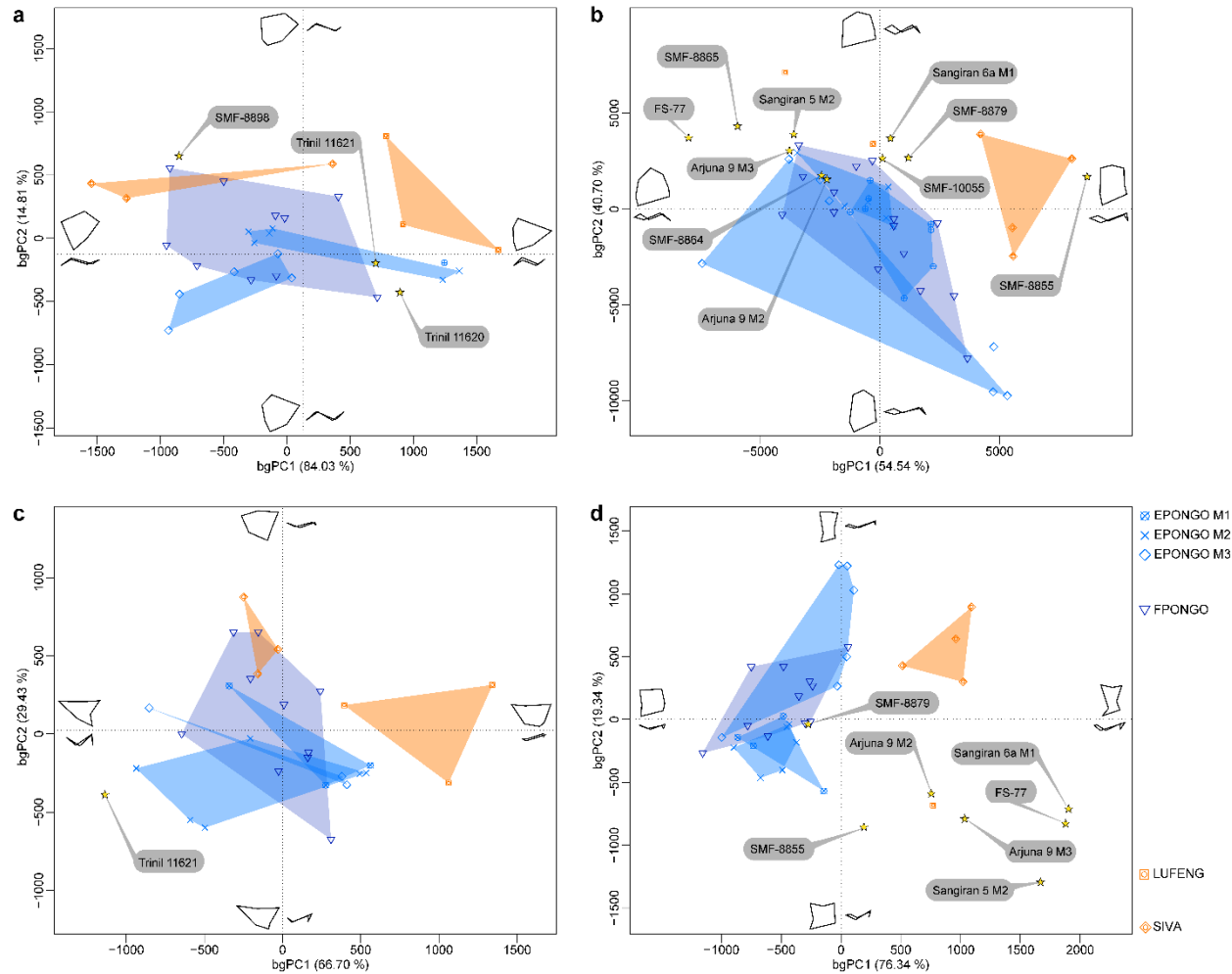
673 (Supplementary Table 2).





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**Figure 5 | Geometric morphometric analyses of the EDJ and pulp chamber. a, b,** Between-group principal component analyses (bgPCA) of the 3D landmarks Procrustes-registered shape coordinates of the Indonesian hominid maxillary (**a**) and mandibular (**b**) molar EDJs (Supplementary Table 1) compared with fossil and extant hominid specimens/samples. **c, d,** bgPCA of the underlying maxillary (**c**) and mandibular (**d**) pulp cavity. The wireframes at the end of the axes illustrate the extreme morphological variation trends along each bgPC in occlusal (mesial aspect upward) and buccal views (mesial aspect rightward). EPONGO, extant *Pongo*; FPONGO, fossil *Pongo*; HEC, *H. erectus* from China; HEE, *H. erectus/ergaster* from Eritrea; HEJ, *H. erectus* from Java; LUFENG, *Lufengpithecus*; MH, modern humans; NAH, North African late Early Pleistocene *Homo*; NEA, Neanderthals; SIVA, *Sivapithecus* (Supplementary Table 2).



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686 **Figure 6 | Geometric morphometric analyses of the EDJ and pulp chamber in non-*Homo* hominids.** **a, b,** Between-group principal  
687 component analyses (bgPCA) of the 3D landmarks Procrustes-registered shape coordinates of the Indonesian hominid maxillary (**a**) and  
688 mandibular (**b**) molar EDJs (Supplementary Table 1) compared with fossil and extant non-*Homo* hominid samples. **c, d,** bgPCA of the underlying  
689 maxillary (**c**) and mandibular (**d**) pulp cavity. The wireframes at the end of the axes illustrate the extreme morphological variation trends along  
690 each bgPC in occlusal (mesial aspect upward) and buccal views (mesial aspect rightward). EPONGO, extant *Pongo*; FPONGO, fossil *Pongo*;

691 LUFENG, *Lufengpithecus*; SIVA, *Sivapithecus* (Supplementary Table 2).  
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