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# A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar

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2 the Wezmeh 1 maxillary premolar

3

4 ABSTRACT

5

6 Wezmeh Cave, in the Kermanshah region of Central Western Zagros, Iran, produced a Late  
7 Pleistocene faunal assemblage rich in carnivorans along with a human right maxillary premolar,  
8 Wezmeh 1, an unerupted tooth from an  $8 \pm 2$  year-old individual. Uranium-series analyses of the  
9 fauna by alpha spectrometry provided age estimates between 70 and 11 ka. Crown dimensions  
10 place the tooth specimen at the upper limits of Late Pleistocene human ranges of variation. Wezmeh  
11 1 metameric position (most likely a P<sup>3</sup>) remains uncertain and only its surficial morphology has  
12 been described so far. Accordingly, we used micro-focus X-ray tomography (12.5  $\mu\text{m}$  isotropic  
13 voxel size) to reassess the metameric position and taxonomic attribution of this specimen. We  
14 investigated its endostructural features and quantified crown tissue proportions. Topographic maps  
15 of enamel thickness (ET) distribution were also generated, and semilandmark-based geometric  
16 morphometric analyses of the enamel-dentine junction (EDJ) were performed. We compared  
17 Wezmeh 1 with unworn/slightly-moderately worn P<sup>3</sup> and P<sup>4</sup> of European Neanderthals, Middle  
18 Paleolithic modern humans from Qafzeh, an Upper Paleolithic premolar, and Holocene humans.  
19 The results confirm that Wezmeh 1 represents a P<sup>3</sup>. Based on its internal conformation and  
20 especially EDJ shape, Wezmeh 1 aligns closely with Neanderthals and is distinct from the fossil  
21 and extant modern human pattern of our comparative samples. Wezmeh 1 is thus the first direct  
22 evidence of Neanderthal presence on the western margin of the Iranian Plateau.

23

24 **Keywords:** Zagros Mountains; Wezmeh Cave; Human premolar tooth; Microfocus X-ray  
25 tomography; Neanderthals  
26

27 **1. Introduction**

28 Since Coon's pioneering excavation in the late 1940s at the Middle Paleolithic site of Bisitun  
29 Cave (Coon, 1951), the Zagros Mountains of Iran and Iraq have produced a number of Late  
30 Pleistocene human remains associated with Middle and Upper Paleolithic technocultural contexts  
31 that represent the main bioanthropological source of information about the populations inhabiting  
32 the region during the oxygen isotope stages (OIS) 3–2 (for a recent chronometric assessment of  
33 some Middle and Upper Paleolithic sites of the region, see Becerra-Valdivia et al., 2017). Among  
34 the excavated sites yielding human remains, with its assemblage of at least ten Neanderthal  
35 individuals, the Shanidar Cave, Iraqi Kurdistan, has produced one of the largest sample of fossil  
36 human remains from Southwestern Asia thus far (Solecki, 1963; Trinkaus, 1983; Cowgill et al.,  
37 2007; Pomeroy et al., 2017).

38 A complex of Paleolithic sites in the Kermanshah region of Central Western Zagros, Iran,  
39 produced the second fossil human sample (Fig. 1). Among these sites, the Middle Paleolithic  
40 sequence of Bisitun Cave, located east-northeast of Kermanshah, was the first that yielded a human  
41 fossil (Coon, 1951), a right radius preserved from just distal of the radial tuberosity to the distal  
42 diaphysis. Although its dimensions overlap the upper end of the earlier Upper Paleolithic range of  
43 variation, comparisons with Neanderthal and Middle Paleolithic early modern human right radii  
44 align it predominantly with Neanderthals, but separate from Middle Paleolithic early modern  
45 humans of Southwestern Asia (Trinkaus and Biglari, 2006).

46 In the course of a reanalysis at the Field Museum of Natural History of the Upper Paleolithic  
47 collections from the Warwasi rockshelter, a site in the northern outskirts of Kermanshah, an isolated  
48 M<sub>2</sub> from a fossil modern human was recently identified in the faunal assemblage from the  
49 Baradostian levels (Tsanova, 2013).

50 Another Paleolithic site in Western Zagros that provided human remains is Gar Arjeneh, near  
51 Khoramabad, in Luristan. First excavated by Hole and Flannery (1967; for a review see Bazgir et  
52 al., 2014), its Baradostian levels have yielded a human premolar and some bone fragments  
53 (Trinkaus, 2018).

54 In the Southern Zagros, the Upper Paleolithic and Epipaleolithic layers of Eshkaft-e Gavi, near  
55 Shiraz, produced an assemblage of fragmentary dental, cranial and postcranial remains sampling a  
56 minimum of four modern human individuals bearing evidence of stone-tool cutmarks and burning  
57 (Rosenberg, 1985; Scott and Marean, 2009).

58 Finally, the catalog of human remains from Paleolithic sites of Central Western Zagros  
59 Mountains includes Wezmeh 1, an isolated maxillary premolar from Wezmeh Cave, southwest of  
60 Kermanshah. Its buccolingual crown diameter places it at the upper limits of Late Pleistocene  
61 human maxillary third (P<sup>3</sup>) and fourth premolar (P<sup>4</sup>) dimensions and above a terminal Pleistocene  
62 Natufian sample (Trinkaus et al., 2008).

63 Given uncertainties concerning the original chronostratigraphic context of Wezmeh 1 (Abdi et  
64 al., 2002; Trinkaus et al., 2008; Mashkour et al., 2009) and the difficulties of assessing its  
65 taxonomic status based on its external features (Trinkaus et al., 2008), we used micro-focus X-ray  
66 tomography ( $\mu$ CT) to reassess the metameric position and taxonomic attribution of this specimen.  
67 Using techniques of virtual imaging coupled with geometric morphometrics, we evaluated its tissue  
68 proportions, enamel thickness topographic distribution, enamel-dentine junction morphology, and  
69 pulp cavity shape. We then compared these data to samples of European Neanderthals, Near  
70 Eastern Middle Paleolithic modern humans, an Upper Paleolithic human, and Holocene humans.

71

72 *1.1. The Wezmeh Cave*

73 Wezmeh Cave is located 10 km southeast of the town of Islamabad-e Gharb (34°03'17.04" N,  
74 46°38'41.03" E), at an elevation of ca. 1430 m asl (Fig. 1). The cave, discovered in 1999 during  
75 archeological survey as a part of the Islamabad Project (director: K.A.), is in a small valley in the  
76 western foothills of the Qazivand Mountain (Fig. 2a). Its entrance (Fig. 2b) faces north and is 2 m  
77 wide and 1.2 m high. The cave is about 27 m long and has about 45 m<sup>2</sup> of floor area (Abdi et al.,  
78 2002; see Fig. 2c). In 2001, following disturbance by clandestine digging, a 3 × 3 m trench was  
79 excavated to the bedrock on the terrace immediately outside of the cave entrance, and six small test  
80 pits at 2 m intervals were dug to bedrock within the cave. These excavations yielded Holocene  
81 (Chalcolithic) archeological materials (Abdi et al., 2002). The surface collecting on the exterior  
82 slope (Fig. 2b) in 1999, 2001 and 2008 yielded an abundant faunal assemblage, particularly rich in  
83 carnivoran and ungulate remains (Trinkaus et al., 2008; Mashkour et al., 2009). The faunal list  
84 includes carnivorans present during the Late Pleistocene in Southwest Asia: Hyenidae (*Crocota*  
85 *crocota*), Canidae (*Vulpes vulpes*, *Canis lupus*), Felidae (*Panthera leo*, *Panthera pardus*,  
86 *Caracal/Lynx/Felis chaus*, *Felis silvestris*), Mustelidae (*Meles meles*, *Martes martes*, *Mustela*  
87 *putorius*), Viverridae (*Herpestes* sp.), and Ursidae (*Ursus arctos*). Artiodactyl remains include  
88 Suidae (*Sus scrofa*), Cervidae (*Cervus elaphus*), Bovidae (*Bos primigenius*, *Gazella* sp., *Capra*  
89 *aegagrus*, *Ovis orientalis*). Among smaller taxa, representatives of Lagomorpha, Rodentia,  
90 Insectivora, and Reptilia were also found. The skeletal remains were mainly collected in disturbed  
91 late Pleistocene deposits and a small number from excavated early Holocene deposits. Three  
92 carnivoran coprolites from disturbed deposits were dated by <sup>14</sup>C (Djamali et al., 2011) to the Last  
93 Glacial Period (19,228 ± 352 cal yr BP and 12,744 ± 370 cal yr BP) and to the recent Holocene  
94 (405 ± 59 cal yr BP). Several fragmented human bones and teeth were discovered among the faunal  
95 remains, including the premolar Wezmeh 1 (Fig. 2d). A few other fragmented human bones and



96 teeth were also found in the cave; one of them was dated to the early Neolithic, at around 9300 cal  
97 yr BP (Broushaki et al., 2016).

98 Because of the exceptional nature, size and taxonomic diversity of the assemblage from  
99 Wezmeh Cave and the joint presence of extinct mammal taxa including human remains (notably  
100 the large and fossilized tooth Wezmeh 1), a program of absolute dating of targeted specimens was  
101 developed. According to uranium-series analyses of the fauna by alpha spectrometry, the site was  
102 occupied by carnivorans within the interval 70–11 ka (OIS 4–2). The human premolar was directly  
103 dated by gamma spectrometry to 25–20 ka (Trinkaus et al., 2008; Mashkour et al., 2009). However,  
104 given that these dates are approximate and may be only minimum ages, Wezmeh 1 is currently  
105 assigned to either OIS 3 or early OIS 2 (Trinkaus et al., 2008).

106

## 107 **2. Materials and methods**

108 Wezmeh 1 is an unerupted right upper premolar from an  $8 \pm 2$  year-old individual (Trinkaus et  
109 al., 2008; see Fig. 2c). The specimen consists of a finely preserved crown and of ca. 7 mm of  
110 growing root (developmental stage between  $R_{1/4}$  and  $R_{1/2}$  following Moorrees et al., 1963), which  
111 is largely complete up to its developing edge despite some local chipping.

112 The specimen was imaged at the University of Poitiers, France, using an EasyTom XL Duo  
113 device (RX-Solutions) set at the PLATINA platform of the IC2MP laboratory. A sealed  
114 Hamamatsu microfocus X-ray source (small focal spot mode) was used, coupled to a Varian  
115 PaxScan 2520DX imager. The acquisition parameters are: 60kV voltage; 166  $\mu$ A current; a 0.35  
116 mm Cu filter; 1280 projections, 4 frames/second; averaging of 13 frames/projection; anti-ring shift  
117 procedure; source-to-detector distance and source-to-object distance of 416 mm and 41 mm,  
118 respectively, and reconstructed with a voxel size of 12.5  $\mu$ m. Reconstruction of the data was done  
119 with the XAct software (RX-solutions) with a filtered back projection algorithm (Felkamp method

120 for cone beam geometry with a Tukey filter) and correction of beam hardening artefacts through  
121 linearization with a polynomial function. A semiautomatic threshold-based segmentation was  
122 conducted using Avizo v.8.0 (FEI Visualization Sciences Group, Hillsboro), following an  
123 adaptation of the half-maximum height method (Spoor et al., 1993; Fajardo et al., 2002; Coleman  
124 and Colbert, 2007). The crown was virtually isolated from the roots (Olejniczak et al., 2008) and  
125 3D surface models of the dental tissues were generated using a constrained smoothing algorithm  
126 (Kupczik and Hublin, 2010).

127 For assessing tissue proportions, the following variables were measured on the 2D buccolingual  
128 virtual tooth section (Feeney et al., 2010) and calculated in 3D (see Kono, 2004; Macchiarelli et  
129 al., 2006; Olejniczak et al., 2008; Bayle et al., 2010; Smith et al., 2012; Skinner et al., 2015): enamel  
130 area (c; mm<sup>2</sup>); coronal dentine and pulp area (b; mm<sup>2</sup>); total crown area (a; mm<sup>2</sup>); percentage of  
131 crown area that is dentine and pulp (b/a; %); enamel-dentine junction (EDJ) length (e; mm);  
132 bicervical diameter (BCD; mm); enamel volume (V<sub>e</sub>; mm<sup>3</sup>); coronal dentine and pulp volume  
133 (V<sub>cdp</sub>; mm<sup>3</sup>); total crown volume (V<sub>c</sub>; mm<sup>3</sup>); percentage of crown volume that is dentine and pulp  
134 (V<sub>cdp</sub>/V<sub>c</sub>; %); EDJ surface area (SEDJ; mm<sup>2</sup>). Enamel thickness was assessed by calculating the  
135 following parameters (Martin, 1985; Olejniczak et al., 2008): 2D average enamel thickness (2D  
136 AET = c/e; mm) and 2D relative enamel thickness (2D RET = 2D AET\*100/(b<sup>1/2</sup>); scale-free); 3D  
137 average enamel thickness (3D AET = V<sub>e</sub>/SEDJ; mm) and 3D relative enamel thickness (3D RET  
138 = 3D AET\*100/(V<sub>cdp</sub><sup>1/3</sup>); scale-free).

139 Three-dimensional maps of topographic enamel thickness distribution were created with the  
140 segmented enamel and crown dentine components (Macchiarelli et al., 2008; Bayle et al., 2011;  
141 Zanolli et al., 2018a, b), where differences in enamel distribution are rendered by a thickness-  
142 related pseudocolor scale ranging from dark blue (thinner) to red (thicker). This method maps  
143 topographic thickness variation at the outer enamel surface and facilitates the site-specific and

144 synthetic comparative assessments of this feature. The topographic variation of standardized  
145 enamel thickness was measured using MPSAK v2.9 (available in Dean and Wood, 2003) in the  
146 lingual and buccal aspects of the virtual buccolingual section (Macchiarelli et al., 2007; Le Luyer  
147 and Bayle, 2017), and the values were calibrated with respect to a bicervical diameter of 6 mm  
148 (Schwartz, 2000; Mazurier et al., 2003; Le Luyer, 2016).

149 Geometric morphometric (GM) analyses of EDJ were performed on the virtual surface by  
150 placing two landmarks at the apices of the paracone and protocone dentine horns and 71  
151 semilandmarks along the marginal ridges (33 on the mesial marginal ridge and 38 on the distal  
152 one). We performed the generalized Procrustes analyses, followed by between-group principal  
153 component analyses (bgPCA) and Jackknife cross-validated canonical variate analyses (CVA)  
154 based on the first 9 (for the separate P<sup>3</sup> and P<sup>4</sup> samples) to 12 (for the combined P<sup>3</sup>–P<sup>4</sup> samples)  
155 first principal components explaining ~90% of the total variance (Mitteroecker and Bookstein,  
156 2011; Krenn et al., 2019). Wezmeh 1 was included a posteriori in the analyses. Multivariate  
157 analyses were performed using the packages ade4 v.1.7-6 (Dray and Dufour, 2007) and Morpho v.  
158 2.7 (Schlager, 2019) for R v.3.6 (R Development Core Team, 2019). Allometry was tested using  
159 the coefficient of determination (R<sup>2</sup>) of a multiple regression (Bookstein, 1991) in which the  
160 explicative variable is the centroid size and the dependent variables are the bgPC scores (see also  
161 Mitteroecker et al., 2013).

162 Because of the uncertainty of the Wezmeh 1 metamer position, the comparative analyses used  
163 the  $\mu$ CT record of selected unworn/slightly-moderately worn crowns (wear stage  $\leq 2$  following  
164 Smith, 1984) of both P<sup>3</sup> and P<sup>4</sup> representing: European Neanderthals (NEA) from Krapina, Sima  
165 de las Palomas, and Spy (Bayle et al., 2017, In press; NESPOS Database, 2019); Middle Paleolithic  
166 modern humans (MPMH) from Qafzeh (Qafzeh 10 and 15 [ESRF, 2019] and Qafzeh 4 [original  
167 data]), and Holocene humans (HH) of Western European origin (Le Luyer, 2016 and original data).

168 Due to the limited  $\mu$ CT-based comparative evidence directly available to us or exploitable from  
169 the literature, the fossil modern human sample (MPMH) is restricted to the material from the site  
170 of Qafzeh, thus resulting in a temporal and geographic gap between the fossil and recent  
171 comparative samples. However, we also exploited the endostructural signal from an unpublished  
172 late Upper Paleolithic (Magdalenian) P<sup>3</sup> from the French site of La Piscine (see Discussion and  
173 conclusions), suggesting that this heterogeneous sample is still representative of the fossil modern  
174 human variation. Information on the three comparative samples (including the variable number of  
175 cases used in the different 2-3D analyses) is reported in Table 1, while Table 2 provides the NEA  
176 and MPMH samples. The sample of Holocene premolars used in this study, consisting of  
177 archaeological and recent specimens from Western Europe, is provided in Supplementary Online  
178 Material (SOM) Table S1.

179 In a few cases, local virtual integrations of the outer enamel surface and/or of the dentine horn  
180 tip contour were made preliminary to the quantitative analyses on 2D virtual sections and 3D  
181 models, respectively. Within each sample, integration of the removed enamel was based on the  
182 preserved morphology of the unworn crowns as revealed by their serial buccolingual cross-sections  
183 (Smith et al., 2012).

184 Adjusted Z-scores (Maureille et al., 2001; Sclan et al., 2012) were computed to compare the  
185 3D dental tissue proportions and enamel thickness values of Wezmeh 1 to the means and standard  
186 deviations of the comparative groups. This method allows the comparison of unbalanced samples,  
187 which is often the case when dealing with the fossil record, by using the Student's t inverse  
188 distribution, where the +1.0 to -1.0 interval comprises 95% of the variation in the reference sample.  
189 Plots of the common logarithm (log) of 2D AET against the log of coronal dentine and pulp area  
190 (b) were used to illustrate the relationship between AET and tooth size (Skinner et al., 2015) and  
191 to show the placement of Wezmeh 1 compared to Neanderthals, MPMH and Holocene humans.

192 For the GM assessment of the EDJ morphology, Wezmeh 1 was projected a posteriori in the bgPCA  
193 analysis.

194

### 195 **3. Results**

196 The virtual reconstructions of the outer enamel surface (OES) and of the internal aspect of  
197 Wezmeh 1 in different views are comparatively shown in Figure 3. The specimen exhibits excellent  
198 preservation of its outer and inner morphology. It also lacks sedimentary infill and displays high  
199 enamel-dentine contrast in all  $\mu$ CT-based reconstructions.

200 On the lateral and occlusal aspects, the undamaged and unworn OES shows several small and  
201 shallow pits representing minor developmental enamel defects. However, these hypoplastic defects  
202 are not visible on the EDJ (Fig. 3). Otherwise, the OES and the dentine surface morphology match  
203 perfectly. Specifically, in occlusal view, they share: a low elevation of the buccal segment of the  
204 mesial marginal ridge, with a short crest running into the mesial fovea; two buccal and two lingual  
205 essential segments of the bifurcated transverse crest; a short distal crest running from the lingual  
206 cusp; and a small cusp-like elevation visible on the lingual part of the distal marginal ridge (Fig.  
207 3).

208 Near the cervix, a shallow subcircular enamel depression is noticeable on the mesiobuccal  
209 aspect of the paracone. The virtual rendering of the coronal dentine shows that its imprint is also  
210 slightly expressed beneath the enamel (Fig. 3). Approximately 2.0 mm from the cervix, this feature  
211 also extends to the root dentine (Trinkaus et al., 2008), where it appears as a larger and deeper  
212 depression (Fig. 3; SOM Fig. S1). Apparently, it does not affect the pulp morphology, the inner  
213 dentine wall being straight and flat at the level of the depression, even if the dentine at this spot is  
214 thinner than measured at other points of the growing root (SOM Fig. S1).

215 2D and 3D measures of crown tissue proportions and enamel thickness in Wezmeh 1 are  
216 reported in Tables 3 and 4, respectively, together with the comparative estimates for each premolar  
217 type of the NEA, MPMH, and HH samples used in this study.

218 For a large majority of the measured/calculated parameters, the values (absolute and  
219 proportions) displayed by the P<sup>3</sup> and P<sup>4</sup> crowns overlap within each sample, or are close. A greater  
220 variation characterizes the MPMH sample, especially for b/a, 2D RET, Vcdp/Vc, SEDJ, and 3D  
221 RET. Whatever its metameric position, Wezmeh 1 shows absolutely higher values for most of the  
222 2D and 3D tissue proportion parameters. It fits better with the Neanderthal P<sup>3</sup> and, to a slightly  
223 lesser extent, the Neanderthal P<sup>4</sup>. The variables that align the Iranian specimen and the  
224 Neanderthals and best discriminate both from the fossil and recent modern human figures are: c, b,  
225 e, Ve, Vcdp, and SEDJ (Tables 3 and 4). For these parameters, Wezmeh 1 is clearly apart from the  
226 HH condition and approaches the NEA pattern, while the MPMH tend to occupy an intermediate  
227 position between the HH and NEA values. However, no substantial differences exist between  
228 Wezmeh 1 and the comparative samples for b/a and Vcdp/Vc, notably among the P<sup>3</sup>. Whatever the  
229 extent of the differences shown in Tables 3 and 4, all of the comparisons with the MPMH and HH  
230 representatives show that the whole inner structural signature of Wezmeh 1 better fits those  
231 expressed by the P<sup>3</sup>, not the P<sup>4</sup>.

232 A closer affinity of Wezmeh 1 with the Neanderthals is revealed by the adjusted Z-scores of the  
233 absolute estimates of nearly all 2D and 3D variables (SOM Figs. S2 and S3). However, this is not  
234 the case for the enamel thickness. In fact, for both 2D and 3D AET, Wezmeh 1 is compatible with  
235 the HH values. Nonetheless, for both size-free 2D and 3D RET indices, the Iranian tooth crown is  
236 slightly closer to the NEA estimates (Tables 3 and 4). Additionally, the affinity of Wezmeh 1 with  
237 NEA is shown by the bivariate graph of log 2D AET against log b (Fig. 4), which also includes

238 two specimens from Qafzeh and where Wezmeh 1 plots among the NEA specimens and apart from  
239 the HH by having larger coronal dentine and pulp areas.

240 The cartographies of enamel thickness distribution in Wezmeh 1 and in representatives of the  
241 comparative samples (NEA, MPMH and HH) are shown in Figures 5 and 6, separately for the P<sup>3</sup>  
242 and P<sup>4</sup> crowns imaged in different projections. As a whole, they reveal only minor differences  
243 among the investigated specimens, including between NEA and HH. At least in the limited  
244 comparative assemblage of premolar crowns available, it appears that the relatively thicker Qafzeh  
245 4 specimen, similar to the HH P<sup>3</sup>, exhibits thicker enamel distributed over the occlusal basin and  
246 at the cusp apices, especially the protocone, whereas in the relatively thinner Qafzeh 10, thicker  
247 enamel is mostly localized on the protocone, as in NEA. Nonetheless, Wezmeh 1 shares with  
248 Qafzeh 4 and NEA P<sup>3</sup>, a relatively thicker enamel on the buccal aspect.

249 A more detailed picture illustrating topographic enamel thickness variation is shown by the site-  
250 specific standardized values comparatively assessed from the cervix towards the apex across the  
251 entire lingual (protocone) and buccal (paracone) mesiodistal virtual sections, respectively (SOM  
252 Figs. S4 and S5). The enamel distribution in Wezmeh 1 follows the NEA pattern revealed by the  
253 pooled P<sup>3</sup> and P<sup>4</sup>, especially for the lingual cross-section (SOM Fig. S4). Conversely, for the buccal  
254 section, its trajectory is less distinct, including when compared to the MPMH and the HH pattern.  
255 In this respect, Wezmeh 1's profile follows a modern-like trajectory along approximately the first  
256 half of its buccal section and a Neanderthal-like trajectory nearing the paracone (SOM Fig. S5).

257 The results of the bgPCA of the geometric morphometric analysis of the EDJ in the shape space  
258 of the P<sup>3</sup> and P<sup>4</sup> are displayed in Fig. 7. The first two components, which account for 88.6% of the  
259 total variation (59.8% for bgPC1 and 31.5% for bgPC2), show a weak allometric signal ( $p < 0.05$ ;  
260  $R^2 = 0.34$ ) and no size-dependent shape variation ( $p > 0.05$ ;  $R^2 = 0.06$ ). The GM analysis combining  
261 P<sup>3</sup> and P<sup>4</sup> thus mostly represents shape variation. By displaying a relatively symmetrical outline of

262 the occlusal basin and a large distal part of the occlusal basin, Wezmeh 1 falls within the NEA P<sup>3</sup>  
263 variation space. It is also relatively close to the NEA P<sup>4</sup> shape, a space characterized by a slightly  
264 more reduced talon, as well as by an acute mesiobuccal angle of the occlusal basin. In this context,  
265 the Iranian tooth differs from the upper premolars from Qafzeh by having a more symmetrical  
266 outline of the EDJ, and is also well separated from the HH P<sup>3</sup> and P<sup>4</sup> by having a more mesiodistally  
267 extended talon and a more marked distolingual extension of the latter. These results are confirmed  
268 by the CVA, in which the predictive accuracy between human groups is robust (100% correct  
269 classification for NEA, 83.3% for MPMH, and 96.3% for HH), and the Iranian specimen is  
270 classified with 100% posterior probability as NEA. We also ran a CVA to assess metameric  
271 variation in the comparative sample (predictive accuracy: 88.5% and 87.5% of correct  
272 classification for P<sup>3</sup> and P<sup>4</sup>, respectively). This analysis indicates a 100% posterior probability of  
273 Wezmeh 1 representing a P<sup>3</sup>.

274 We also analyzed Wezmeh 1 separately with the P<sup>3</sup> (SOM Fig. S6) and the P<sup>4</sup> (SOM Fig. S7).  
275 Again, only a weak allometric signal is found along the bgPC1 ( $R^2 = 0.48$  and  $0.34$  for the P<sup>3</sup> and  
276 the P<sup>4</sup> analyses, respectively), while no allometry is recorded along the bgPC2 for both analyses ( $p$   
277  $> 0.05$ ;  $R^2 < 0.03$ ). When compared with the P<sup>3</sup>, Wezmeh 1 is much closer to the NEA condition  
278 than to the MPMH and HH groups. More specifically, the Iranian premolar exhibits the typical  
279 Neanderthal square outline of the occlusal basin, whereas the other groups have a more ovoid  
280 pattern (SOM Fig. S6). Compared with the P<sup>4</sup> (SOM Fig. S7), Wezmeh 1 again fits the NEA shape  
281 and sets apart from both the three MPMH (displaying a more rounded outline of the occlusal basin)  
282 and the HH sample (characterized by a shorter talon and no angulation of the distolingual corner).

283

#### 284 **4. Discussion and conclusions**



285 A number of sites in Central and Southern Zagros have yielded variably rich Mousterian lithic  
286 assemblages (e.g., Biglari, 2007; Otte et al., 2009; Scott and Marean, 2009; Bazgir et al., 2014,  
287 2017; Shidrang et al., 2016; Becerra-Valdivia et al., 2017; Heydari-Guran and Ghasidian, 2017).  
288 Within an approximate 30 km radius of Wezmeh Cave, 13 Middle Paleolithic sites have been  
289 recorded; among them, the nearest sites (cluster of Cham Souran and Cham Barzeh) are located  
290 about 10 km to the northwest (Biglari and Abdi, 1999). Surface collected lithic artifacts from these  
291 cave, rockshelter and open-air sites generally resemble excavated Zagros Mousterian assemblages  
292 from sites situated in the neighboring intermountain plain of Kermanshah. However, the physical  
293 record of their producers remains elusive (review in Trinkaus, 2018).

294 The first description of the isolated immature human upper premolar Wezmeh 1 suggested it  
295 more likely represents a P<sup>3</sup> (Trinkaus et al., 2008). Our comparative observations combining outer  
296 morphology and inner structural organization corroborate this attribution. Importantly, the new  
297 analyses add relevant information to more confidently assess the taxonomic status of this specimen.  
298 Even if the possibility that Wezmeh 1 "could derive from an earlier OIS 3 Neandertal" (Trinkaus  
299 et al., 2008: 376) was evoked because of its large buccolingual crown diameter, based solely on its  
300 outer crown characteristics, its attribution to a late archaic or an early modern human was unclear  
301 (Trinkaus et al., 2008). However, our analyses of the internal structure confirm that Wezmeh 1  
302 belongs to a Neanderthal.

303 Because of its discriminant value, quantitative information on the inner tooth structural  
304 organization and tissue proportions is increasingly used in paleoanthropological research as a  
305 reliable tool of taxonomic significance, including among species within the genus *Homo* (e.g.,  
306 Macchiarelli et al., 2006; Olejniczak et al., 2008; Skinner et al., 2008; Smith et al., 2009; Bayle et  
307 al., 2010; Benazzi et al., 2011; Liu et al., 2013; Crevecoeur et al., 2014; Martín-Torres et al.,

308 2014; Weber et al., 2016; Hublin et al., 2017; Martin et al., 2017; Martínez de Pinillos et al., 2017;  
309 Pan et al., 2017; Hershkovitz et al., 2018; Xing et al., 2018; Zanolli et al., 2018a).

310 Our  $\mu$ CT-based analyses indicate that the Iranian premolar most likely derives from a  
311 Neanderthal-like individual to a degree of reliability comparable to that usually accepted for  
312 discriminating Neanderthal from extant and fossil modern human molar teeth (e.g., Olejniczak et  
313 al., 2008; Smith et al., 2012; Weber et al., 2016; Bayle et al., 2017; Martin et al., 2017; Zanolli et  
314 al., 2018a). In this context, the results of the 3D geometric morphometric analysis of the EDJ  
315 conformation are of special value, as EDJ topography approximates the inner enamel epithelium  
316 of the developing tooth and provides useful information about taxon-specific processes underlying  
317 crown growth (e.g., Skinner et al., 2008; Crevecoeur et al., 2014; Zanolli, 2015; Martin et al., 2017;  
318 Zanolli et al., 2019).

319 Studies of the outer crown morphology indicate that there are no particular non-metric features  
320 enabling to diagnostically attribute an isolated upper premolar to a Neanderthal or to an early  
321 modern human (e.g., Bailey, 2006; Bailey and Hublin, 2013). However, the bifurcated essential  
322 crest slightly visible in Wezmeh 1, notably at the EDJ level, is generally present in Neanderthals  
323 but, to the best of our knowledge, has not been recorded in early modern humans thus far (Bailey,  
324 2006), evidence that strengthens our endostructurally-based attribution of Wezmeh 1 to a  
325 Neanderthal individual.

326 Besides the limited size of the available comparative fossil samples, information currently is  
327 rare for coronal tissue proportions and enamel thickness variation of upper premolar crowns,  
328 including in recent humans (Feeney et al., 2010; Le Luyer, 2016). Importantly for this study, no  
329 data suitable for direct comparisons have been published so far on tooth tissue proportions of fossil  
330 modern human P<sup>3</sup>. The  $\mu$ CT record of an unpublished right P<sup>3</sup> (specimen H3) from the  
331 Magdalenian (OIS 2) site of La Piscine, in Montmorillon, Central-Western France (Henry-

332 Gambier, 2010; Delage, 2011), allowed us to use this otherwise worn tooth (stage 4) for the GM-  
333 based comparative analysis of the EDJ. Following a virtual integration of its slightly eroded  
334 protocone (SOM Fig. S8a)—according to the geometric method described in Zanolli et al.  
335 (2018a)—the bgPCA results (SOM Fig. S8b) show that this latest Pleistocene tooth plots together  
336 with the MPMH P<sup>3</sup>, distant from Wezmeh 1.

337 In our analyses, a Neanderthal vs. modern human-like signature is less distinct for the enamel  
338 thickness, whatever the parameter used. The absolute enamel volume of Neanderthal upper and  
339 lower molars is comparable to that of modern humans, but in Neanderthals it is deposited over a  
340 larger volume of coronal dentine, thus resulting in lower average and relative enamel thickness  
341 values (Olejniczak et al., 2008). However, the possibility exists that enamel thickness in upper  
342 premolars is not as powerful to discriminate between Neanderthals and modern humans. This  
343 hypothesis should be tested in larger samples. Unfortunately, no directly comparable quantitative  
344 information on the inner tooth structural organization and topographic enamel thickness variation  
345 is available so far on Neanderthal premolars from Southeast Asia.

346 An additional limiting aspect in our study is the fact that Wezmeh 1 is from a still growing  
347 individual bearing a modest portion of radicular dentine (Trinkaus et al., 2008). This prevents the  
348 possibility of virtually unrolling and projecting it into a standardized morphometric map for  
349 assessing its topographic thickness variation, a feature which tends to discriminate Neanderthal  
350 from non-Neanderthal teeth (e.g., Bayle et al., 2010; Bondioli et al., 2010; Macchiarelli et al., 2013;  
351 Zanolli et al., 2014, 2018a).

352 As first noted by Trinkaus et al. (2008), an interesting feature in Wezmeh 1 is represented by a  
353 distinct depression located on its mesial root aspect. In this study we investigated its occurrence in  
354 two comparative P<sup>3</sup> and P<sup>4</sup> samples representing 20 Western European Neanderthals (Rougier,  
355 2003; Toussaint, 2014; NESPOS Database, 2019) and 48 Western European Holocene humans (Le

356 Luyer, 2016 and original data; SOM Table S2). According to our record, a similar and  
357 topographically homologous feature occurs more frequently on the P<sup>3</sup>, either in Neanderthals (7/12)  
358 or extant humans (7/28), whereas it is rarely present on the P<sup>4</sup> (1/8 and 0/20, respectively).  
359 Additionally, at least among the samples available to us, this radicular depression is more frequent  
360 in European Neanderthals (8/18) than in Holocene humans (7/48). However, further studies are  
361 necessary to elucidate its nature and significance as a possible taxon/population-related feature.

362 Along with the Shanidar remains from further north, the Wezmeh 1 maxillary premolar, from  
363 the Central Western Zagros of Iran, provides solid evidence for the presence of Neanderthals  
364 through the Zagros Mountains in the Late Pleistocene. Although undated other than to at least OIS  
365 3, or OIS 2 (Trinkaus et al., 2008), its morphological affinities and the presence of a Late  
366 Pleistocene faunal assemblage from Wezmeh Cave (Mashkour et al., 2009) strongly imply that it  
367 derives from the earlier OIS 3 and therefore relates to the increasingly documented Middle  
368 Paleolithic of the region. As such, it adds to the limited evidence for Neanderthals in Southwest  
369 Asia east of the Mediterranean region.

370

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## Figure captions

**Figure 1.** a) Map of Paleolithic sites having yielded human remains in the Zagros Mountains across Iraq and Iran. b) The enlarged Iranian area showing the location of Wezmeh Cave.

**Figure 2.** a) The Wezmeh cave (white arrow) at the western foothills of the Qazivand Mountain, Kermanshah region of Central Western Zagros. b) Entrance of the cave and original location of the Late Pleistocene skeletal remains redeposited at the front of the cave mouth. c) Plan of the Wezmeh Cave with the areas of excavation (after Abdi et al., 2002); the area of the clandestine excavation is indicated at the top (black arrow). d) The Wezmeh 1 maxillary premolar in mesial (M), distal (D), buccal (B), lingual (L) and occlusal views (after Trinkaus et al., 2008).

**Figure 3.**  $\mu$ CT-based 3D virtual rendering of Wezmeh 1 a) external morphology; b) the specimen imaged with the virtually removed enamel cap revealing the morphology of the coronal dentine. The correspondence between the outer enamel and the inner dentine morphology can be appreciated in occlusal view for (1) the elevation of the mesial marginal ridge attached to a low short crest running into the mesial fovea and (2) a cusp-like relief on the distal marginal ridge. The arrows show the segments of the bifurcated transverse crest and the asterisks indicate the position of small pits representing minor enamel defects.

**Figure 4.** Plot of log 2D average enamel thickness (2D AET) against log coronal dentine and pulp area (b) for Wezmeh 1 and the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic



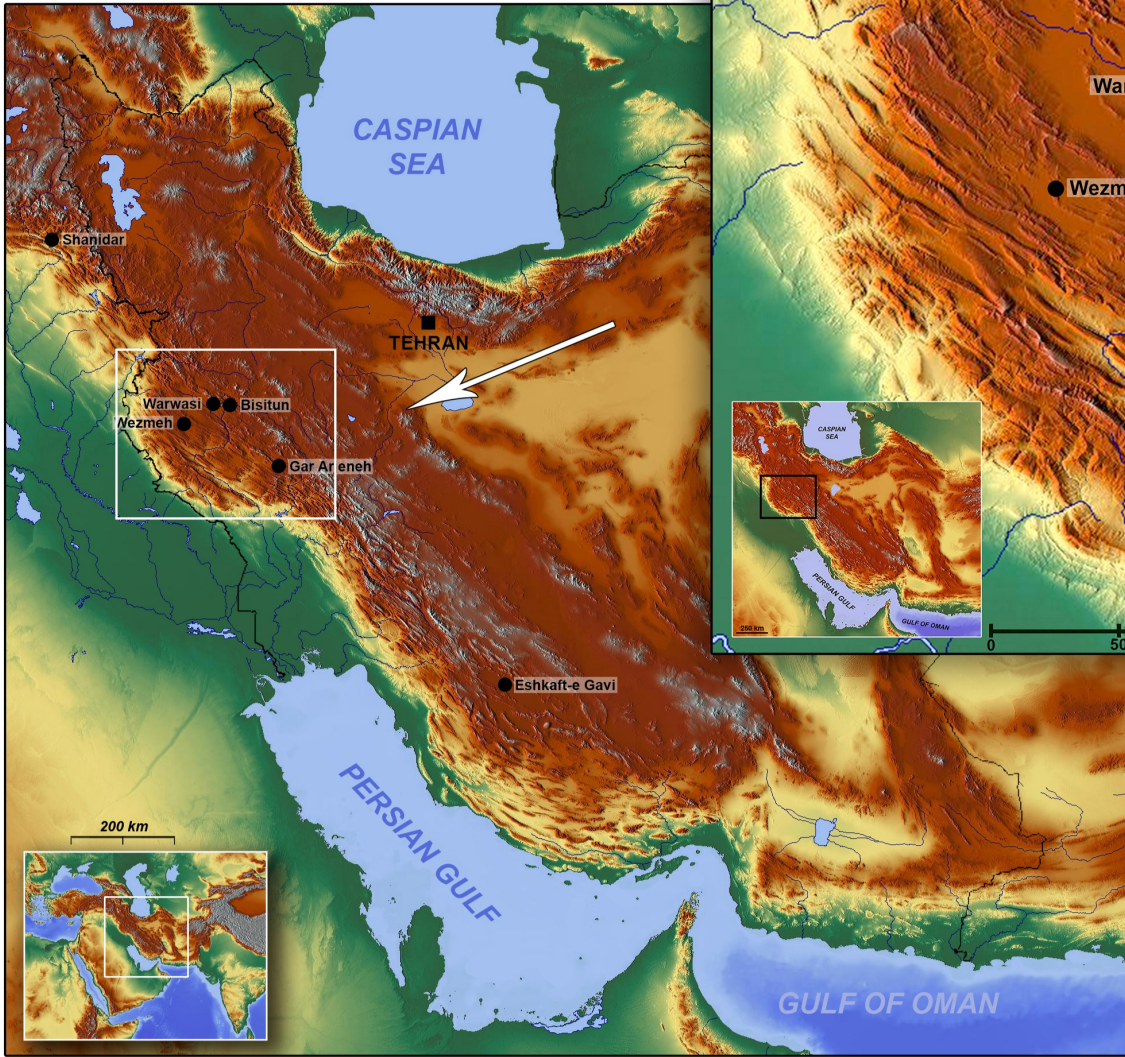
modern human (MPMH), and Western European Holocene human (HH) samples. See Tables 1 and 2 and SOM Table S1 for sample composition.

**Figure 5.** Enamel thickness cartographies of Wezmeh 1 in occlusal (O), buccal (B), mesial (M), lingual (L), and distal (D) views compared with selected P<sup>3</sup> from the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. Topographic thickness variation is rendered by a pseudocolor scale ranging from thinner dark blue to thicker red; isolated spots correspond to wear-related enamel removal. Independently from their original side, all crowns are shown as right.

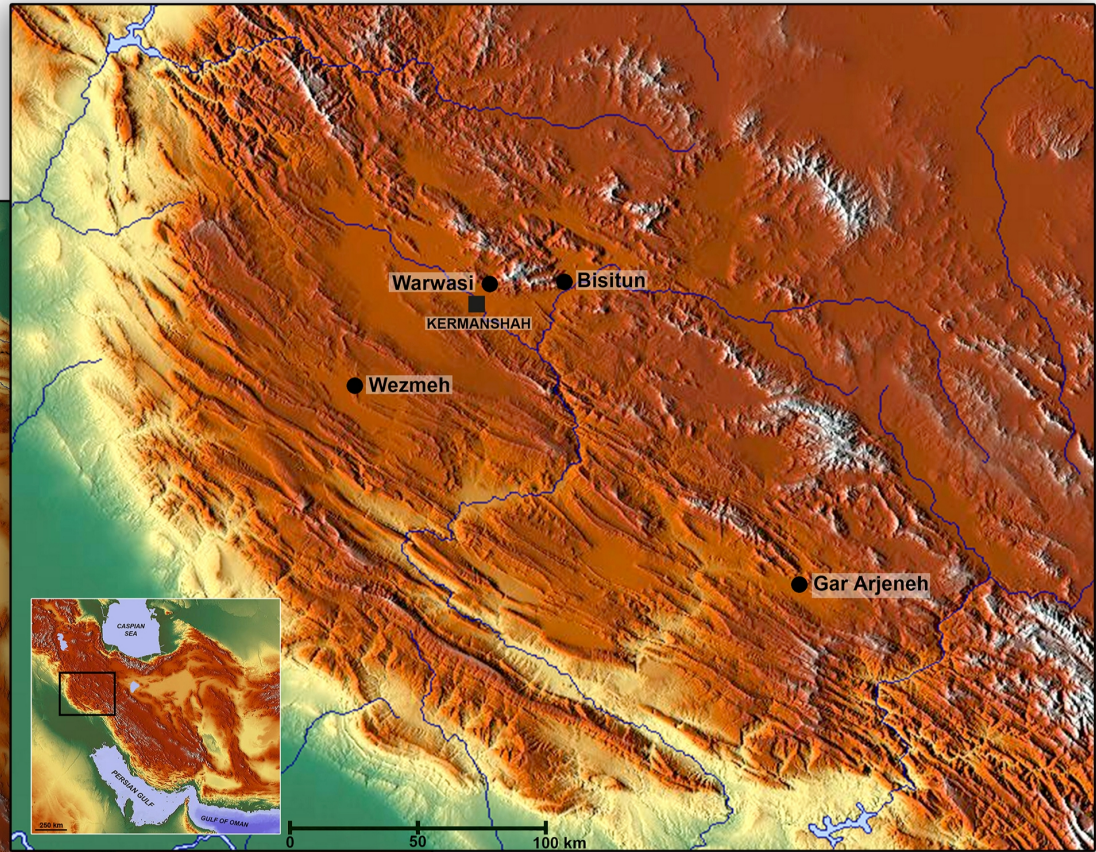
**Figure 6.** Enamel thickness cartographies of Wezmeh 1 in occlusal (O), buccal (B), mesial (M), lingual (L), and distal (D) views compared with selected P<sup>4</sup> from the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. Topographic thickness variation is rendered by a pseudocolor scale ranging from thinner dark blue to thicker red; isolated spots correspond to wear-related enamel removal. Independently from their original side, all crowns are shown as right.

**Figure 7.** Between-group principal component analysis (bgPCA) of the Procrustes shape coordinates of the enamel-dentine junction (EDJ) of Wezmeh 1 compared with the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. See Tables 1 and 2 and SOM Table S1 for sample composition. The extremes of morphological variation are illustrated at the ends of each bgPC axis in occlusal (mesial aspect, upward) and buccal views (mesial aspect, rightward).

a

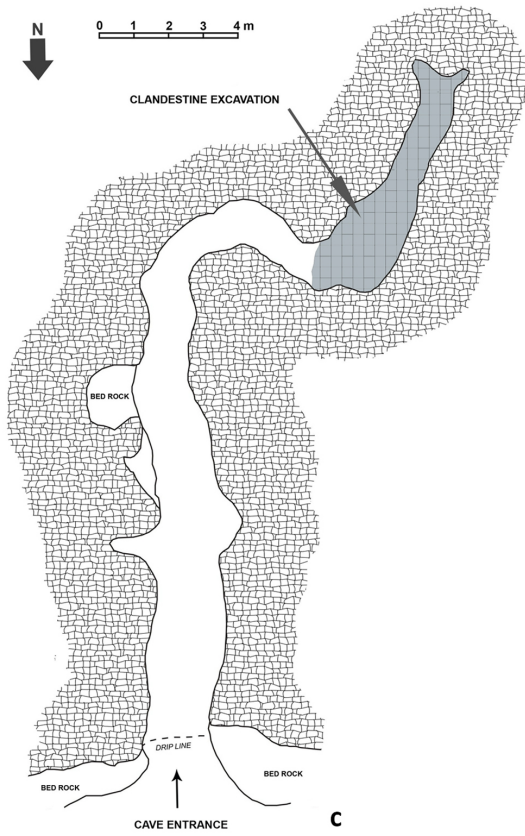


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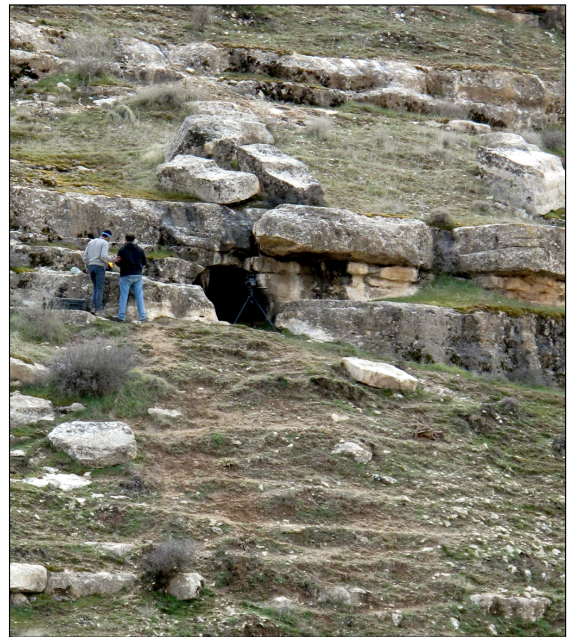




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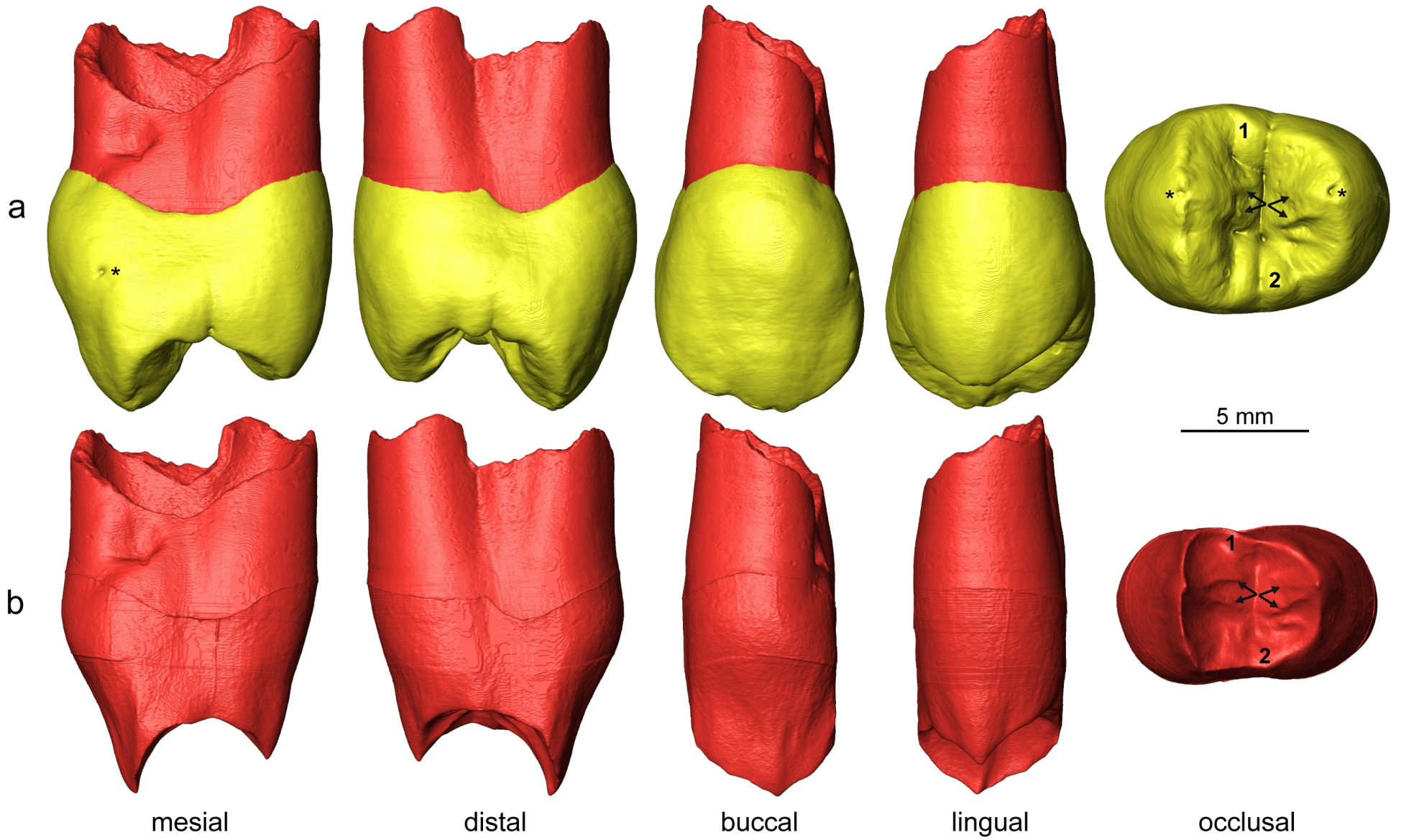
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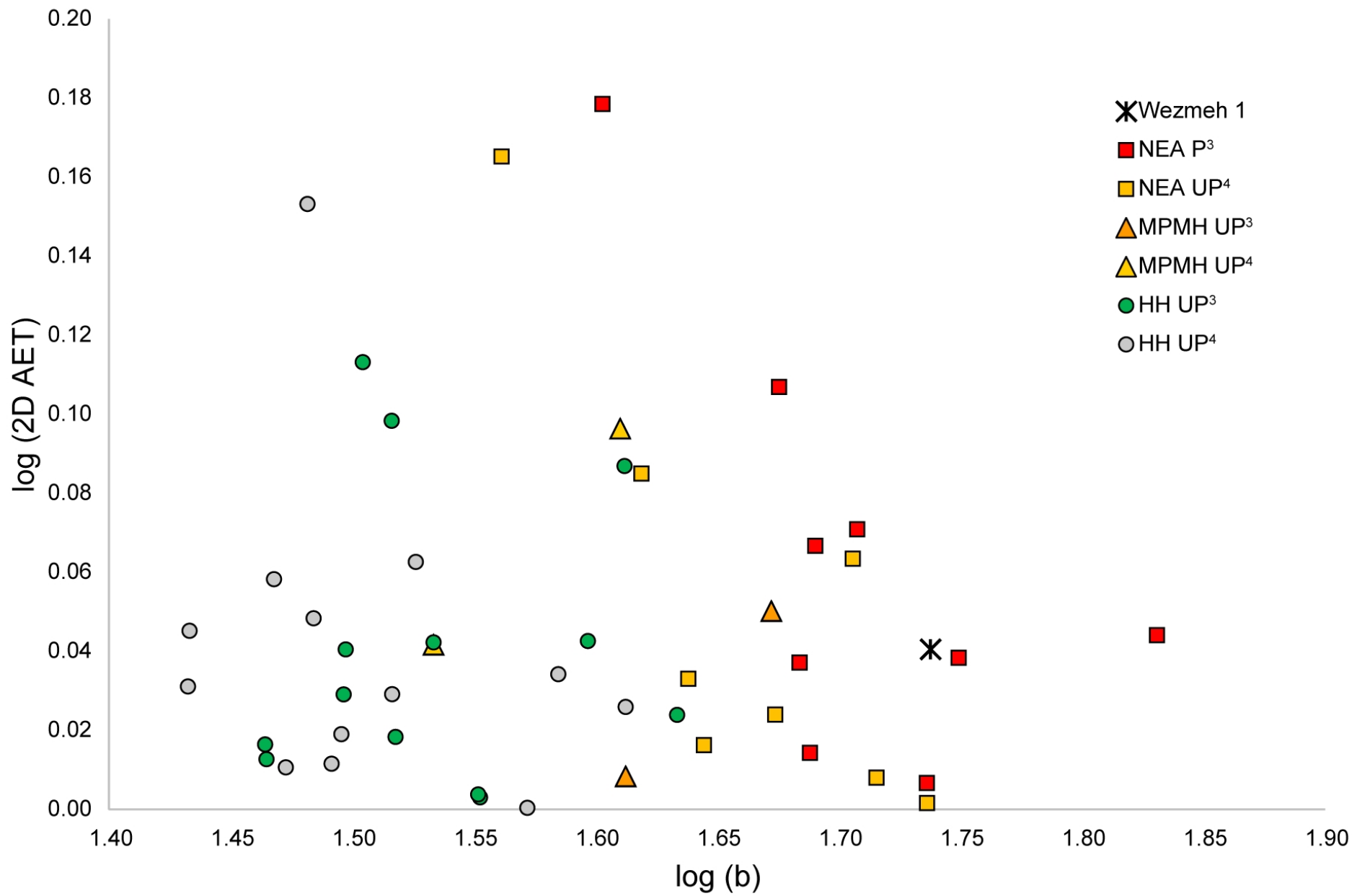


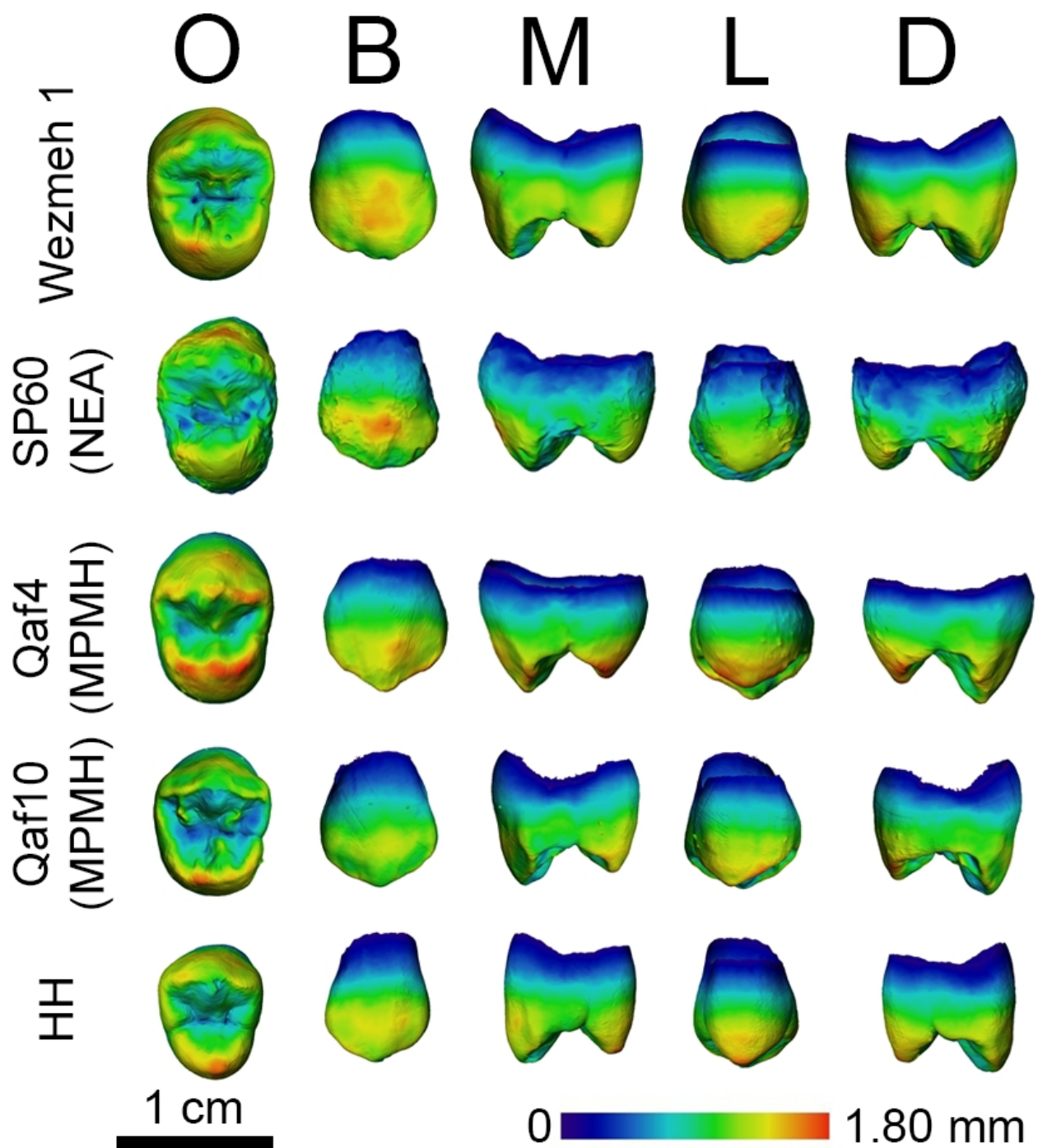
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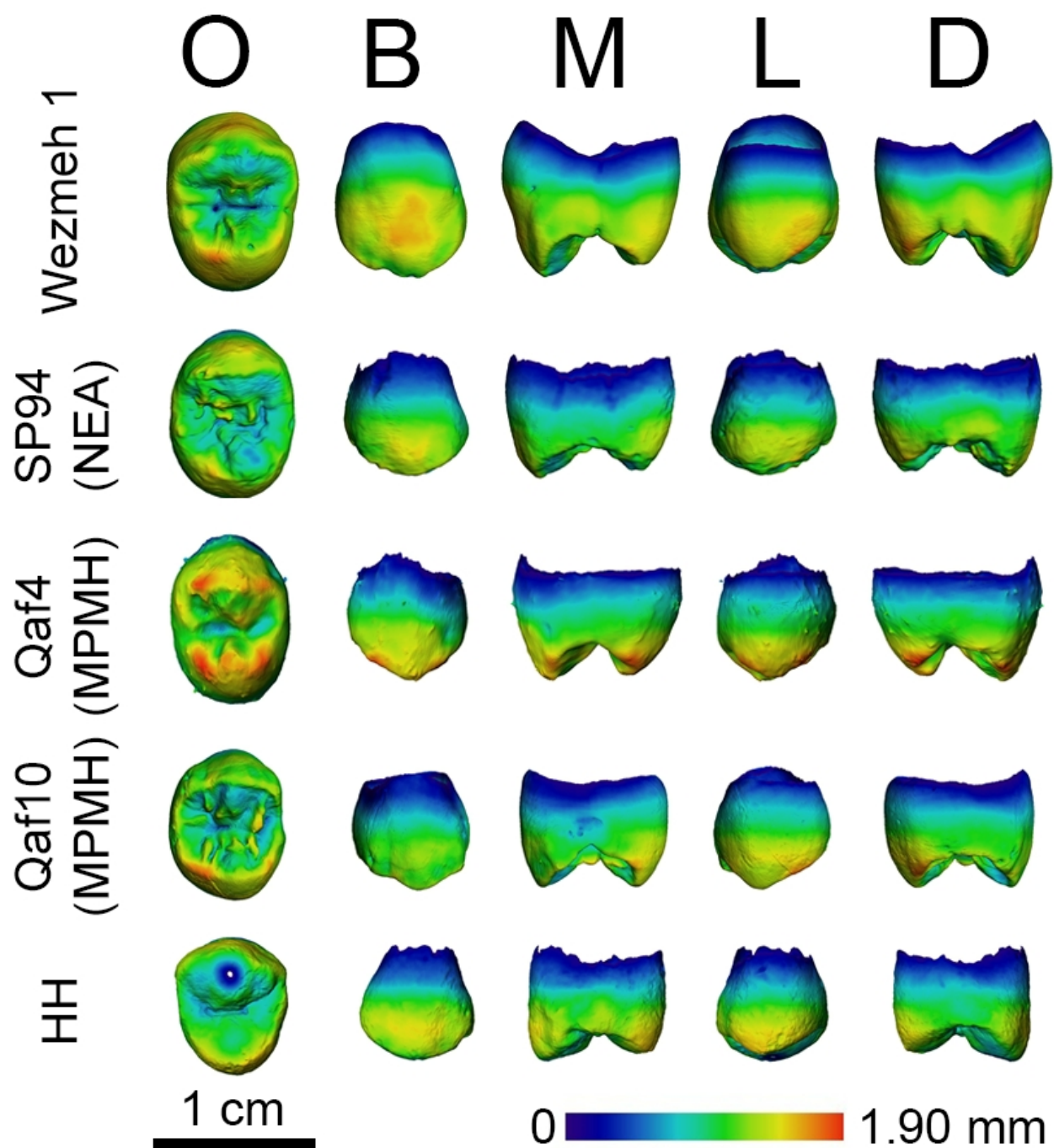


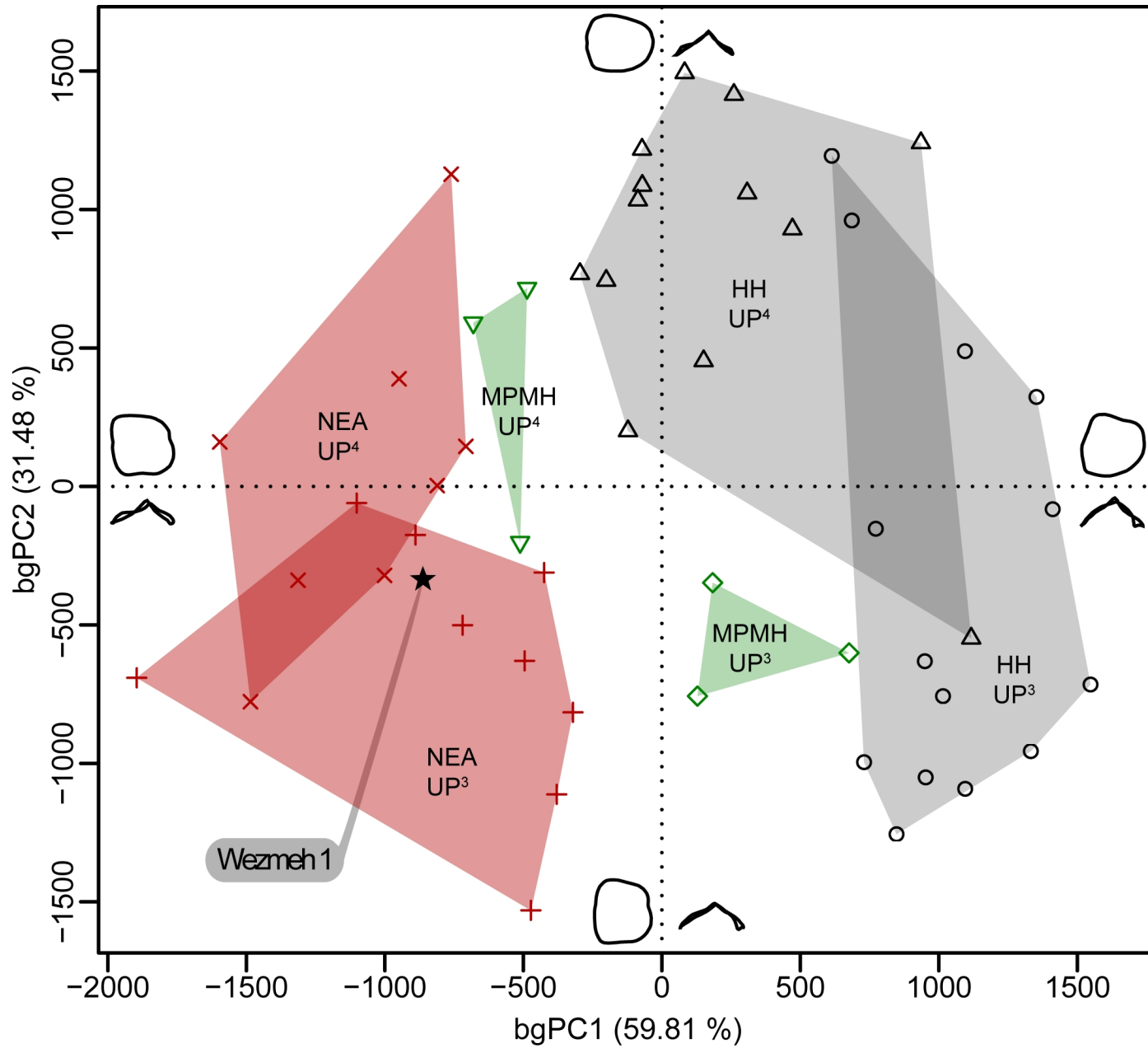
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**Table 1**

Number of specimens (*n*) and degree of occlusal wear (range; Smith, 1984) of the P<sup>3</sup> and P<sup>4</sup> forming the three comparative samples used in the 2-3D analyses. The samples represent Neanderthals (NEA), Middle Paleolithic modern humans (MPMH) and Western European Holocene humans (HH).

Tooth	Sample	<i>n</i>	Wear degree	<i>n</i> GM EDJ	<i>n</i> DTP and ET 2D	<i>n</i> DTP and ET 3D (wear degree ≤ 2)	<i>n</i> TOPO ET 2D	2-3D data sources
P <sup>3</sup>	NEA	9	1–4	9	9	4	9	Bayle et al., 2017, 2019; NESPOS Database, 2019
	MPMH	3	1	3	2	2	3	ESRF Paleontological Microtomographic Database, 2019; original data
	HH	14	1–4	14	13	11	13	Le Luyer, 2016; original data
P <sup>4</sup>	NEA	8	1–4	8	8	4	8	Bayle et al., 2017, 2019; NESPOS Database, 2019

							ESRF Paleontological
MPMH	3	1	3	2	2	3	Microtomographic Database, 2019; original data
HH	13	1–4	13	13	11	13	Le Luyer, 2016; original data

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Abbreviations: GM EDJ = geometric morphometrics of the enamel-dentine junction shape; DTP dental tissue proportions; ET = enamel thickness;

TOPO ET: standardized enamel thickness topographic variation.

**Table 2**

List of the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA) and the Middle Paleolithic modern human (MPMH) samples used in the comparative analyses.

See Table 1 for the data sources.

	p <sup>3</sup>	p <sup>4</sup>
	KRD38, KRD39, KRD43, KRD45,	KRD41, KRD42, KRD44, KRD46,
NEA	KRD48, Palomas 53, Palomas 60, Palomas 68, Spy11F	KRD47, Palomas 68, Palomas 94, Spy 11E
MPMH	Qafzeh 4, Qafzeh 10, Qafzeh 15	Qafzeh 4, Qafzeh 10, Qafzeh 15

**Table 3**

2D dental tissue proportions and enamel thickness in Wezmeh 1 compared to the values of the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. See Tables 1 and 2 for sample composition.

		c (mm <sup>2</sup> )	b (mm <sup>2</sup> )	a (mm <sup>2</sup> )	b/a	e (mm)	BCD (mm)	2D AET (mm)	2D RET
Wezmeh 1		27.16	54.72	81.88	66.83	24.75	9.86	1.10	14.83
NEA P <sup>3</sup>	mean	22.21	51.44	73.66	69.98	22.78	9.83	0.97	13.59
	range	13.73–26.93	40.08–67.76	53.81–91.60	65.25–74.48	20.71–26.39	8.52–10.94	0.66–1.18	10.47–16.65
NEA P <sup>4</sup>	mean	21.50	46.26	67.76	68.37	21.47	9.75	1.00	14.70
	range	13.37–25.42	36.43–54.49	49.80–76.56	62.06–73.15	19.56–22.52	8.04–11.44	0.68–1.22	11.32–18.86
MPMH P <sup>3</sup>	mean	22.34	44.00	66.34	66.29	20.86	8.90	1.07	16.15
	range	21.33–23.35	40.97–47.03	62.30–70.38	65.76–66.82	20.80–20.92	7.74–10.05	1.02–1.12	15.93–16.37
MPMH P <sup>4</sup>	mean	23.43	37.46	60.89	61.51	19.93	8.81	1.18	19.20
	range	21.63–25.22	34.16–40.76	55.79–65.98	61.23–61.78	19.65–20.20	7.99–9.63	1.10–1.25	18.83–19.56
HH P <sup>3</sup>	mean	18.62	34.44	53.06	64.85	19.48	7.61	0.96	16.43
	range	14.31–21.55	29.12–43.02	45.66–64.17	59.44–70.34	17.18–22.35	6.84–8.42	0.77–1.10	12.80–19.58
HH P <sup>4</sup>	mean	19.99	32.27	52.26	61.72	18.88	7.87	1.06	18.79
	range	15.27–26.81	27.07–40.97	45.43–62.99	53.06–66.63	17.07–21.94	7.08–8.60	0.89–1.42	14.91–25.85

Abbreviations: 2D AET = 2D average enamel thickness; 2D RET = 2D relative enamel thickness; a = total crown area; b =: coronal dentine and pulp area;  $b/a$  = percentage of crown area that is dentine and pulp; c = enamel area; e = enamel-dentine junction length; BCD = bicervical diameter.

**Table 4**

3D dental tissue proportions and enamel thickness in Wezmeh 1 compared to the values of the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. See Tables 1 and 2 for sample composition.

		Ve (mm <sup>3</sup> )	Vcdp (mm <sup>3</sup> )	Vc (mm <sup>3</sup> )	Vcdp/Vc	SEDJ (mm <sup>2</sup> )	3D AET (mm)	3D RET
Wezmeh 1		204.48	208.89	413.37	50.53	177.27	1.15	19.44
NEA P <sup>3</sup>	mean	141.04	165.28	306.32	54.66	145.07	0.95	17.27
	range	85.15–202.97	111.97–199.26	197.12–402.23	49.54–57.72	112.80–168.28	0.75–1.23	15.64–21.02
NEA P <sup>4</sup>	mean	143.72	166.92	310.64	53.56	137.92	1.02	18.76
	range	83.94–179.04	96.16–221.02	180.10–383.33	51.39–57.66	102.55–154.54	0.82–1.18	17.37–20.40
MPMH P <sup>3</sup>	mean	147.15	153.11	300.25	51.00	136.38	1.08	20.14
	range	134.91–159.38	140.58–165.63	275.49–325.00	50.96–51.03	132.01–140.75	1.02–1.13	19.65–20.62
MPMH P <sup>4</sup>	mean	141.15	131.50	272.64	48.19	119.05	1.19	23.31
	range	132.42–149.87	120.11–142.88	252.53–292.75	47.56–48.81	115.80–122.29	1.14–1.23	23.18–23.44
HH P <sup>3</sup>	mean	115.04	111.73	226.76	49.27	113.86	1.02	21.23
	range	80.93–141.78	88.37–144.50	186.93–282.73	41.00–56.70	98.68–135.26	0.75–1.29	15.81–28.93
HH P <sup>4</sup>	mean	117.22	102.65	219.86	46.61	107.41	1.09	23.51
	range	88.65–152.91	80.88–134.07	181.95–281.97	41.84–53.68	93.19–126.66	0.85–1.29	17.85–27.89

Abbreviations: 3D AET = 3D average enamel thickness; 3D RET = 3D relative enamel thickness; SEDJ = EDJ surface area;  $V_c$  = total crown volume;  $V_{cdp}$  = coronal dentine and pulp volume;  $V_{cdp}/V_c$  = percentage of crown volume that is dentine and pulp;  $V_e$  = enamel volume.

## Supplementary Online Material (SOM):

A Neanderthal from the Central Western Zagros, Iran. Structural reassessment of the Wezmeh 1 maxillary premolar

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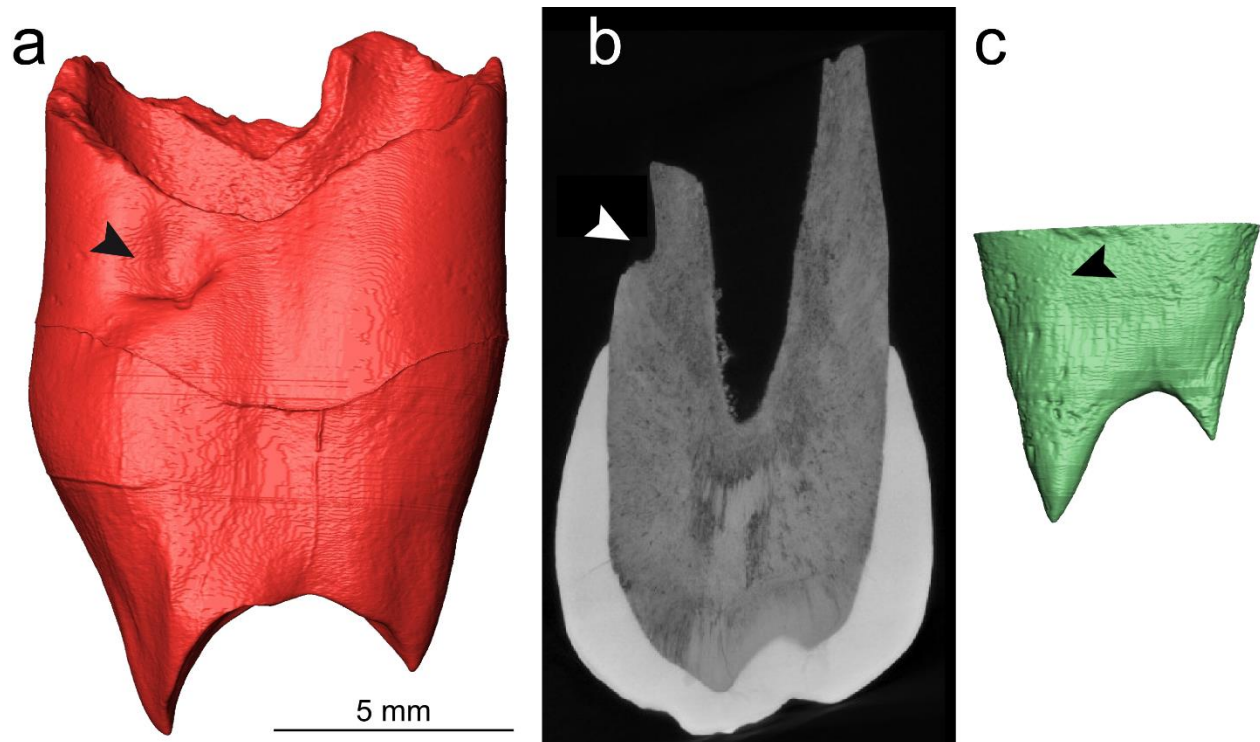
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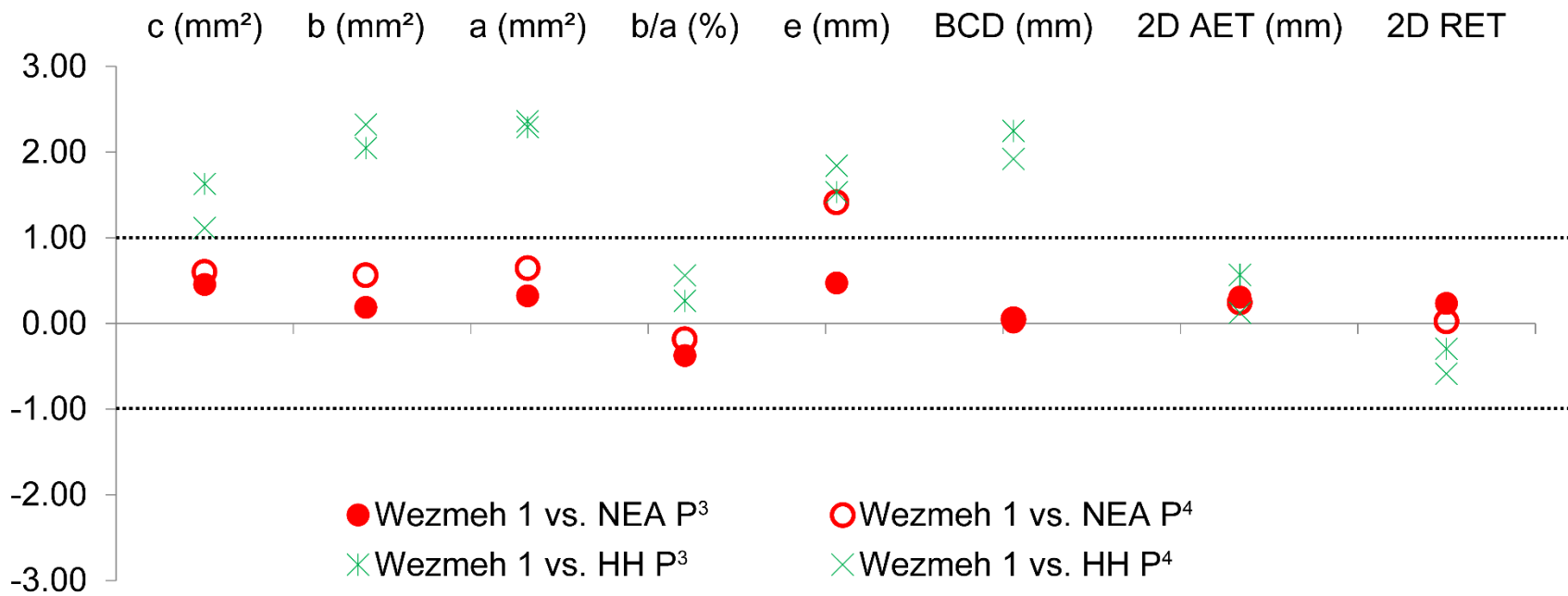
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E-mail addresses: [clement.zanolli@gmail.com](mailto:clement.zanolli@gmail.com) (C. Zanolli), [fbiglari@gmail.com](mailto:fbiglari@gmail.com) (F. Biglari).

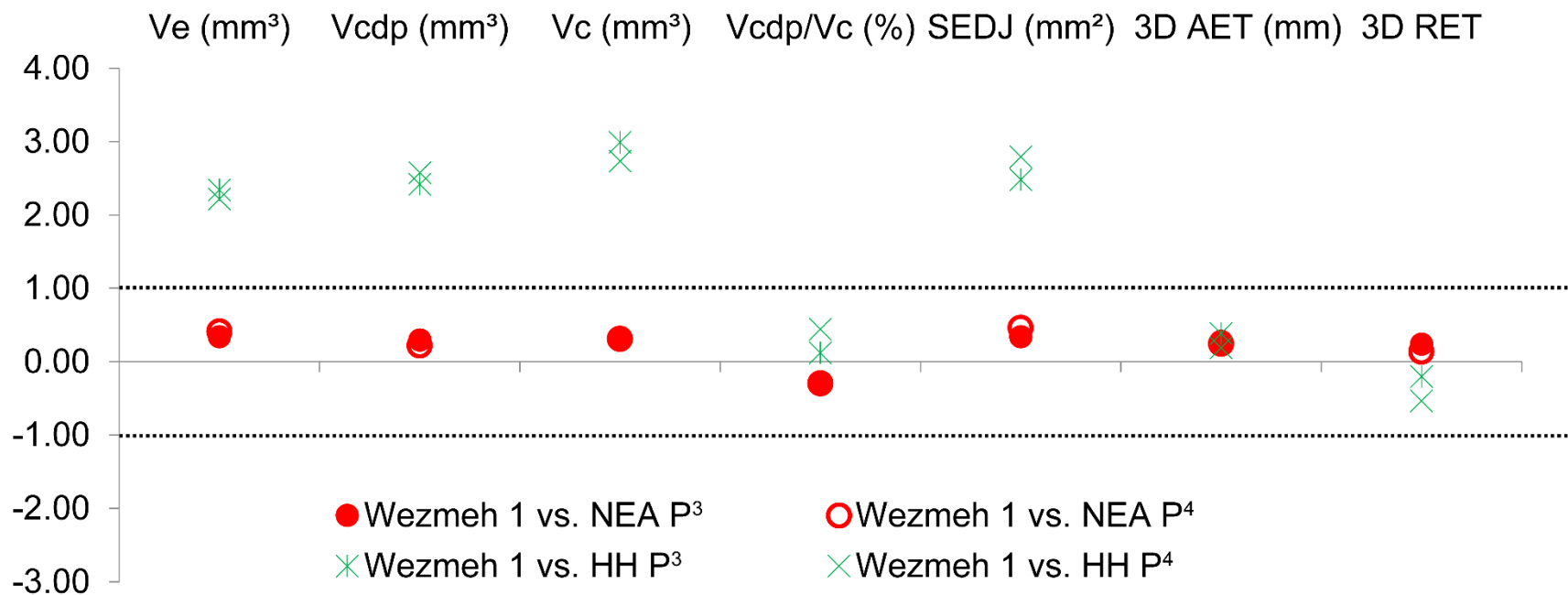




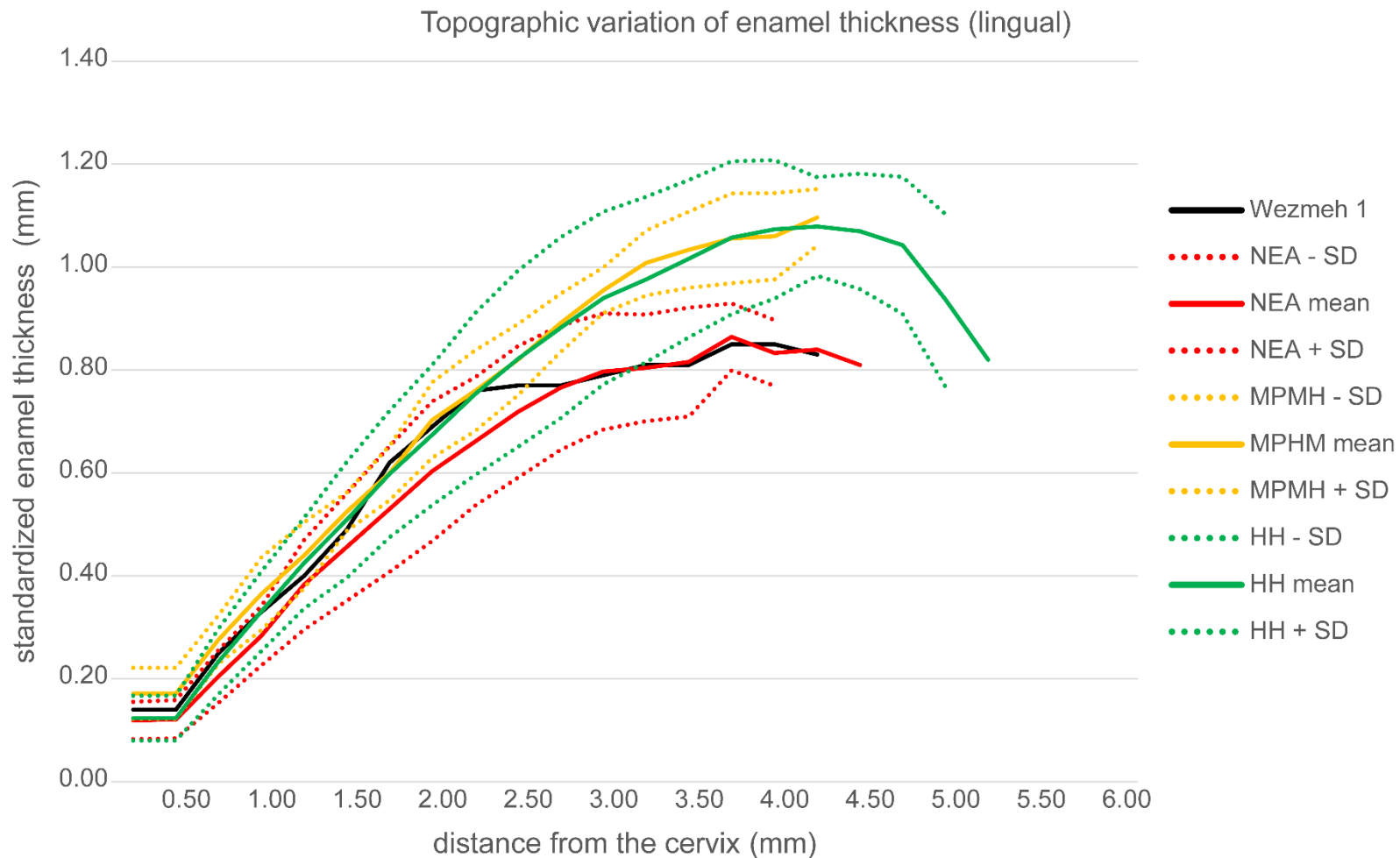
**SOM Figure S1.** a)  $\mu$ CT-based 3D virtual rendering of the Wezmeh 1 coronal and radicular dentine in mesial view showing the relatively large and deep depression on the root, approximately 2.0 mm from the cervix (arrow). b) Virtual section across the depression (arrow) revealing that it does not reach the inner dentine wall (dentine-pulp junction). c) As visible on the section, this defect does not affect the still forming pulp chamber.



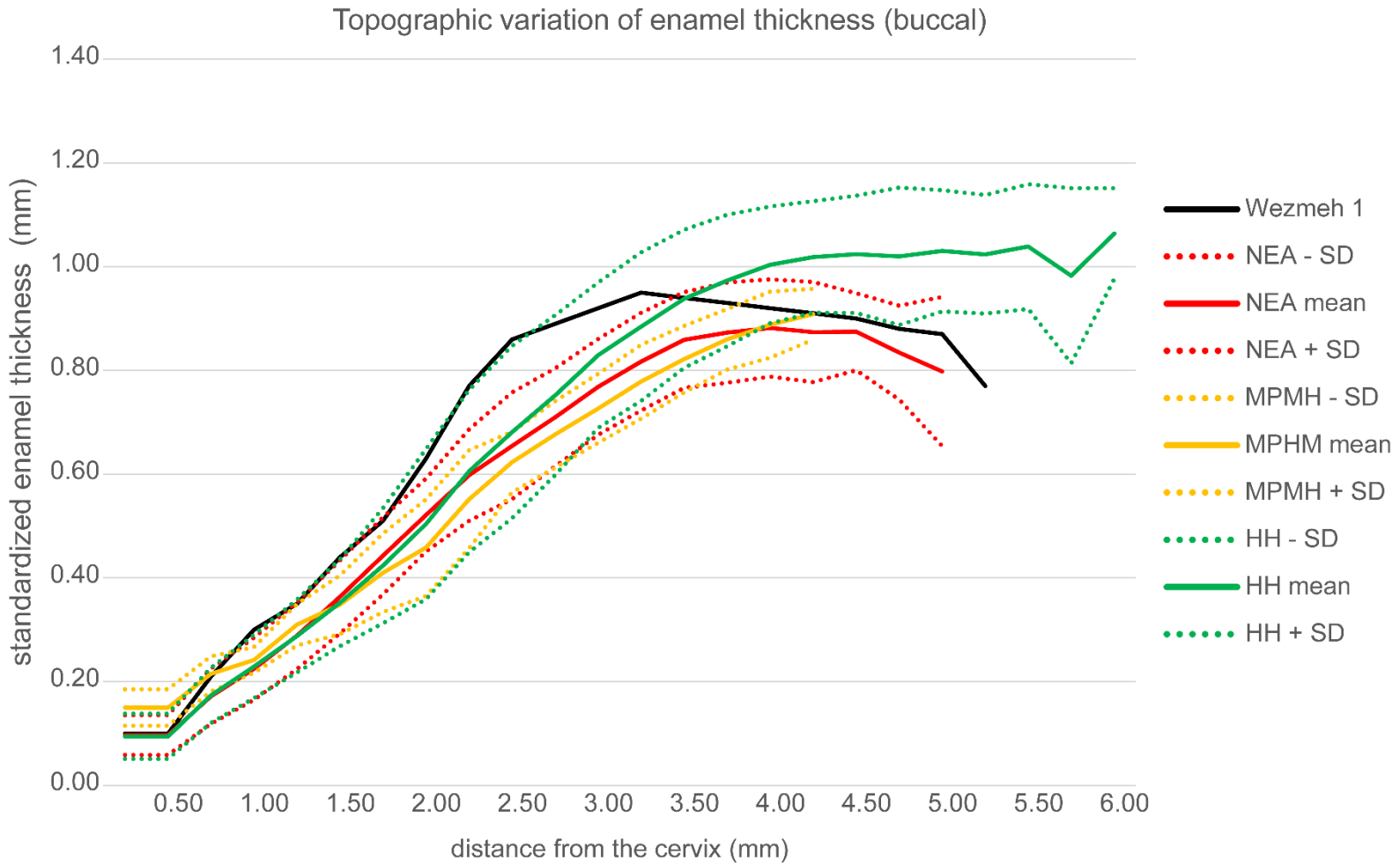
**SOM Figure S2.** Adjusted Z-scores of the 2D dental tissue proportions and enamel thickness variables in Wezmeh 1 compared to the variation expressed by the P<sup>3</sup> and P<sup>4</sup> premolars forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. The line passing through zero represents the mean; the dotted lines correspond to the estimated 95% limit of variation expressed by the comparative samples. See Materials and methods for variable abbreviations and Tables 1 and 2 and SOM Table S1 for sample composition.



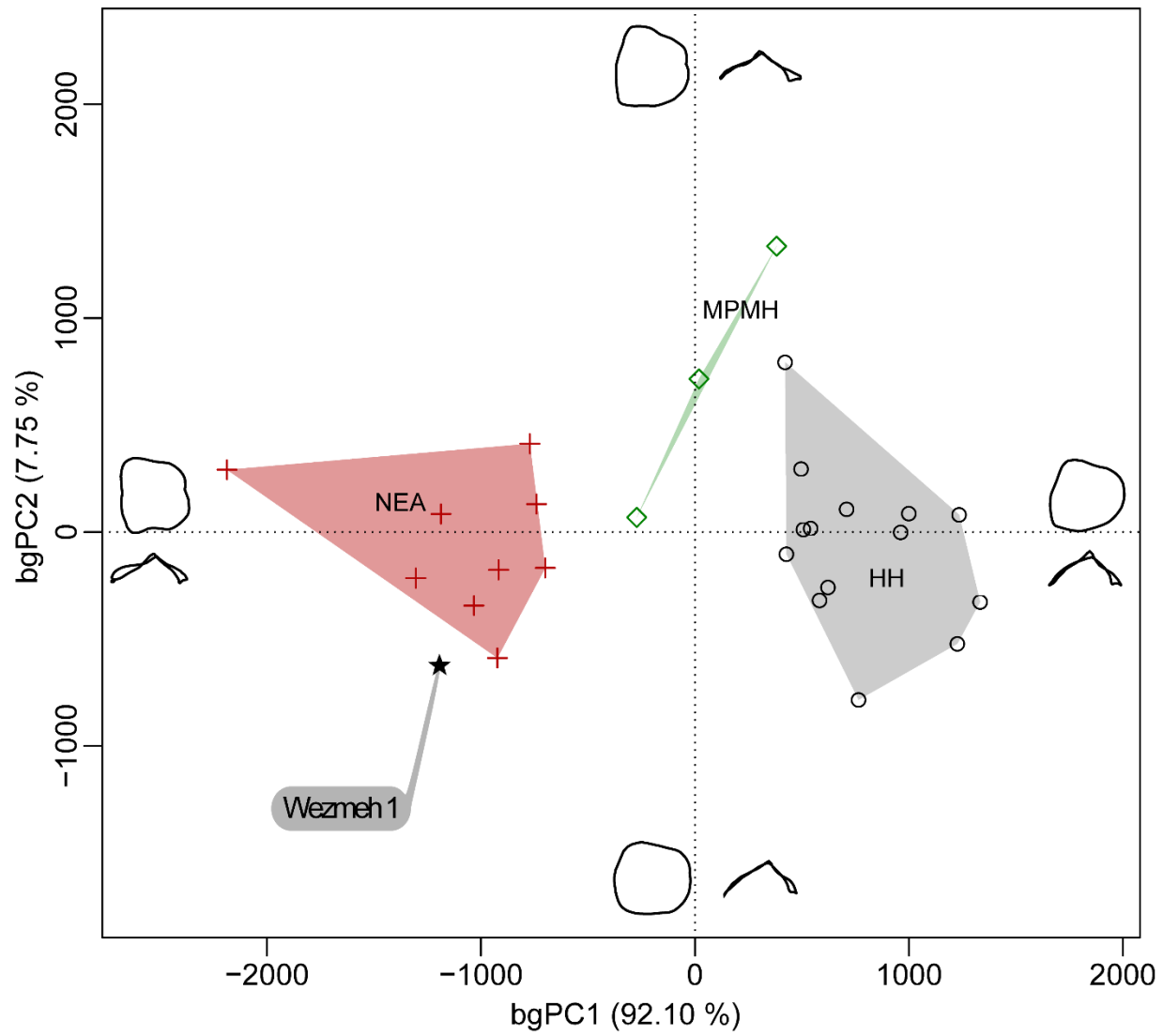
**SOM Figure S3.** Adjusted Z-scores of the 3D dental tissue proportions and enamel thickness variables in Wezmeh 1 compared to the variation expressed by the P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples. The line passing through zero represents the mean; the dotted lines correspond to the estimated 95% limit of variation expressed by the comparative samples. See Materials and methods for variable abbreviations and Tables 1 and 2 and SOM Table S1 for sample composition.



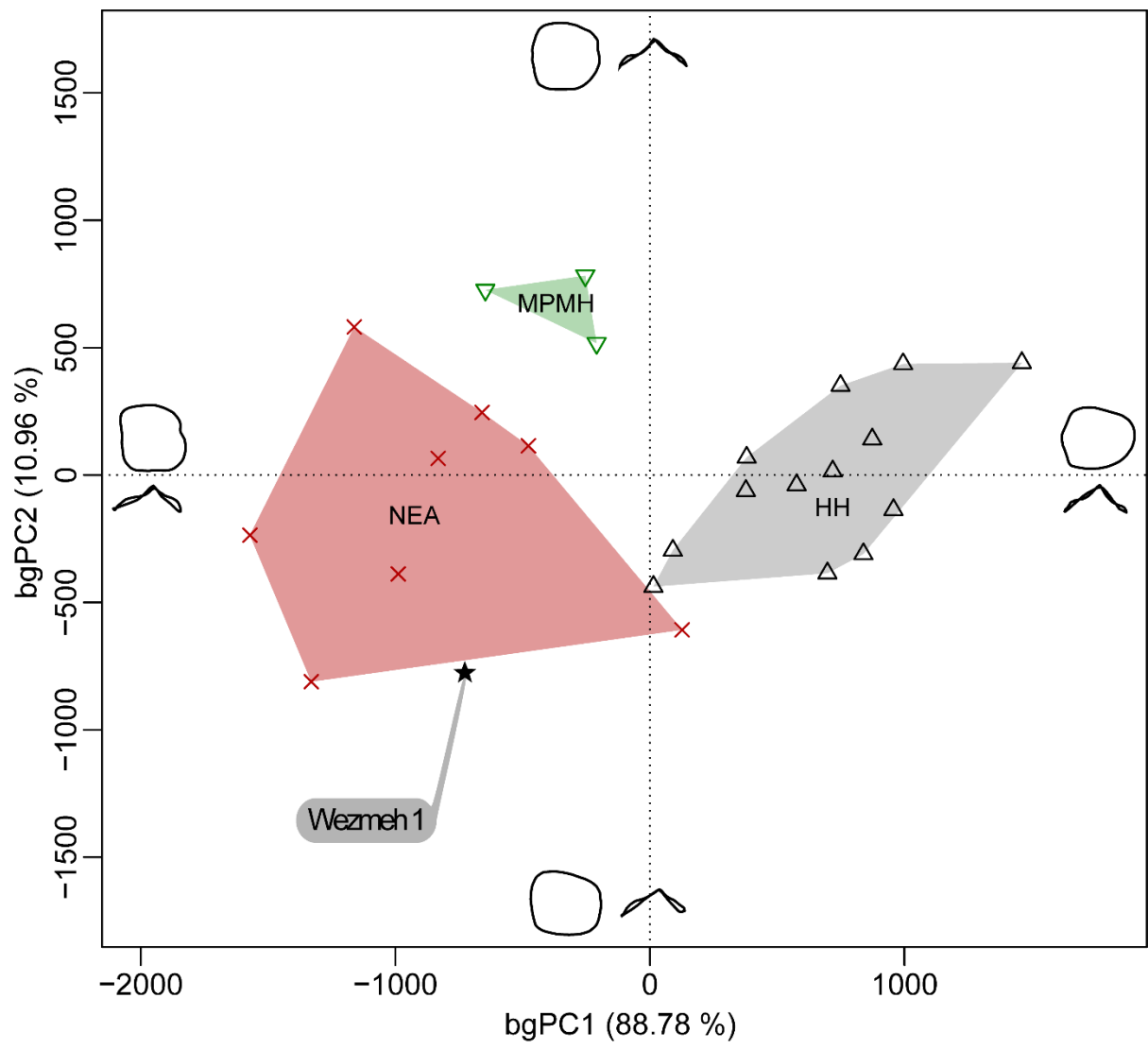
**SOM Figure S4.** Standardized enamel thickness topographic variation (in mm) measured across the entire virtual lingual section in Wezmeh 1 compared with the values measured on the homologous virtual sections of the pooled P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA; mean  $\pm$  1 SD), Middle Paleolithic modern human (MPMH; mean  $\pm$  1 SD), and Western European Holocene human (HH; mean  $\pm$  1 SD) samples.



**SOM Figure S5.** Standardized enamel thickness topographic variation (in mm) measured across the entire virtual buccal section in Wezmeh 1 compared with the values measured on the homologous virtual sections of the pooled P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA; mean  $\pm$  1 SD), Middle Paleolithic modern human (MPMH; mean  $\pm$  1 SD), and Western European Holocene human (HH; mean  $\pm$  1 SD) samples.

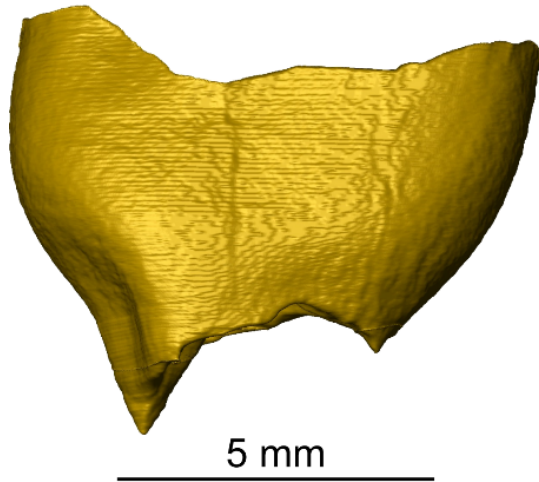
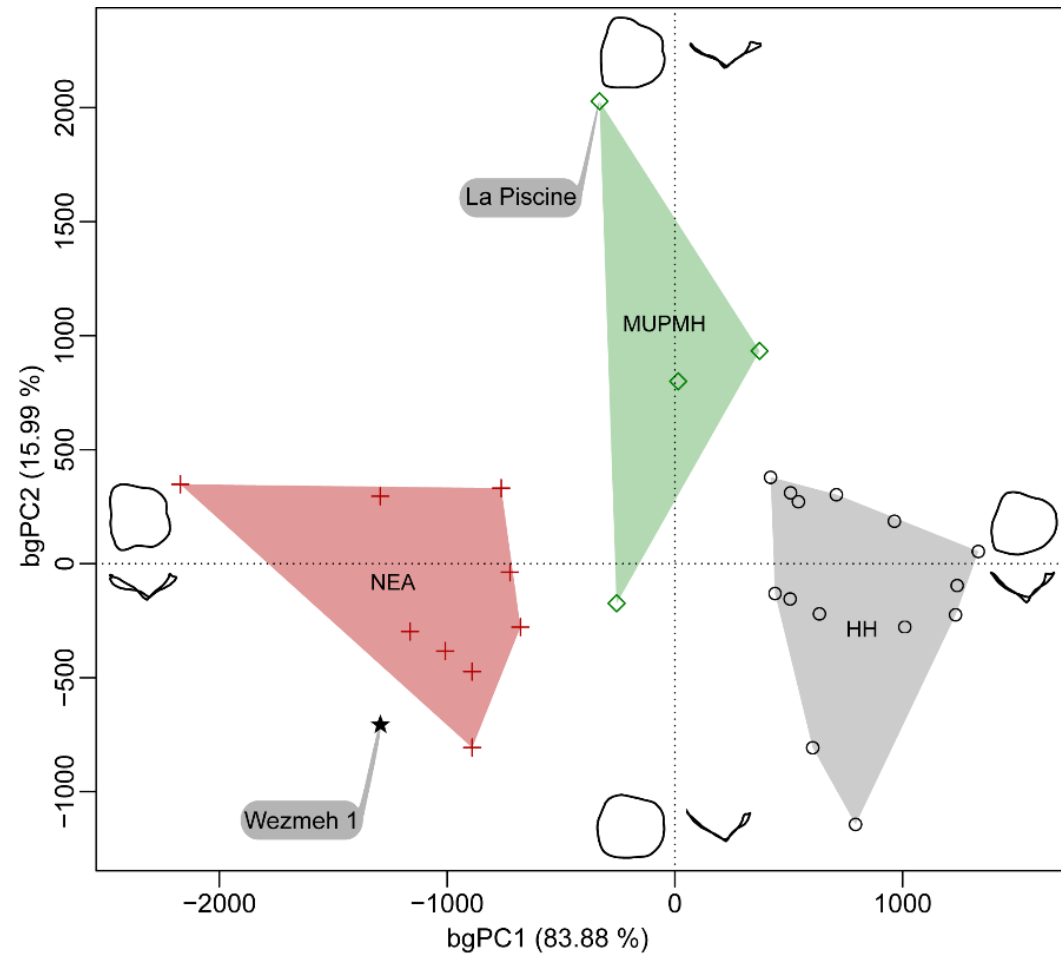


**SOM Figure S6.** Between-group principal component analysis (bgPCA) of the Procrustes shape coordinates of the enamel-dentine junction (EDJ) of Wezmeh 1 compared with the P<sup>3</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples.





**SOM Figure S7.** Between-group principal component analysis (bgPCA) of the Procrustes shape coordinates of the enamel-dentine junction (EDJ) of Wezmeh 1 compared with the P<sup>4</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples.

**a****b**

**SOM Figure S8.** a) Virtual rendering of the EDJ of the late Upper Paleolithic (Magdalenian) P<sup>3</sup> H3 from the French site of La Piscine. Stored at the Musée d'Art et d'Histoire de Montmorillon (<http://sitearcheo-la-piscine.blogspot.com>), H3 was  $\mu$ CT-scanned in 2010 at the University of Poitiers (voxel size of 14.46  $\mu$ m) thanks to the scientific collaboration provided by C. Delage. b) Between-group principal component analysis (bgPCA) of the Procrustes shape coordinates of the enamel-dentine junction (EDJ) of H3 compared with Wezmeh

1 and the P<sup>3</sup> forming the Neanderthal (NEA), Middle Paleolithic modern human (MPMH), and Western European Holocene human (HH) samples.

**SOM Table S1**

List of P<sup>3</sup> and P<sup>4</sup> forming the Western European Holocene human sample (HH) used in the comparative analyses.

	UP3	UP4	References
Neolithic	Gurgy Les Noisats (GLN04-201, GLN04-277, GLN06-215B, GLN06-215B3, GLN05-308), Mykolas cave (LBGM10)	Gurgy Les Noisats (GLN04-201, GLN04-277, GLN05-308), Mykolas cave (LBGM10-5)	Le Luyer, 2016
Roman Empire	Bosco Pontini (BP 5, BP 6, BP 7)	Bosco Pontini (BP 5, BP 6, BP 7, BP 8, BP 9)	original data
19th-20th centuries	France and Italy (4)	France and Italy (2)	original data

**SOM Table S2**

List of P<sup>3</sup> and P<sup>4</sup> forming the Neanderthal (NEA) and Western European Holocene human (HH) samples investigated for the presence of a dentine depression on the mesial root aspect.

	P <sup>3</sup>	P <sup>4</sup>	References
NEA	Krapina (D38, D39, D43, D45, D48, D51, D53, D54, D55, D116), Biache-Saint-Vaast 1 (both UP3s)	Krapina (D40, D41, D42, D44, D46, D47, D49), Scladina (Scla 4A-2/P <sup>4</sup> )	Rougier, 2003; Toussaint, 2014; Nespos Database, 2019
HH	<i>n</i> = 28	<i>n</i> = 20	Le Luyer, 2016; original data