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Taxonomic differences in deciduous lower first molar crown outlines of *Homo sapiens* and *Homo neanderthalensis*

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1 **Abstract**

2

3           Recent studies have demonstrated that the outline shapes of deciduous upper and lower  
4 second molars and the deciduous upper first molar are useful for diagnosing hominin taxa –  
5 especially *Homo neanderthalensis* and *H. sapiens*. Building on these studies, we use geometric  
6 morphometric methods to assess the taxonomic significance of the crown outline of the lower  
7 first deciduous molar (dm<sub>1</sub>). We test whether the crown shape of the dm<sub>1</sub> distinguishes *H.*  
8 *neanderthalensis* from *H. sapiens* and explore whether dm<sub>1</sub> crown shape can be used to  
9 accurately assign individuals to taxa. Our fossil sample includes 3 early *H. sapiens*, 7 Upper  
10 Paleolithic *H. sapiens* and 13 *H. neanderthalensis* individuals. Our recent human sample  
11 includes 103 individuals from Africa, Australia, Europe, South America and South Asia. Our  
12 results indicate that *H. neanderthalensis* dm<sub>1</sub>s cluster fairly tightly and separate well from those  
13 of Upper Paleolithic *H. sapiens*. However, we also found that the range of shapes in the recent  
14 human sample completely overlaps the ranges of all fossil samples. Consequently, results of the  
15 quadratic discriminant analysis based on the first 8 PCs representing more than 90% of the  
16 variation were mixed. Lower dm<sub>1</sub>s were correctly classified in 87.3% of the individuals: the  
17 combined *H. sapiens* sample had greater success (90.2%) in assigning individuals than did the *H.*  
18 *neanderthalensis* sample (61.5%). When the analysis was run removing the highly variable  
19 recent human sample, accuracy increased to 84.6% for *H. neanderthalensis* and 57.1% of Upper  
20 Paleolithic *H. sapiens* were classified correctly by using the first four PCs (70.3%). We conclude  
21 that caution is warranted when assigning isolated dm<sub>1</sub> crowns to taxa: while an assignment to *H.*  
22 *neanderthalensis* has a high probability of being correct, assignment to Upper Paleolithic *H.*  
23 *sapiens* is less certain.

24

25 Key Words: *Homo sapiens*, Neanderthals, Tooth shape, Deciduous molars, Geometric  
26 morphometrics

27

## 28 **1. Introduction**

29 Before we can test evolutionary hypotheses explaining patterns in, and distribution of,  
30 morphological variation in our fossil relatives we must first be able to accurately identify  
31 hominin species from a fragmentary fossil record. Recent studies have demonstrated this need by  
32 showing the importance of accurately associating a culture with the species that made it (Benazzi  
33 et al., 2011a; Benazzi et al., 2015). Correctly identifying isolated dental remains has also shed  
34 important light on the timing of dispersals of our species (Benazzi et al., 2011b). The ability to  
35 accurately assign isolated skeletal and dental elements to taxa may also result in larger fossil  
36 sample sizes, which provide greater power to statistical tests aimed at testing the significance of  
37 differences among taxa.

38 Skeletons recovered from the Late Pleistocene, especially during the European Upper  
39 Paleolithic, are often incomplete and fragmentary (Churchill and Smith, 2000). Complicating  
40 matters is the fact that fragmentary skeletal elements often are morphologically undiagnostic and  
41 may be unusable unless they preserve ancient hominin DNA. Dental elements, on the other hand,  
42 are more frequently recovered and, due to their durable enamel, are often complete.

43 Although tooth size alone is not very informative for diagnosing Late Pleistocene taxa  
44 (Bailey and Hublin, 2005), tooth crown and root morphology has proven to be quite useful,  
45 especially in distinguishing *Homo neanderthalensis* (hereafter: Neanderthals) from *H. sapiens*  
46 during the periods in which they overlapped in time and space (Bailey et al., 2009; Been et al.,  
47 2017; Benazzi et al., 2011b, 2014; Fabbri et al., 2016; Hublin et al., 2020; Kupczik and Hublin,  
48 2010; Le Cabec et al., 2013 ; Margherita et al., 2016). When complete dentitions are found and

49 crowns are relatively unworn, assigning specimens to taxa is fairly straightforward because  
50 Neanderthals have diagnostic combinations of dental characters (Bailey, 2002a; 2002b, 2006).  
51 Even incomplete dentitions can be diagnostic if the appropriate teeth and/or characters are  
52 preserved (Bailey et al., 2009). However, while many tooth crowns are found complete, they  
53 often suffer from wear that obscures or eliminates minor morphological features on the crown  
54 (e.g., occlusal crests and small accessory cusps).

55         Early studies of molar crown shape relied on the position of, and relationships between,  
56 cusp tips, which required relatively unworn teeth (Bailey, 2004; Morris, 1981). More recently,  
57 methods of assessing crown shape (e.g., Elliptical Fourier Analysis - EFA, semi-landmark-based  
58 methods) from crown outlines have allowed for the inclusion of both worn and unworn molar  
59 crowns in analyses (Benazzi et al., 2012). Studies using these methods have shown that crown  
60 outlines of permanent molars are quite useful for partitioning out variation and assigning  
61 specimens to taxa (Bailey and Lynch, 2005; Benazzi et al., 2011a; Gómez-Robles et al., 2007;  
62 Gómez-Robles et al., 2008, 2011).

63         The small size and thin enamel of deciduous molars make them especially prone to loss  
64 of surface information through attrition, especially in paleoanthropological and archaeological  
65 samples that predate the advent of processed food. For this reason, the crown outline is  
66 particularly useful for assessing shape differences among groups. Over the past decade several  
67 studies have confirmed that the outlines of postcanine deciduous crowns can be used to  
68 accurately assign individuals to taxa (Bailey et al., 2014b, 2016; Fornai et al., 2016; Moroni et  
69 al., 2018a).

70 In hominins, the deciduous second molar (dm2 or dp4<sup>1</sup>) is remarkably similar to the  
71 permanent first molar (M1) in both crown outline and morphology (Fig. 1A). While about 15%  
72 smaller in size than the M1 (Bailey et al., 2014a), within individuals the dm2 preserves the same  
73 number of primary cusps; and the number and expression of accessory features are highly  
74 correlated between the two (Edgar and Lease, 2007; Kieser, 1984; Paul et al., 2017). Because the  
75 dm2 forms early during ontogeny (Liversidge and Molleson, 2004) it is presumed to be little  
76 influenced by environmental variation. Moreover, studies have shown it to be less variable in  
77 size and morphology than the deciduous first molar (Farmer and Townsend, 1993; Liversidge  
78 and Molleson, 1999; Margetts and Brown, 1978). Thus, it is perhaps not surprising that just like  
79 the M1, the dm2 has proven to discriminate between Neanderthals and *H. sapiens* quite well  
80 (Bailey et al., 2014a, 2015; Benazzi, 2012; Moroni et al., 2018a).

81 In contrast to the dm2, the dm1 can be more premolar-like than molar-like in form, at  
82 least in later *Homo* (Fig. 1B). The dm1 often preserves fewer cusps, with the distal aspects of  
83 both upper and lower dm1 reduced compared to the dm2. The dm<sup>1</sup> may even be bicuspid  
84 (preserving only mesial cusps) in some *H. sapiens* groups. Like the dm<sup>1</sup>, the distal cusps of the  
85 dm1 may be completely missing, preserving only the protoconid and metaconid. This variation in  
86 cusp number and expression is reflected in the crown's shape.

87

88 [FIGURE 1A and 1B ABOUT HERE]

89

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<sup>1</sup>Here we follow terminology in the dental anthropological literature, which refers to this tooth as a molar. We are aware that in the paleontological literature this tooth is referred to as a premolar.

90 An earlier study of  $dm_1^1$  shape of Neanderthals and *H. sapiens* resulted in 96.3% accuracy  
91 in separating the two groups (Benazzi et al., 2011b). The current study builds on our previous  
92 studies of the diagnostic utility of deciduous molar shape for taxonomic affiliation by examining  
93 variation of the  $dm_1$  ( $dp_3$ ). We analyze the crown shapes of Neanderthals and early, Upper  
94 Paleolithic and recent *H. sapiens*, applying geometric morphometric (GM) methods to crown  
95 outlines taken from digital occlusal images. Based on our previous research, we expect that the  
96  $dm_1$  will distinguish Neanderthals from *H. sapiens* with a high degree of accuracy (80% or  
97 higher). Based on results of our earlier study showing that the  $dm_2$  and  $M_1$  were slightly less  
98 diagnostic than the  $dm_2^2$  and  $M_1^1$  (Bailey et al., 2016), we expect this may also to be the case for  
99 the  $dm_1$ . The ability of the  $dm_1$  to discriminate among taxa will rely, at least in part, on the  
100 amount of variation within each group. At a broader level, knowing the degree of variability  
101 within groups may allow us to test hypotheses about the evolutionary forces, or the relaxation of  
102 such forces, driving this variation.

103 If the  $dm_1$  crown outline proves to discriminate well between Neanderthals and *H.*  
104 *sapiens*, it will add to the tools available for assessing isolated teeth and assigning them to fossil  
105 taxa. If, unlike the  $dm_1^1$  (Benazzi et al., 2011b), the  $dm_1$  crown outline cannot accurately assign  
106 teeth to taxa, future work will focus on exploring the possible reasons why the lower molars are  
107 less distinctive than the upper molars.

108

## 109 **2.0 Materials**

### 110 *2.1. Samples*

111 The materials used in this study include occlusal photographs of  $dm_1$ s from 126 recent  
112 and fossil *H. sapiens* and Neanderthals (Table 1). Our recent *H. sapiens* (RHS) sample includes

113 103 individuals representing Africa, Australia, Europe, South America and South Asia.  
114 Deciduous teeth are scarce in the fossil record and our comparative fossil sample, while small,  
115 includes nearly all relevant fossil dm1s available for study: 3 early *H. sapiens* (EHS), 7 Upper  
116 Paleolithic *H. sapiens* (UPHS) and 13 Neanderthals. We assigned specimens to taxa based on  
117 assignments made in the published literature. These assignments were based on a combination of  
118 criteria including: cranial morphology, age, cultural association, and/or their association with  
119 taxonomically diagnostic adult human remains.

120 We included only complete and undamaged crowns in our samples. With one exception  
121 (Die Kelders 6291), these crowns ranged in status from unworn to moderately worn (three or  
122 more small dentine patches, stages 1–4; Molnar, 1971). Figure 2 illustrates the single crown with  
123 stage 5 wear (see Methods below for how worn outlines were reconstructed). Even in moderately  
124 worn crowns it was primarily the distal aspect that required correction. We did not consider sex  
125 as a variable in this study due to the difficulty in assigning sex to fossil individuals, especially  
126 those represented by isolated teeth.

127

128 [TABLE 1 ABOUT HERE]

129

130 We arbitrarily chose to use the left dm1 to represent each individual. If the left side was  
131 not represented or was damaged, we used the right side and mirror-imaged the crown using  
132 Adobe PhotoShop® before the analysis. Although the left and right sides may be asymmetrical  
133 in size and/or shape, studies have shown that dental asymmetry occurs randomly with regard to  
134 side. This phenomenon is known as fluctuating asymmetry (Van Valen, 1962). To date we know  
135 of no study quantifying the differences in crown shapes between left and right antimeres.



136 However, we assume that crown shape asymmetry is randomly distributed — as it is for tooth  
137 size and dental nonmetric traits, which influence crown shape (see Scott and Turner, 1997 for  
138 review).

139

## 140 *2.2. Methods of data collection and analysis*

141 All but seven occlusal images were taken using a Canon EOS Rebel XT digital 8 MP  
142 camera equipped with a macro lens (see Supplementary Online Material [SOM] Table S1). All  
143 images were taken from original skeletal and fossil materials (i.e., no casts were used).  
144 Photographic images of the fossils were taken by SEB. Some images of recent humans  
145 (primarily the African samples) were taken by Caroline Souday (see acknowledgements) under  
146 the supervision of SEB. Individual teeth were oriented so that the cervical border was  
147 perpendicular to the camera's optical axis. A bubble device was used to level the camera and  
148 each image included a similarly leveled millimeter scale that was placed at approximately the  
149 same height as the cusp tips. Bailey et al. (2004) have shown that inter-observer error due to  
150 differences in image orientation and camera equipment is low (2.4%–4.5%) and not significantly  
151 greater than intra-observer error.

152 In seven cases (SOM Table S1) occlusal images were acquired from  
153 microtomographic ( $\mu$ CT) image data of original specimens performed by the Department of  
154 Human Evolution of the Max Planck Institute for Evolutionary Anthropology. In those cases,  
155 either an industrial  $\mu$ CT system or a desktop system was used, and the subsequent voxel  
156 resolutions ranged from 14 to 70  $\mu$ m. The image stacks of each tooth were filtered to improve  
157 tissue grayscale homogeneity and then segmented into enamel and dentine components manually  
158 with Avizo® v.9 (Thermo Fisher Scientific). The crown surface was extracted as a 3D digital

159 surface model (.ply format). The models of the  $\mu$ CT scans were opened in Avizo® v.9 and then  
160 manipulated in 3D space so that the cervical border was perpendicular to the optical axis in both  
161 mesiodistal and buccolingual directions (Benazzi et al., 2009). Avizo® v.9 was used to add an  
162 appropriate scale and then a screen shot of the occlusal surface (analogous to taking a digital  
163 photograph) was taken and saved as a .jpg file. A recent study has shown that there is no  
164 significant difference between crown outlines obtained from photos and 3D digital models (Buti,  
165 2013).

166 Screen shots and digital images were imported into Adobe Photoshop®. Backgrounds  
167 were removed and image contrast was adjusted to provide a clear distinction between the crown  
168 outline and the background. Finally, each image was scaled to approximately the same size and  
169 resolution (300 dpi).

170 Even in moderately worn dm1s, interproximal wear sometimes distorted the distal aspect  
171 of the crown outline. Less often, the mesial aspect was also affected. In these cases, the outline  
172 was reconstructed by estimating the original mesial and/or distal borders (see Bailey, 2004;  
173 Gómez-Robles et al., 2007; Wood and Abbott, 1983; Wood and Engleman, 1988). These  
174 estimations were based on the buccolingual extent of the wear facet and the overall contour of  
175 the tooth (Fig. 2); all estimations were made by SEB.

176

177

[FIGURE 2 ABOUT HERE]

178

179 The occlusal images of the dm1s were imported in Rhino 4.0 Beta CAD environment  
180 (Robert McNeel & Associates, Seattle, WA), placed on the xy-plane of the Cartesian coordinate  
181 system, and rotated along the z-axis to have its lingual aspect parallel to the x-axis. Then, for

182 each tooth the crown outline was manually digitized using the curve function. The outlines were  
183 centered on their centroid, and equiangularly spaced radial vectors emanating from their  
184 superimposed centroids (the first radius parallel to the y-axis and buccally directed) intersected  
185 the outlines. Ultimately 24 pseudolandmarks were identified for each outline (Fig. 3; Benazzi et  
186 al., 2011a). Finally, the pseudolandmark configurations were scaled to unit centroid size (i.e.,  
187 Procrustes shape coordinates) and variation in crown outline shape was explored by principal  
188 components analysis (PCA) of the matrix of shape coordinates (Bailey et al., 2014a, b, 2016;  
189 Benazzi et al., 2011b; Benazzi et al., 2012; Lacy et al., 2018; Moroni et al., 2018b).

190

191

[FIGURE 3 ABOUT HERE]

192

193 We conducted two separate PCAs. The first analysis included all samples to examine  
194 variation among fossil and recent groups. The second analysis used only the recent *H. sapiens*  
195 sample to investigate the role of geographic origin in the variation observed.

196 To identify potentially significant differences in crown shape of the dm<sub>1</sub> between groups,  
197 permutation tests ( $n = 10,000$ ) were conducted using the first three PCs. These tests compared  
198 the distance between two group means to the distances obtained by random assignment of  
199 observations to this groups (using Morpho v. 2.8 in R). Values were considered significant at  $p <$   
200 0.05. Because Neanderthal molars are, on average, slightly larger than those of *H. sapiens* and  
201 because size and shape may be related, we also conducted an analysis examining the relationship  
202 between shape variables (PCs) and size allometry (logarithm of crown base area). This analysis  
203 was investigated by Procrustes ANOVA with permutation procedures ( $n = 1,000$ ) using the R  
204 package geomorph v. 3.2.1 (Adams and Otárola-Castillo, 2013).

205 The Shapiro-Wilks test was used to assess the normality of distribution of Procrustes  
206 shape coordinates for each group in the sample (Ghasemi and Zahediasl, 2012). Fligner-Killeen's  
207 test was performed to test the homogeneity of variances across the groups, rejecting the null  
208 hypothesis  $H_0$  (variances homogeneity) if  $p < 0.05$ . Since both assumption of normality and  
209 homogeneity of variance were violated, we used leave-one-out cross-validation Quadratic  
210 Discriminant Analysis (QDA) to test how well crown shape discriminates taxa (see Results for  
211 details). The QDA used the first eight PCs representing about 90% of the variation in the  
212 comparison of *H. sapiens* (fossil and recent) and Neanderthals. Whereas, considering the small  
213 sample size of UPHS ( $n = 7$ ), the QDA used the first four PCs (70.3%) in the comparison among  
214 recent *H. sapiens*, UPHS and Neanderthals, as well as between UPHS and Neanderthals. The  
215 number of PCs used for QDA was chosen in order to find the minimum optimal combination of  
216 variables (i.e., PCs) within the sensible cutoff in the range of 70% to 90% of variation (Jolliffe,  
217 2002; Sorrentino et al., 2020). Posterior probabilities were calculated using equal prior  
218 probability of 0.5. The data were processed and analyzed through software routines written in R  
219 v. 3.4.3 (R Core Team, 2017).

220  
221

### 222 **3. Results**

#### 223 *3.1. Principal components analysis*

224 Figure 4 illustrates the results of the PCA. The first three principal components account  
225 for about 60% of the variance (PC1 = 31.6%, PC2 = 15.5%, and PC3 = 12.4%; Fig. 4a).

226 Allometry is responsible for only 2.1% of overall crown variation ( $F = 2.72$ ,  $R^2 = 0.021$ ,  $df = 1$ ,  $p$   
227  $< 0.05$ ) considering the whole sample; and it remains similar (2.3%) when excluding EHS ( $F =$   
228  $2.86$ ,  $R^2 = 0.023$ ,  $df = 1$ ,  $p < 0.05$ ) in Procrustes ANOVA. The contribution of allometry

229 increases to 10.8% in the comparison of Neanderthals and UPHS ( $F = 2.19$ ,  $R^2 = 0.108$ ,  $df = 1$ ,  $p$   
230  $> 0.05$ ), but the effects of shape variation due to size allometry are not significant in this case. It  
231 is, therefore, unlikely that size is a significant driver of shape differences between the two  
232 groups.

233

234

[FIGURE 4 ABOUT HERE]

235 The range of variation in recent humans is wide and spans all four quadrants of the PCA  
236 plot. With the exception of two *H. sapiens* individuals (Die Kelders 6291 and La Madeleine) all  
237 fossil individuals, regardless of taxon, fall within the RHS range. Recent humans appear to be  
238 distributed randomly but it is possible that their distribution reflects the geographic range  
239 sampled in this study. The results of a PCA exploring the RHS distribution further by grouping  
240 RHS samples by geographic region are provided in Figure 5 and discussed below (3.3 Recent  
241 human variation).

242

243

[FIGURE 5 ABOUT HERE]

244

245 In Figures 4b and 5 positive PC1 scores represent a relatively rectangular crown shape,  
246 whereas negative PC1 scores reflect a more trapezoidal shape with a mesiobuccal projection  
247 related to the tuberculum molare. Along PC2, positive scores reflect an asymmetrical crown with  
248 a somewhat reduced trigonid portion and unreduced talonid, while negative PC2 scores are  
249 associated with a somewhat triangular shape with a reduction in the talonid portion of the crown.

250

251 *3.2. Fossil hominin variation*

252           The three EHS individuals are variable for PC1. However, none have particularly high  
253 negative PC1 scores, indicating the absence of a strong mesiobuccal projection (i.e., tuberculum  
254 molare). All three individuals have negative scores for PC2, which reflect relatively large mesial  
255 cusps. The three EHS individuals fall closer to the range of Neanderthals than they do to the  
256 range of UPHS. All of the UPHS individuals possess negative PC1 scores, which reflect the  
257 presence of a prominent tuberculum molare. Along PC2 UPHS individuals have mainly positive  
258 scores (or low negative scores), indicating crowns with a relatively wider talonid than trigonid.  
259 Neanderthal individuals have both positive and negative PC1 scores and mainly negative PC2  
260 scores. Along PC1 the Neanderthal  $dm_1$  scores range from moderately positive to moderately  
261 negative, reflecting the observation that some possess a strong tuberculum molare, while others  
262 are more rectangular and/or symmetrically shaped. Table 2 presents the results of a permutation  
263 test of the significance of differences among groups. Significant differences are obtained  
264 between the UPHS sample and all the other groups ( $p < 0.05$ ). Significant differences are also  
265 found between Neanderthals and the UPHS and RHS samples ( $p < 0.05$ ), but not between the  
266 Neanderthal and the EHS samples ( $p > 0.05$ ).

267

268

[TABLE 2 ABOUT HERE]

269

270

          The PCA plots in Figure 4 shows that the UPHS and Neanderthal samples are less  
271 variable than the RHS sample despite their wider temporal sampling, although small sample  
272 sizes may play a role this result. In fact, the two fossil groups separate quite well in shape space  
273 (especially in the 3D plot of the first three PCs: Fig 4a), with only one individual falling in the  
274 range of both. Figure 6 provides the mean  $dm_1$  crown shapes of UPHS and Neanderthals. As

275 suggested from the PCA plots, the mean shape of UPHS reflects the marked mesiobuccal  
276 projection frequently observed in that sample, whereas the mean shape in Neanderthals reflects  
277 the wider range of expression in this feature.

278

279 [FIGURE 6 ABOUT HERE]

### 280 3.3. Recent human variation

281 Figure 5 provides a PCA plot of the geographic subgroups within the RHS sample.  
282 Figure 7 illustrates the wide range of shape variation within the subgroups. Procrustes ANOVA  
283 showed no significant effects (1.8%) of crown variation due to size allometry in the RHS sample  
284 ( $F = 1.84$ ,  $R_2 = 0.018$ ,  $df = 1$ ,  $p > 0.05$ ). Table 3 presents the results of the permutation test of  
285 significant differences among recent human subgroups in which the two Australian individuals  
286 were not included. With the exception of South America, all subgroups span the four quadrants  
287 of the PCA graph. Significant differences were obtained between the Sub Saharan African and  
288 European ( $p < 0.05$ ), South American ( $p < 0.05$ ) and South Asian ( $p < 0.05$ ) subgroups.  
289 Significant differences were also found between South American and European ( $p < 0.05$ ) and  
290 South Asian ( $p < 0.05$ ) subgroups. The North African subsample differs significantly from the  
291 European ( $p < 0.05$ ) and South Asia ( $p < 0.05$ ) subgroups. Even though significant differences  
292 were found, Figure 5 suggests the geographic patterning to the variation is not very strong.  
293 Among the recent geographic subgroups, the South American sample shows the narrowest  
294 distribution: individuals have positive and negative PC1 scores but only positive PC2 scores.

295

296

[FIGURE 7 and TABLE 3 ABOUT HERE]

297

### 298 3.4. Quadratic Discriminant Functions Analysis

299 Shapiro-Wilks tests show that the distribution of Procrustes shape coordinates of the RHS  
300 violate the assumption of normality ( $W = 0.945, p < 0.05$ ), whereas UPHS ( $W = 0.879, p > 0.05$   
301 and Neanderthals ( $W = 0.894, p > 0.05$ ) do not. The variances of the groups are not  
302 homogeneous ( $\chi^2 = 555.7, df = 3, p < 0.05$ ), even if EHS are excluded ( $\chi^2 = 321, df = 2, p <$   
303  $0.05$ ). Furthermore, Fligner-Killeen's test shows different variance between RHS and  
304 Neanderthals ( $\chi^2 = 8.65, df = 1, p < 0.05$ ), RHS and UPHS ( $\chi^2 = 112.79, df = 1, p < 0.05$ ), and  
305 between UPHS and Neanderthals ( $\chi^2 = 4.8, df = 1, p < 0.05$ ).

306 Results of the QDA are provided in Tables 4 and 5. When grouped according to taxon (*H.*  
307 *neanderthalensis* and *H. sapiens*), individuals were correctly assigned 87.3% of the time (Table  
308 4). The classification for *H. sapiens* was better (90.2%) than it was for Neanderthals (61.5%).  
309 When *Homo sapiens* was separated into fossil and recent groups and reanalyzed, RHS were  
310 correctly classified 76.7% of the time, but only 42.9% of the UPHS individuals and 53.8% of the  
311 Neanderthals classified correctly (Table 5). EHS was not considered in this second analysis, due  
312 to its small sample size.

313

[TABLES 4 and 5 ABOUT HERE]

314

315 To explore the effect of the recent human variation on our results, and because our  
316 primary goal was to ascertain whether  $dm_1$  shape can accurately distinguish between  
317 Neanderthals and fossil *H. sapiens*, we re-ran the QDA focusing only on Neanderthal and UPHS  
318 groups. Doing this increased the accuracy substantially (Table 6). Correct assignment to the



319 Neanderthal group rose to 84.6% while correct assignment to UPHS increased to 57.1%, with  
320 two Neanderthals (Bruniquel and Roc du Marsal) and three UPHS individuals (Estelas, Isturitz  
321 and Solutre) misclassified.

322 [INSERT TABLE 6 ABOUT HERE]

## 323 **Discussion**

324 Results of the present study are in agreement with previous ones, which have  
325 demonstrated that there are significant differences between the deciduous molar crown shapes of  
326 UPHS and Neanderthals. As was the case for other deciduous molars, we found that assessment  
327 of the  $dm_1$  shape provides a relatively accurate method for identifying Neanderthal individuals.  
328 However, and in contrast to our previous studies, the success rate in classifying UPHS based on  
329  $dm_1$  shape is substantially lower. This leads us to conclude that a  $dm_1$  assigned to ‘Neanderthal’  
330 is very likely to be correct, but a  $dm_1$  assigned to ‘UPHS’ is less certain to be correct.

331 We are somewhat surprised at the mediocre classification accuracy for the UPHS  
332 individuals, especially given that in the PCA the UPHS and Neanderthal samples appear to be  
333 well separated in shape space (Fig. 4). We believe that our QDA results reflect, at least in part,  
334 the choice of PCs and the variance for the QDA. We chose a number of PCs (4) that was both  
335 less than the smallest group size ( $n = 7$ ) and also accounted for at least 70% of the variance. Re-  
336 running the QDA with five and six PCs (accounting for a slightly higher amount of variation) did  
337 not improve the results. Re-running the QDA with only the first three PCs (which are illustrated  
338 in Fig. 4a) led to better classificatory results, but the first three PCs accounted for only 60% of  
339 the variance. Therefore, we do not have confidence in those results. Since both number of PCs  
340 and variance are affected by the size of samples used, we believe that small sample size is

341 responsible, at least in part, for the lower classification accuracy indistinguishing Neanderthals  
342 and UPHS in this study compared to previous ones (e.g., Bailey et al 2016).

343 Results from the present study are consistent with those of our previous studies, which  
344 found that lower molars are less powerful in discriminating *H. sapiens* (both fossil and recent)  
345 and Neanderthal groups than are the upper molars. The first study using  $dm^1$  crown shape to  
346 distinguish Neanderthals from UPHS showed the method to be successful 96% of the time  
347 (Benazzi et al 2011a). In the same study, the shape of the  $dm^2$  proved to be 100% accurate at  
348 discriminating individuals from these two groups. In a follow-up study that included a wide  
349 geographic range of recent *H. sapiens*, the accuracy of the  $dm^2$  was only slightly lower (97%;  
350 Bailey et al 2014). Subsequent studies that assessed the lower dentition suggested that  $dm_2$   
351 shape was also a powerful discriminator of Neanderthals and UPHS and recent European *H.*  
352 *sapiens*, but it was slightly less accurate (92%) than the upper deciduous molars (Benazzi et al.,  
353 2012). And in a study comparing  $dm_2$  and  $M_1$  shapes, Bailey et al. (2016) confirmed that both  
354 lower molars discriminated between these two species less successfully than the upper molars.  
355 The results of the present study show that the  $dm_1$  is the least powerful in terms of discriminating  
356 Neanderthals from *H. sapiens*.

357 The mediocre discriminatory power of the  $dm_1$  in the present study is at least somewhat  
358 related to the wide range of shape variation in recent humans (more than has been observed in  
359 the other deciduous molars) and the greater similarity of EHS  $dm_1$  shape to that of Neanderthals,  
360 at least as far as can be determined with this small EHS sample. A previous study of the  $dm_2$  and  
361  $M_1$  (Bailey et al., 2016) also suggested that EHS and Neanderthal  $dm_2$  shapes do not differ  
362 significantly. However, in that study EHS specimens plotted well within the variation of both  
363 RHS and UPHS groups, which makes the dissimilarity between EHS and UPHS  $dm_1$  shapes

364 found in this study somewhat surprising. The similarities between EHS and Neanderthals may  
365 suggest that the lower dentition has undergone less change in EHS than it has in UPHS and RHS.  
366 Additional specimens from the Middle Pleistocene would help clarify the polarity of dm<sub>1</sub> crown  
367 shapes and confirm that this is the case.

368

## 369 **Conclusions**

370         Based on the recent series of studies of molar crown shapes, we conclude that the lower  
371 deciduous molars and the lower permanent M1 are less reliable than the upper molars for  
372 discriminating between Neanderthals and *H. sapiens*. Although our results for the dm<sub>1</sub> are  
373 somewhat mediocre over all, from a practical standpoint we can say that crown shape of the dm<sub>1</sub>  
374 is useful for identifying Neanderthals in a Late Pleistocene European context. Unfortunately, we  
375 would hesitate to use the dm<sub>1</sub> to identify *H. sapiens* from the same time period/region because  
376 the success rate is not much better than chance. In addition, we would not recommend using the  
377 dm<sub>1</sub> crown shape to discriminate between these two groups where they co-occur in the Near  
378 East, since the early *H. sapiens* dm<sub>1</sub> crown outline does not differ significantly from that of  
379 Neanderthals. In sum, the dm<sub>1</sub> crown shape is only of limited use for assigning isolated teeth to  
380 taxa.

381

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389

390 REFERENCES CITED

- 391 Adams, D.C., Otárola-Castillo, E., 2013. Geomorph: an R package for the collection and analysis  
392 of geometric morphometric shape data. *Methods in Ecology and Evolution* 4, 393-399.
- 393 Bailey, S.E., 2002a. A closer look at Neanderthal postcanine dental morphology. I. The  
394 mandibular dentition. *Anatomical Record* 269, 148-156.
- 395 Bailey, S.E., 2002b. Neandertal dental morphology: implications for modern human origins,  
396 Ph.D. Dissertation, Arizona State University.
- 397 Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle-Late  
398 Pleistocene hominins. *Journal of Human Evolution* 47, 183-198.
- 399 Bailey, S.E., 2006. Beyond shovel shaped incisors: Neandertal dental morphology in a  
400 comparative context. *Periodicum Biologorum* 108, 253-267.
- 401 Bailey, S.E., Benazzi, S., Buti, L., Hublin, J.-J., 2016. Allometry, merism, and tooth shape of the  
402 lower second deciduous molar and first permanent molar. *American Journal of Physical*  
403 *Anthropology* 159, 93-105.
- 404 Bailey, S.E., Benazzi, S., Hublin, J.-J., 2014a. Allometry, Merism and tooth shape of the upper  
405 deciduous M2 and permanent M1. *American Journal of Physical Anthropology* 154, 104-114.
- 406 Bailey, S.E., Benazzi, S., Souday, C., Astorino, C., Paul, K., Hublin, J.-J., 2014b. Taxonomic  
407 differences in deciduous upper second molar crown outlines of *Homo sapiens*, *Homo*  
408 *neanderthalensis* and *Homo erectus*. *Journal of Human Evolution* 72, 1-9.
- 409 Bailey, S.E., Hublin, J.-J., 2005. Who made the Early Aurignacian? A reconsideration of the  
410 Brassempouy dental remains. *Bulletins et mémoires de la Société d'anthropologie de Paris* 17,  
411 115-121.
- 412 Bailey, S.E., Lynch, J.M., 2005. Diagnostic differences in mandibular P4 shape between  
413 Neandertals and anatomically modern humans. *American Journal of Physical Anthropology* 126,  
414 268-277.
- 415 Bailey, S.E., Pilbrow, V.C., Wood, B.A., 2004. Interobserver error involved in independent  
416 attempts to measure cusp base areas of *Pan* M1s. *Journal of Anatomy* 205, 323-331.
- 417 Bailey, S.E., Weaver, T.D., Hublin, J.-J., 2009. Who made the Aurignacian and other early  
418 Upper Paleolithic industries? *Journal of Human Evolution* 57, 11-26.
- 419 Been, E., Hovers, E., Ekshtain, R., Malinski-Buller, A., Aghna, N., Barash, A., Bar-Yosef, Y.,  
420 Mayer, D., Benazzi, S., Hublin, J.-J., Leven, L., Greenbaum, N., Mitki, N., Oxilia, G., Porat, N.,  
421 Roskin, J., Soudack, M., Yeshurun, R., Shahack-Gross, R., Nir, N., Stahlschmidt, M.C., Rak, Y.,  
422 Barzilai, O., 2017. The first Neanderthal remains from an open-air Middle Palaeolithic site in the  
423 Levant. *Scientific Reports* 7, 1-8.

- 424 Benazzi, S., 2012. The first modern Europeans. *Journal of Anthropological Sciences* 90, 3-6.
- 425 Benazzi, S., Bailey, S.E., Peresani, M., Mannino, M.A., Romandini, M., Richards, M.P., Hublin,  
426 J.-J., 2014. Middle Paleolithic and Uluzzian human remains from Fumane Cave, Italy. *Journal of*  
427 *Human Evolution* 70, 61-68.
- 428 Benazzi, S., Coquerelle, M., Fiorenza, L., Bookstein, F., Katina, S., Kullmer, O., 2011a.  
429 Comparison of dental measurement systems for taxonomic assignment of first molars. *American*  
430 *Journal of Physical Anthropology* 144, 342-354.
- 431 Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F.,  
432 Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011b. Early  
433 dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479,  
434 525-528.
- 435 Benazzi, S., Fantini, M., De Crescenzo, F., Persiani, F., Gruppioni, G., 2009. Improving the  
436 spatial orientation of human teeth using a virtual 3D approach. *Journal of Human Evolution* 56,  
437 286-293.
- 438 Benazzi, S., Fornai, C., Buti, L., Toussaint, M., Mallegni, F., Ricci, S., Gruppioni, G., Weber,  
439 G.W., Condemi, S., Ronchitelli, A., 2012. Cervical and crown outline analysis of worn  
440 Neanderthal and modern human lower second deciduous molars. *American Journal of Physical*  
441 *Anthropology* 149, 537-546.
- 442 Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta,  
443 D., Vicino, G., Starnini, E., Mannino, M.A., Salvadori, P.A., Meyer, M., Pääbo, S., Hublin, J.-J.,  
444 2015. The makers of the Protoaurignacian and implications for Neanderthal extinction. *Science*  
445 348, 793-796.
- 446 Buti, L., 2013. Nuove prospettive di indagine tassonomica di denti decidui usurati attraverso  
447 analisi di immagine e tecnologie tridimensionali. Ph.D. Dissertation, Università di Firenze.
- 448 Churchill, S., Smith, F., 2000. Makers of the early Aurignacian of Europe. *Yearbook of Physical*  
449 *Anthropology* 43, 61-115.
- 450 Edgar, H.J.H., Lease, L.R., 2007. Correlations between deciduous and permanent tooth  
451 morphology in a European sample. *American Journal of Physical Anthropology* 133, 726-734.
- 452 Fabbri, P.F., Panetta, D., Sarti, L., Martini, F., Salvadori, P., Caramella, D., Fedi, M., Benazzi,  
453 S., 2016. Middle Paleolithic human deciduous incisor from Grotta del cavallo, Italy. *American*  
454 *Journal of Physical Anthropology* 161, 506-512.
- 455 Farmer, V., Townsend, G., 1993. Crown size variability in the deciduous dentition of South  
456 Australian children. *American Journal of Human Biology* 5, 681-690.
- 457 Fornai, C., Benazzi, S., Gopher, A., Barkai, R., Sarig, R., Bookstein, F.L., Hershkovitz, I.,  
458 Weber, G.W., 2016. The Qesem Cave hominin material (part 2): a morphometric analysis of  
459 dm2-QC2 deciduous lower second molar. *Quaternary International* 398, 175-189.

- 460 Ghasemi, A., Zahediasl, S., 2012. Normality tests for statistical analysis: a guide for non-  
461 statisticians. *International Journal of Endocrinology and Metabolism* 10, 486-489.
- 462 Gómez-Robles, A., Martínón-Torres, M., Bermúdez De Castro, J.M., Margvelashvili, A., Bastir,  
463 M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., Martínez, L.M., 2007. A geometric  
464 morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution* 55, 627-  
465 638.
- 466 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Prado-Simón, L., Arsuaga,  
467 J.L., 2011. A geometric morphometric analysis of hominin upper premolars. Shape variation and  
468 morphological integration. *Journal of Human Evolution* 61, 688-702.
- 469 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Prado, L., Sarmiento, S.,  
470 Arsuaga, J.L., 2008. Geometric morphometric analysis of the crown morphology of the lower  
471 first premolar of hominins, with special attention to Pleistocene *Homo*. *Journal of Human*  
472 *Evolution* 55, 627-638.
- 473 Hublin, J.-J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Enderova, E., Fagault,  
474 Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N., Paskulin,  
475 L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Svoboda, S., Skinner, M.,  
476 Smith, G., Spasov, R., Talamo, S., Tuna, T., Wacker, L., Welker, F., Wilcke, A., Zaharieva, N.,  
477 McPherron, S., Tsanova, T., 2020. Initial Upper Paleolithic *H. sapiens* from Bacho Kiro Cave,  
478 Bulgaria. *Nature*. 581, 299-302. doi.org/10.1038/s41586-020-2259-z
- 479 Jolliffe, I.T. 2002. *Principal Component Analysis*. Springer, New York.
- 480 Kieser, J.A., 1984. An analysis of the Carabelli trait in the mixed deciduous and permanent  
481 human dentition. *Archives of Oral Biology* 29, 403-406.
- 482 Kupczik, K., Hublin, J.-J., 2010. Mandibular molar root morphology in Neanderthals and Late  
483 Pleistocene and recent *Homo sapiens*. *Journal of Human Evolution* 59, 525-541.
- 484 Lacy, S.A., Bailey, S., Benazzi, S., Delage, C., 2018. Newly Recognized Human Dental Remains  
485 at Les Fadets (Lussac-les-Châteaux, Vienne, France). *Bulletins et mémoires de la Société*  
486 *d'anthropologie de Paris* 30, 180-191.
- 487 Le Cabec, A., Gunz, P., Kupczik, K., Braga, J., Hublin, J.-J., 2013 Anterior tooth root  
488 morphology and size in Neanderthals: taxonomic and functional implications. *Journal of Human*  
489 *Evolution* 64, 169-193.
- 490 Liversidge, H.M., Molleson, T., 1999. Deciduous tooth size and morphogenetic fields in children  
491 from Christ Church, Spitalfields. *Archives of Oral Biology* 44, 7-13.
- 492 Liversidge, H.M., Molleson, T., 2004. Variation in crown and root formation and eruption of  
493 human deciduous teeth. *American Journal of Physical Anthropology* 123, 172-180.
- 494 Margetts, B., Brown, T., 1978. Crown diameters of the deciduous teeth in Australian  
495 Aboriginals. *American Journal of Physical Anthropology* 48, 493-502.

496 Margherita, C., Talamo, S., Wiltshcke-Schrotta, K., Senck, S., Oxilia, G., Sorrentino, R.,  
497 Mancuso, G., Gruppioni, G., Lindner, R., Hublin, J.-J., Benazzi, S., 2016. A reassessment of the  
498 pre-seumed Torrenere Bärenhöhle's Paleolithic human tooth. *Journal of Human Evolution* 93, 120-  
499 125.

500 Molnar, S., 1971. Human tooth wear, tooth function and cultural variability. *American Journal of*  
501 *Physical Anthropology* 34, 27-42.

502 Moroni, A., Ronchitelli, A., Simona, A., Aureli, D., Bailey, S.E., Boscato, P., Boschin, F.,  
503 Capecchi, G., Crezzini, J., Douka, K., Marciani, G., Panetta, D., Ranaldo, F., Ricci, S.,  
504 Scaramucci, S., Spagnolo, V., Benazzi, S., Gambassini, P., 2018b. Grotta del Cavallo (Apulia –  
505 Southern Italy). The Uluzzian in the mirror. *Journal of Anthropological Sciences* 96, 125 - 160.

506 Morris, D.H., 1981. Maxillary first premolar angular differences between North American  
507 Indians and non-North American Indians. *American Journal of Physical Anthropology* 54, 431-  
508 433.

509 Paul, K.S., Astorino, C.M., Bailey, S.E., 2017. The Patterning Cascade Model and Carabelli's  
510 trait expression in metamerer of the mixed human dentition: exploring a morphogenetic model.  
511 *American Journal of Physical Anthropology* 162, 3-18.

512 R Core Team., 2017. R: A language and environment for statistical computing. R Foundation for  
513 Statistical Computing., Vienna, Austria.

514 Scott, G.R., Turner, C.G., II, 1997. *The Anthropology of Modern Human Teeth. Dental*  
515 *Morphology and its Variation in Recent Human Populations.* Cambridge University Press,  
516 Cambridge.

517 Sorrentino R, Belcastro MG, Figus C, Stephens NB, Turley K, Harcourt-Smith W, Ryan T,  
518 Benazzi S. 2020. Exploring sexual dimorphism of the modern human talus through geometric  
519 morphometric methods. *PLoS ONE* 15(2): e0229255.

520 Van Valen, L., 1962. A study of fluctuating asymmetry. *Evolution* 16, 125-142.

521 Wood, B.A., Abbott, S.A., 1983. Analysis of the dental morphology of Plio-Pleistocene  
522 hominids. I. Mandibular molars: crown area measurements and morphological traits. *Journal of*  
523 *Anatomy* 136, 197-219.

524 Wood, B.A., Engleman, C.A., 1988. Analysis of the dental morphology of Plio-Pleistocene  
525 hominids. V. Maxillary postcanine tooth morphology. *Journal of Anatomy* 161, 1-35.

526

527



528 Figure Legends

529 Figure 1. Comparison of A) upper and lower left dm2 and M1, and B) upper and lower left dm1  
530 and dm2 (all images represent the same recent *H. sapiens* from Peru). In both photos, upper is on  
531 the left, lower is on the right. For orientation: B = buccal, L = lingual, M = mesial, D = distal.

532 Figure 2. Illustration showing the most worn crown (stage 5 wear: Molnar, 1971) in our sample  
533 and how minor corrections were made to the outline before analysis (Early *H. sapiens* Die  
534 Kelders 6291). For orientation: B = buccal, L = lingual, M = mesial, D = distal.

535 Figure 3. Illustration showing methods for acquisition of pseudolandmarks on the left dm1 of the  
536 Kebara 1 Neanderthal. For orientation: B = buccal, L = lingual, M = mesial, D = distal.

537 Figure 4. Results of the Principal Components Analysis: all samples. The range of variation in  
538 recent *H. sapiens* encompasses that of nearly all fossil samples, whereas the fossil samples are  
539 more tightly constrained along the first three PCs. Center plot: PC1 against PC2. Upper left: PC1,  
540 PC2 and PC3. N, Neanderthal; EHS, Early *Homo sapiens*; RHS, Recent *Homo sapiens*; UPHS,  
541 Upper Paleolithic *Homo sapiens*. For orientation: B = buccal, L = lingual, M = mesial, D =  
542 distal.

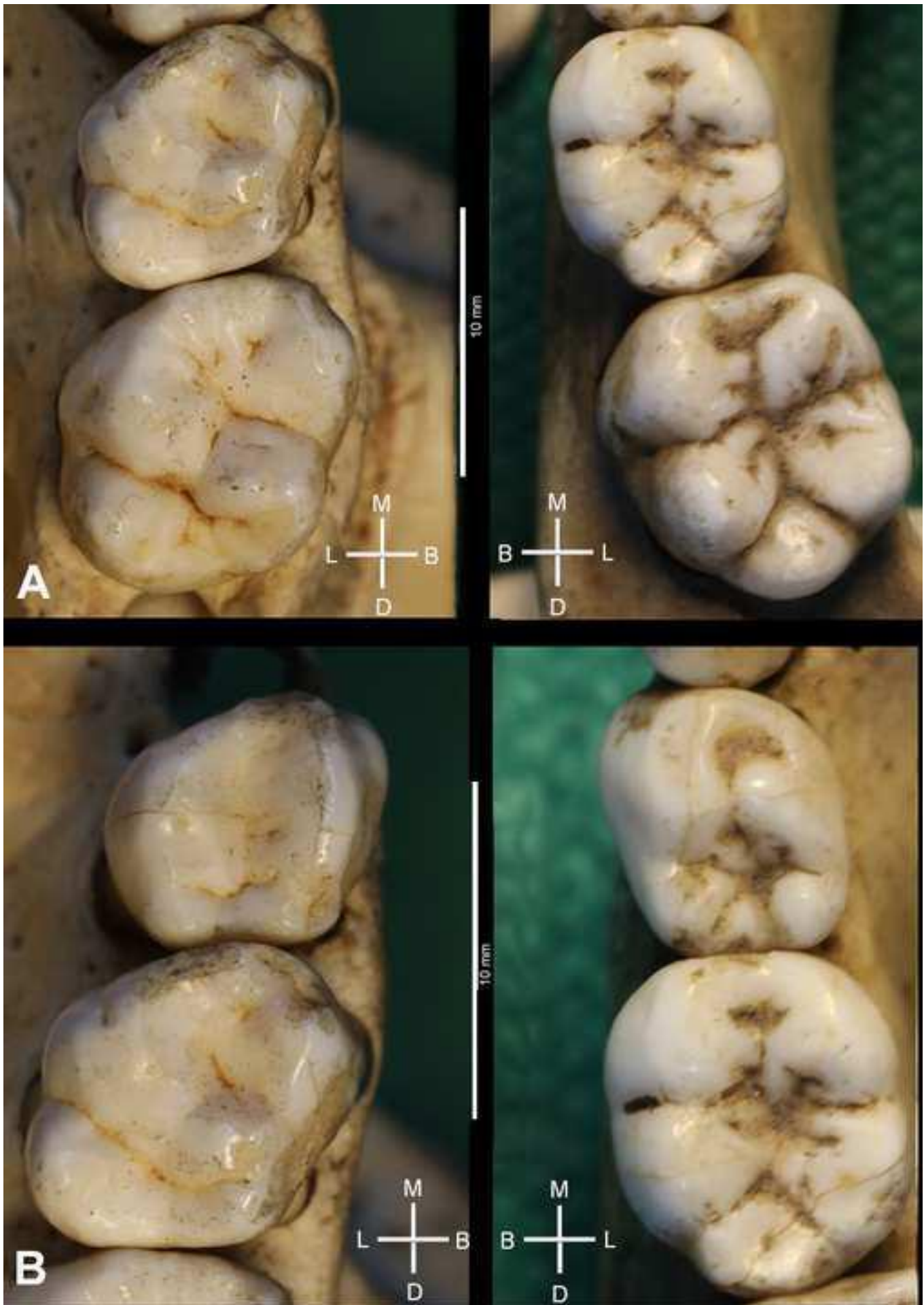
543 Figure 5. Results of the Principal Components Analysis of recent *H. sapiens* grouped by  
544 geographic origin. With the exception of the South American sample, which has only positive  
545 PC2 scores, there appears to be no geographic patterning to ldm1 shape based on the first two  
546 principal components. For orientation: B = buccal, L = lingual, M = mesial, D = distal.

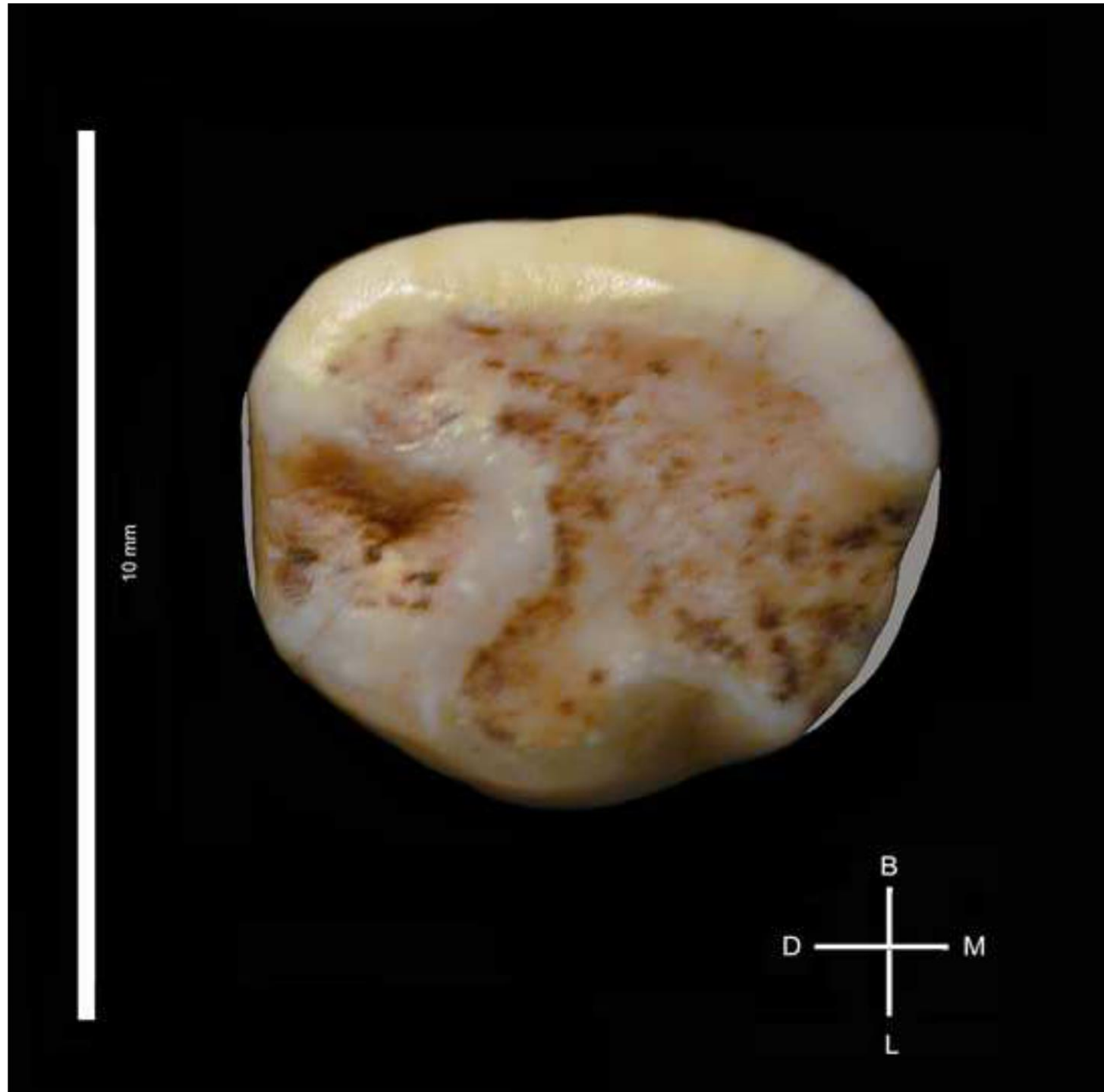
547 Figure 6. Comparison of mean shapes between Neanderthals (left) and Upper Paleolithic *H.*  
548 *sapiens* (right). Right arrow indicates mesiobuccal expansion (tuberculum molare) in Upper  
549 Paleolithic *H. sapiens*. Left arrow indicates more equal sized buccal and lingual cusps in  
550 Neanderthals. For orientation: B = buccal, L = lingual, M = mesial, D = distal.

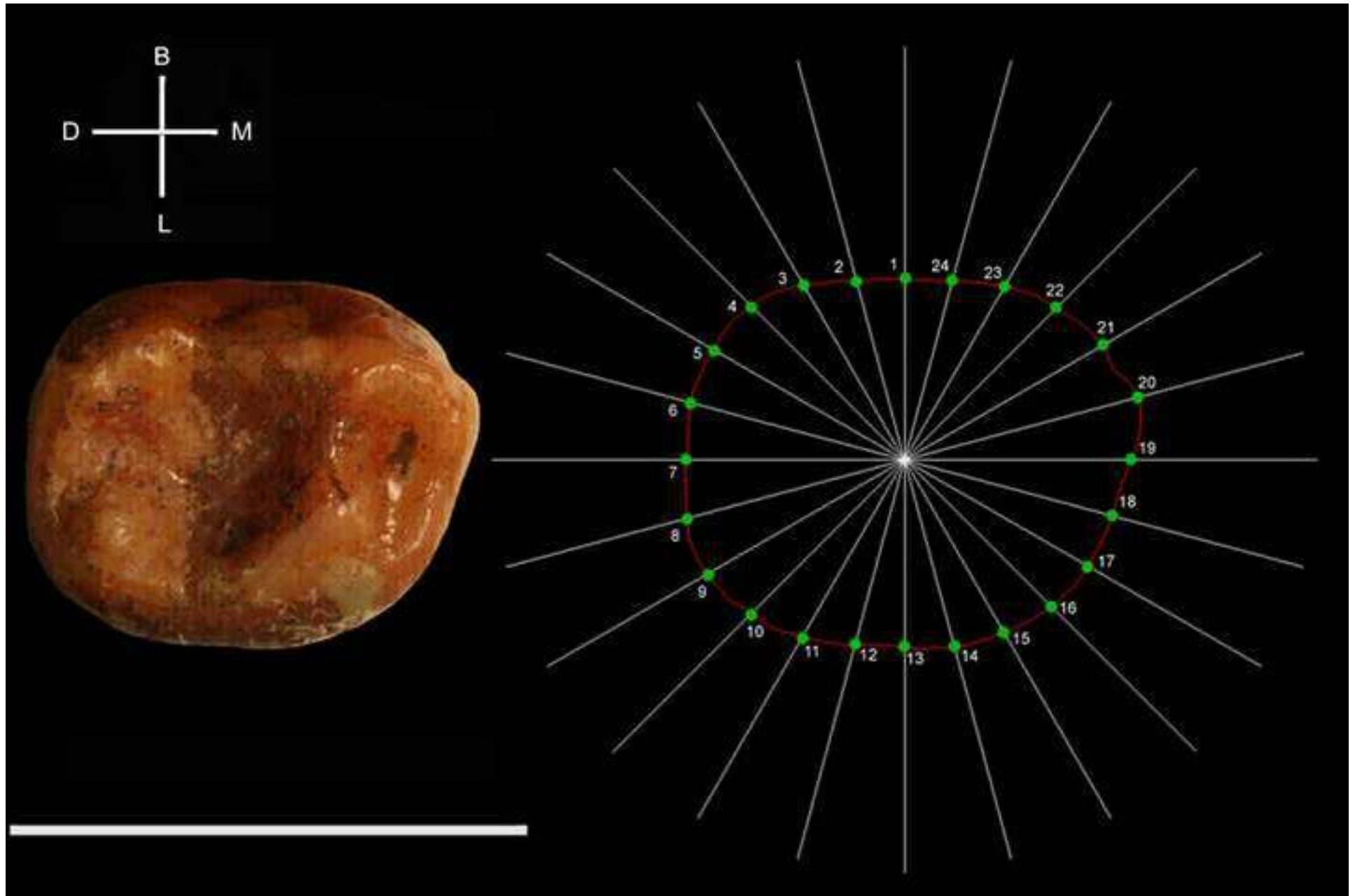
551 Figure 7. Variation of left dm1 crown shape within recent *H. sapiens* geographic populations. For  
552 orientation: B = buccal, L = lingual, M = mesial, D = distal.

553

554







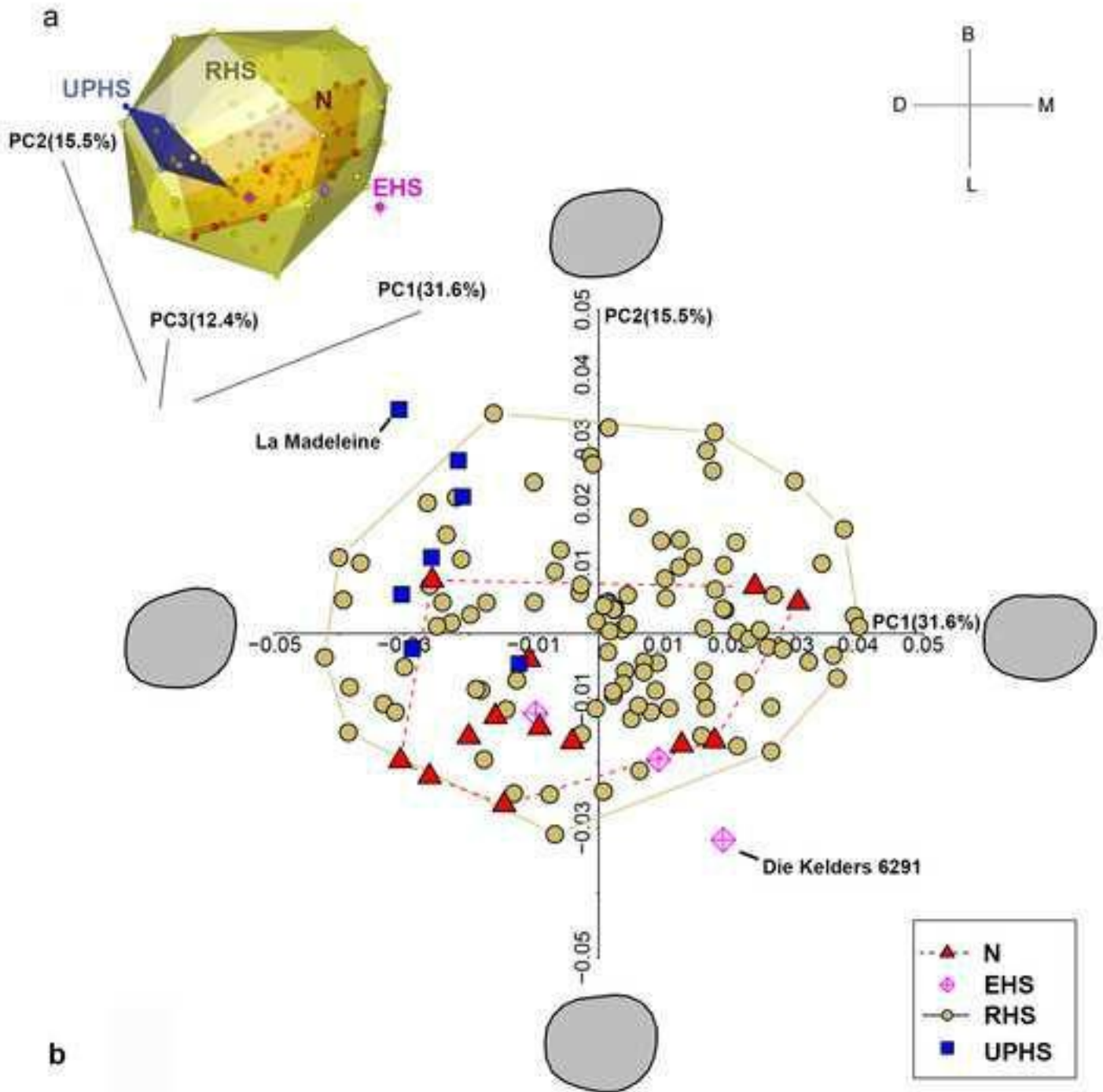
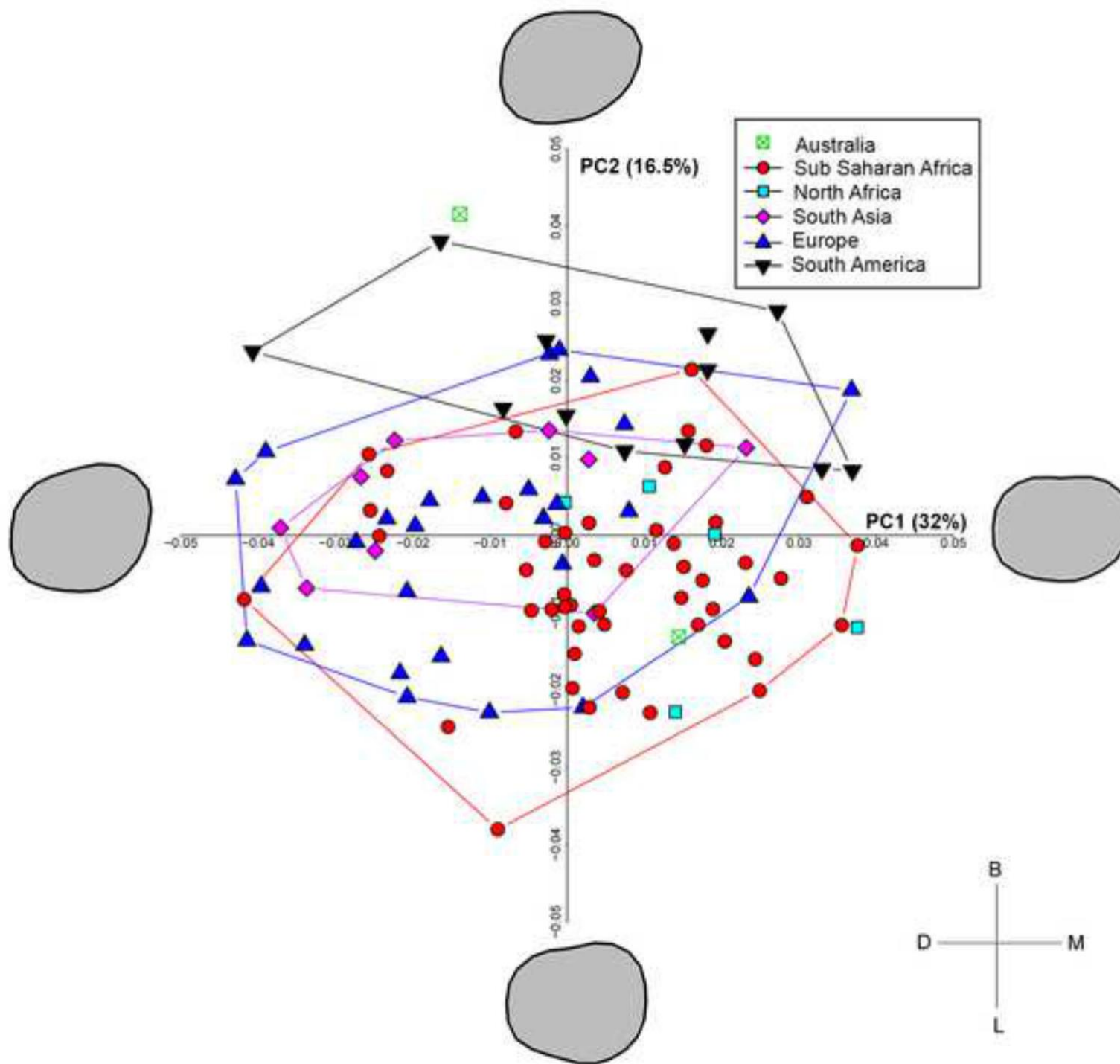
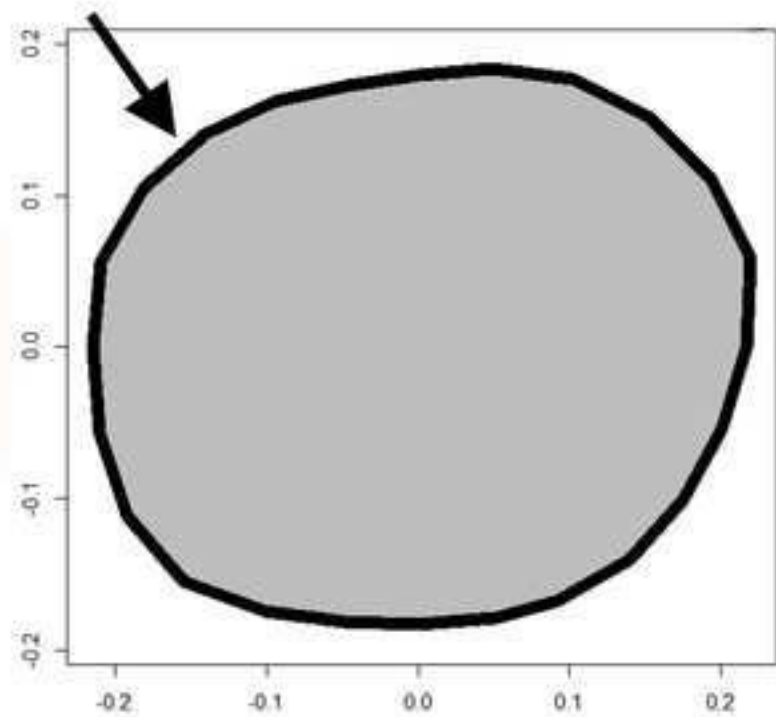
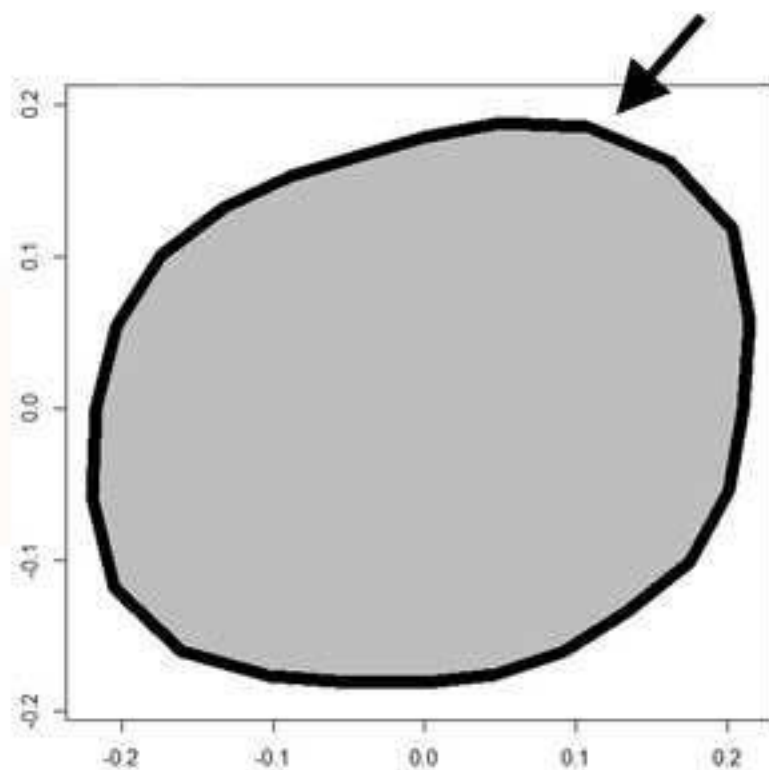
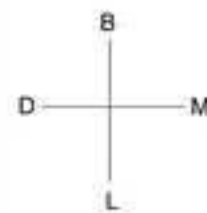


Figure 5





NEANDERTHAL MEAN SHAPE

UPPER PALEOLITHIC *H. SAPIENS* MEAN SHAPE





**Table 1**Materials used in this study.<sup>a</sup>

	No.	Sites sampled
Early <i>H. sapiens</i>	3	Die Kelders, Qafzeh
Upper Paleolithic <i>H. sapiens</i>	7	Balla Barlang, Estelas, La Grotte du Figuier, Isturitz, Lagar Velho, Abri de la Madeleine, Roche de Solutré
<i>H. neanderthalensis</i>	13	Archi, Arcy-sur-Cure, Barakai Cave, Bruniquel, Combe Grenal, Engis, Kebara, La Ferrassie, La Chaise, Riparo del Molare, Peche de l'Azé, Roc de Marsal, Mezmaiskaya
Recent <i>H. sapiens</i>	103	Africa, Asia, Australia, Europe, South America

<sup>a</sup> See SOM for sources of materials.**Table 2**Permutation tests of differences in crown shape of the  $dm_1$  between fossil and recent human samples.<sup>a</sup>

	Early <i>H. sapiens</i>	Neanderthal	Recent <i>H. sapiens</i>
<i>H. neanderthalensis</i> (n=13)	0.502		
Recent <i>H. sapiens</i> (n=103)	0.182	<b>0.010</b>	
Upper Paleolithic <i>H. sapiens</i> (n=7)	<b>0.002</b>	<b>0.002</b>	<b>0.001</b>

<sup>a</sup>Significant differences ( $p < 0.05$ ) are in bold.**Table 3**Permutation tests of differences in crown shape of the  $dm_1$  between recent human geographic subsamples.<sup>a-b</sup>

	Europe	North Africa	South America	South Asia
Europe (n=28)				
North Africa (n=5)	<b>0.025</b>			
South America (n=12)	<b>0.001</b>	0.054		
South Asia (n=9)	0.884	<b>0.040</b>	<b>0.032</b>	
Sub-Saharan Africa (n=49)	<b>0.001</b>	0.884	<b>0.001</b>	<b>0.032</b>

<sup>a</sup>The Australia sample is excluded in the permutation test because of its small (n=2) sample size'<sup>b</sup>Significant differences ( $p < 0.05$ ) are in bold.**Table 4**Results of quadratic discriminant functions assignments (fossil and recent *H. sapiens* combined) based on crown shape of the  $dm_1$  by using 8 PCs (accounting for 90.7% of the variation).

	<i>H. neanderthalensis</i>	<i>H. sapiens</i>	% correct
<i>H. neanderthalensis</i> (n=13)	8	5	61.5
<i>H. sapiens</i> (n=113)	11	102	90.2

**Table 5**

Results of quadratic discriminant functions assignments (fossil and recent *H. sapiens* separated) based on crown shape of the  $dm_1$  using 4 PCs (accounting for 70.3% of the variation). Early *H. sapiens* are excluded due to small sample size.

	<i>H. neanderthalensis</i>	<i>H. sapiens</i>	Upper Paleolithic <i>H. sapiens</i>	% correct
<i>H. neanderthalensis</i> (n = 13)	7	4	2	53.8
Recent <i>H. sapiens</i> (n = 103)	4	79	16	76.7
Upper Paleolithic <i>H. sapiens</i> (n = 7)	0	4	3	42.9

**Table 6**

Results of quadratic discriminant functions assignments (Upper Paleolithic *H. sapiens* and *H. neanderthalensis* only) by using 4 PCs (accounting for 70.3% of the variation). Early *H. sapiens* are excluded due to small sample size.

	<i>H. neanderthalensis</i>	Upper Paleolithic <i>H. sapiens</i>	% correct
<i>H. neanderthalensis</i> (n = 13)	11	2	84.6
Upper Paleolithic <i>H. sapiens</i> (n = 7)	3	4	57.1