

1 The morphology of the Late Pleistocene hominin remains from the site of La Cotte de St
2 Brelade, Jersey (Channel Islands)

3

4 **ABSTRACT**

5 Thirteen permanent fully-erupted teeth were excavated at the Paleolithic site of La Cotte de
6 St Brelade in Jersey in 1910 and 1911. These were all found in the same location, on a ledge
7 behind a hearth in a Mousterian occupation level. They were originally identified as being
8 Neanderthal. A fragment of occipital bone was found in a separate locality in a later season.
9 Recent dating of adjacent sediments gives a probable age of <48 ka. The purpose of this
10 paper is to provide an updated description of the morphology of this material, and consider its
11 likely taxonomic assignment from comparison with Neanderthal and *Homo sapiens* samples.
12 One of the original teeth has been lost, and we identify one as non-hominin. At least two
13 adult individuals are represented. Cervix shape and the absence of common Neanderthal traits
14 in several teeth suggest affinities with *H. sapiens* in both individuals, while crown and root
15 dimensions and root morphology of all the teeth are entirely consistent with a Neanderthal
16 attribution, pointing towards a possible shared Neanderthal and *H. sapiens* ancestry (the
17 likely date of this material corresponds with the time in which both Neanderthals and *H.*
18 *sapiens* were present in Europe). The occipital fragment is stratigraphically more recent and
19 does not exhibit any diagnostic Neanderthal features.

20

21 **Keywords:** Hominin teeth; Late Pleistocene; Neanderthal; European Pleistocene *Homo*
22 *sapiens*; La Cotte de St. Brelade; Hominin morphology.

23

24 **1. Introduction**

25 The timing and duration of overlaps between *Homo sapiens* and Neanderthals in Europe,
26 and the nature of their interaction, have long been debated by archaeologists and
27 anthropologists (e.g., Stringer, 2006; Hoffercker, 2009). Recent evidence points towards
28 contemporaneity or alternation of occupation of the two populations (Benazzi et al., 2011;
29 Harvati et al., 2019). The application of improved radiocarbon dating methods has shown that
30 the Mousterian ended by ~41–39 ka cal BP across much of Europe (Higham et al., 2014).
31 Furthermore, new data from Bulgaria suggest that *H. sapiens* were already in Eastern Europe
32 by ~45 ka, several millennia before the physical disappearance of the Neanderthals from the
33 region. Hominin fossils from Bacho Kiro were identified as *H. sapiens* from morphology and
34 mtDNA analysis, and directly dated to ~46.8–42.8 ka cal BP (Fewlass et al., 2020; Hublin et
35 al., 2020). Radiocarbon dating shows a clear overlap of the initial Upper Paleolithic at Bacho
36 Kiro with the late Mousterian and Châtelperronian attributed to late Neanderthal populations
37 (Fewlass et al., 2020). In central and northwestern Europe, the Châtelperronian (~44–40 ka)
38 overlaps with both the Early Aurignacian, starting at ~43–42 ka, and the Proto-Aurignacian,
39 starting at ~42 ka (Hublin, 2015). In Western Europe, there is direct fossil evidence for the
40 presence of both *H. sapiens* and Neanderthals at ~41–40.4 ka. A tooth discovered in a Proto-
41 Aurignacian context at the site of Grotta di Fumane in northern Italy and dated to ~41–38.5
42 ka cal BP was found to have *H. sapiens* DNA (Benazzi et al., 2015), while a Neanderthal
43 tibia from Saint-Césaire in western France was directly dated to ~42–40.6 ka cal BP (Hublin
44 et al., 2012) and Neanderthal fossils from Spy in Belgium have been directly dated to
45 ~42.2–40.4 ka cal BP (Semal et al., 2013). The Oase 1 *H. sapiens* from Romania, dated to
46 ~42.5–40.5 ka cal BP (Zilhão et al., 2007), had a Neanderthal ancestor within the previous six
47 generations (Fu et al., 2015), which demonstrates that these populations probably did overlap
48 in Europe before 40 ka. In support of this, Peter (2019) has determined that, while the
49 majority of Neanderthal ancestry entered *H. sapiens* populations between ~55 and ~48 ka,

50 there was a lesser amount of gene flow within Europe, ending at ~40 ka. Interestingly,
51 Hajdinjak et al. (2018) found no evidence of recent gene flow from *H. sapiens* in four very
52 late Neanderthals, dated to <45 ka cal BP, from Goyet, Spy, Les Cottés and Mezmaiskaya.

53 The hominin remains from La Cotte de St Brelade on Jersey (Fig. 1) probably fall within
54 this key time period when both Neanderthals and *H. sapiens* were present in Western Europe.
55 Their taxonomic status is therefore of considerable interest. The hominin remains ~~from La~~
56 ~~Cotte de St Brelade~~ originate from an area of complex sedimentation close to where the
57 North and West Ravines meet (Fig. 2). Members of the Société Jersiaise undertook
58 excavation in this area in 1910–1911 after the cave entrance had been cleared of clay and
59 granite rubble deposits. The investigators located a series of fine-grained deposits, some of
60 which were rich in ash and carbonized wood, which they described as hearths (Nicolle and
61 Sinel, 1910). The excavations of these deposits continued until 1920 and produced at least
62 20,000 stone artifacts (Callow, 1986a), but it appears that smaller debitage elements were
63 largely discarded during the initial seasons. These artifacts were described at the time as
64 Mousterian in character (Marett, 1916), and more recent analysis has confirmed that all the
65 stone artifacts are consistent with Late Middle Paleolithic technological practices (Callow,
66 1986a). The assemblage contains both Levallois and discoidal production elements, as well as
67 formal tools, including side scrapers and two bifaces. No artifacts consistent with Upper
68 Paleolithic technology have been identified among the artifact collections of La Cotte de St
69 Brelade.

70 It is not possible to determine what fauna were found within deposits directly associated
71 with the hominin remains from the surviving archive of the excavations carried out between
72 1910 and 1920. However, the faunal material recovered from ‘Weichselian’ units as a whole
73 includes *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp., *Rangifer tarandus*,
74 *Crocuta crocuta*, and *Vulpes vulpes* (see Callow, 1986b), species which would be consistent

75 with a Marine Isotope Stage (MIS) 3 attribution in northern France (Auguste, 2009).
76 Mammoth, woolly rhinoceros and horse are specifically mentioned as coming from the same
77 general area as the hominin teeth (Nicolle and Sinel, 1910; Keith and Knowles, 1911).

78 The hominin teeth were discovered over two seasons. In 1910, nine teeth were found in a
79 mass of poorly preserved bone (for which no identifications are recorded) on a rock ledge
80 above the layer identified as a hearth (Fig. 3; Nicolle and Sinel, 1910). They were described
81 as lying side by side in original position, but with no trace of once supporting bone apparent.
82 A further four teeth were found in clay adhering to the rock at the same location in 1911
83 (Nicolle and Sinel, 1912). An occipital fragment, together with two other bone fragments,
84 were discovered in a ravine 6 ft (1.8 m) beyond the entrance of the cave and 18 ft (5.4 m)
85 above the Mousterian cave floor level by Ernest Daghorn in 1915 (Marett, 1916).

86 Analysis of the surviving archive and a modern survey of the site have allowed us to
87 broadly identify the location and position in the stratigraphic succession from which the
88 hominin teeth were recovered and, more generally, the position and context of the hominin
89 occipital fragment (Table 1). Although the deposits from this part of the site were removed
90 during the early 20th century, their stratigraphic equivalents appear to extend into areas of
91 remaining sediment within the main West Ravine (Bates et al., 2013). Optically stimulated
92 luminescence (OSL) dating undertaken in 2011 within the middle parts of this sequence,
93 approximately 4 m below the location where the teeth were discovered, suggests that the
94 deposits containing the teeth and the occipital fragment both postdate ~48 ka (Bates et al.,
95 2013). In view of the vertical extent of sediments between the lower dated horizon and the
96 location from which we understand the teeth to have been discovered, a date that is clearly
97 younger than 48 ka for the teeth is the only tenable proposition. It is plausible that these
98 deposits span a period in which both late Neanderthal populations and those of *H. sapiens*
99 were present in Western Europe, and during which sea levels were low enough for Jersey to

100 be part of a continuous landmass with France (Fig. 1B; Scott et al., 2014; Shaw et al., 2016).
101 Consequently, understanding the exact date and taxonomic affinity of these hominin fossils is
102 important for understanding Pleistocene population replacement at a regional scale.

103 The teeth were originally described by Keith and Knowles (1911, 1912). The 1912 paper
104 is a reprint of the 1911 paper, with additional details of the four teeth found in 1911. Keith
105 (1913) further addressed the considerable level of taurodontism in the molar teeth. The teeth
106 were briefly described in Marett (1911) and Oakley et al. (1975), and more recently were
107 studied by Stringer and Carrant (1986), who noted that by this date two of the teeth were only
108 represented by casts and one other tooth was missing. The missing tooth was a left I¹,
109 represented only by the root. The crown of this tooth had disintegrated before it was seen by
110 Arthur Keith, as the result of an accident during conservation (letter from J. Sinel to Keith
111 dated 1st September 1911, in the archives of the Royal College of Surgeons). In 1929 Tom
112 Watson, an amateur paleontologist/archaeologist on Jersey, sent a hominin lower canine that
113 he had found at La Cotte to Arthur Keith for identification (letter dated 17th January 1929, in
114 the archives of the Royal College of Surgeons). Although Tom Watson left all his finds to the
115 Jersey Museum, this tooth has not come to light. This letter also states that Tom Watson had
116 previously sent teeth and bones that he had discovered at La Cotte to Arthur Keith for
117 identification, but no record of these has been found. The three bone fragments recovered in
118 1915 were initially identified as parts of an occipital, malar and mandible from a single
119 juvenile skull (Marett, 1916). Angel and Coon (1954) reanalyzed the material and concluded
120 that only the occipital fragment was human, and that it belonged to a child about 5 years old.
121 This opinion was supported by Stringer and Carrant (1986), who agreed that the other two
122 fragments did not represent any part of the human skeleton.

123 The purpose of this paper is to provide an updated description of the morphology of the La
124 Cotte teeth and the occipital fragment, and present data relevant to their taxonomic
125 attribution.

126

127 **2. Materials and methods**

128 *2.1. Described material from La Cotte*

129 The material available for study consists of ten isolated permanent fully erupted teeth
130 (Table 2), and a fragment of occipital. These are held by the Jersey Museum, and were
131 temporarily loaned to the Natural History Museum, London, in 2015. Two other teeth,
132 SJMJ2462 (right I₁) and SJMJ2467 (left M³), are represented by casts. The casts made in
133 1911 and now held by the Natural History Museum, London, were used in this study because,
134 of several casts available, they are the most similar to the teeth described and illustrated by
135 Keith and Knowles (1912). The right I₁ (SJMJ2462) is thought to be non-hominin and is not
136 included in the analysis (see Supplementary Online Material [SOM] S1). With permission of
137 Jersey Heritage, the microtomographic scans of the La Cotte de St Brelade specimens
138 published in this paper are publically available (under a CC BY-NC 4.0 license) through the
139 Human Fossil Record online archive (<https://human-fossil-record.org/>).

140

141 *2.2. Comparative material*

142 Comparative samples for morphological traits scored at the outer enamel surface (OES)
143 principally come from Bailey (2006a) and, where the trait is not scored by Bailey (2006a),
144 from Martín-Torres et al. (2012)—see SOM Tables S1 and S2. These samples consist of
145 Neanderthals and fossil (primarily European Late Pleistocene) *H. sapiens*. Comparative CT-
146 scan samples employed for geometric morphometrics, and occurrence of Tomes' root
147 (Arizona State University dental anthropology system [ASUDAS] grades 4–5: Turner et al.,

148 1991) and taurodontism in P₃ and P₄, consist of Neanderthals, fossil (Pleistocene) *H. sapiens*
149 and recent (Holocene) *H. sapiens* (SOM Tables S1, S3, S4). Comparative metrics data for the
150 early Neanderthal site of Krapina, late Neanderthals and fossil (European Late Pleistocene)
151 *H. sapiens* were taken from the literature and the NESPOS database (2013), identified in
152 table legends and in SOM Tables S1–S3, S5, S6. For crown dimensions, the site of Krapina
153 was separated from late Neanderthals because of the distorting effect caused by the relatively
154 large size of the Krapina tooth crowns, and in some cases their different shape, together with
155 the fact that the Krapina teeth make up approximately one third of the total Neanderthal
156 sample.

157

158 2.3. Methods

159 Definitions We use the terms pre-Neanderthal (e.g., Atapuerca-SH, Pontnewydd), early
160 Neanderthal (e.g., Krapina, Bourgeois-Delaunay), and classic/late Neanderthal, as proposed
161 by Dean et al. (1998). Although this assumed a linear and almost certainly oversimplified
162 model of Neanderthal evolution (Hublin and Roebroeks, 2009), Compton and Stringer (2015)
163 found it useful in classifying morphological differences observed in Neanderthal dentitions.

164 Dental morphological traits Most of the morphological traits were assessed using the Arizona
165 State University Dental Anthropology System (ASUDAS), and associated reference plaques
166 (Turner et al., 1991; Scott and Turner, 1997; Scott et al., 2018). Additional traits described by
167 other authors and not included in the ASUDAS were also utilized (see SOM S2 for
168 descriptions of the traits studied). Wherever possible, traits were scored at the OES but, due
169 to wear, some traits could only be scored at the enamel dentine junction (EDJ). There are few
170 comparative data available for the frequency of traits at the EDJ, and they are only provided
171 here for P⁴. In other cases, traits scored at the EDJ were compared to frequencies of traits at
172 the OES. Several authors have found a strong positive correlation between the EDJ and the

173 OES in the expression of morphological traits in hominins (Krenn et al., 2019 for lower
174 premolars; Guy et al., 2015 for upper molars; Skinner et al., 2008, 2010 for lower molars) but
175 we recognize that wear obscures the OES and can lead to misidentification of trait
176 expression. For each trait, 95% confidence limits were calculated for trait frequency in each
177 taxon, and for the difference in frequencies between the two taxa (SOM S3). Traits that are of
178 potential use in making inferences about taxonomic affiliation are those where the confidence
179 intervals for the two comparative samples do not overlap, or where the confidence limits for
180 the difference in frequencies between the two comparative samples are both either above or
181 below zero (i.e., do not include zero; Altman et al., 2000).

182 Relative cusp areas and occlusal polygon Relative cusp areas, and the angles and relative size
183 of the occlusal polygon, on SJMJ2456 (right M¹) were measured from a high definition
184 photograph of the occlusal surface taken perpendicular to the plane of the cervix, using
185 ImageJ software (Rasband, 2008), according to the methodology described by Bailey (2004).
186 The original positions of the cusp tips were estimated by determining the point of intersection
187 of the principal ridges of each cusp visible at the EDJ,

188 Taurodontism The degree of taurodontism of the molars was determined using the method of
189 Shifman and Chananel (1978). Shifman and Chananel's (1978) method was employed (SOM
190 S2) because it provides an absolute measurement, rather than a relative measurement that
191 requires complete roots. The distance between the bicervical line and the highest point on the
192 floor of the pulp cavity of the molar teeth was measured from the CT scans (Table 2: pulp
193 chamber height). This is preferable to taking the measurement from the roof of the pulp
194 chamber, where secondary dentine may form as the tooth wears. The method presented by
195 Keene (1966; see SOM S2) was used to measure the degree of taurodontism in SJMJ2461
196 (right M₂), because the original root length could be estimated. The original length of the root

197 of this tooth ~~SJMJ2461 (right M₂)~~, where the broken sides of the tooth's root are converging,
198 was estimated by extending these on a scaled photograph, and assuming a rounded tip.
199 Geometric morphometrics of cervix shape Microtomography was used to examine the
200 internal structures of the teeth. Specimens were scanned at the Natural History Museum using
201 an XTekCT scanner (180 kV, 205 μA, 0.25mm copper filter, 3000 projections) with a
202 resultant isometric voxel size of ~30 μm. To facilitate segmentation, each image stack was
203 filtered using a mean-of-least-variance filter (kernel size one) or a median and mean-of least
204 variance filter (each with kernel size three; Wollny et al., 2013). Each tooth was segmented
205 into its enamel and dentine components in Avizo 6.3 (ThermoFisher Scientific, Waltham).
206 Surface models of the EDJ were produced using the surface generation module
207 (unconstrained smoothing) and saved as PLY files.

208 Geometric morphometric analysis of cervix shape (in almost all cases the dentine horns,
209 and the ridges between, were too worn for landmark-based measurement) was conducted in
210 Mathematica 10 (Wolfram, Long Hanborough) following protocols outlined in previous
211 publications (Skinner and Gunz, 2010; Martin et al., 2017). Thirty semilandmarks were
212 placed around the cervix of each tooth. For the mandibular molars, the initial cervix landmark
213 was placed on the mesiobuccal corner of the crown (beneath the protoconid) and continued
214 mesially. In the maxillary molars, the initial landmark was placed on the middle part of the
215 buccal face of the crown (between the paracone and metacone) and continued mesially. For
216 mandibular and maxillary premolars the initial landmark was placed at the mid-point of the
217 buccal face and continued mesially. Estimations of missing portions of the cervix were made
218 for SJMJ 2457 (left P⁴), 2456 (right M¹) and 2461 (right M₂; SOM Fig. S1), and subjected to
219 Procrustes superimposition and then slid (Gunz and Mitteroecker, 2013) to create a
220 geometrically homologous set of shape variables. Principal components analysis (PCA) was
221 conducted to assess variation in cervix shape. Canonical variate analysis (CVA) was

222 conducted to assess taxonomic affinity using inclusive sets of principal component scores
223 (i.e., first set using 1–5 PCs, second set using 1–6 PCs, etc.) that represented ~95% of overall
224 shape variation. PCA was conducted in both shape space and form space; the latter including
225 the log of centroid size as a variable. CVA was only conducted in shape space and attempted
226 to assign La Cotte teeth to either Neanderthals or *H. sapiens*.

227 Crown and root measurements Measurements of the La Cotte teeth were taken with sliding
228 calipers to the nearest 0.1 mm. The crown dimensions and root lengths were measured using
229 the method of Moorrees (1957): crown = maximum dimensions parallel to and at right angles
230 to the buccal surface; root = maximum vertical dimension from the cervix of the mesiobuccal
231 root on the buccal aspect. In multirouted teeth, the term ‘trunk’ is used to describe the portion
232 of the root between the cervix and the point at which the individual roots furcate, and root
233 trunk length was measured as the distance between the cervix and the root furcation on the
234 aspect of the tooth on which this was at a minimum. The dimensions of the root at the cervix
235 were measured as the maximum dimensions at right angles to the mesial and buccal surfaces.
236 This definition was also used to measure cervical dimensions from CT scans of comparative
237 samples. Where the measurements for both left and right antimeres are available, the average
238 was used. Mesiodistal crown dimensions of the La Cotte teeth were adjusted for wear using
239 the method of Wood and Abbott (1983), in which the estimated original margins of the tooth
240 are drawn on a scaled photograph of the occlusal surface and the difference between these
241 and the actual margins measured. The adjusted measurements were used for comparisons
242 with other teeth. Where the length of the La Cotte teeth could not be estimated, only the
243 buccolingual dimension is used for comparison with other teeth. The level of occlusal wear
244 was quantified using Murphy's method, as summarized by Smith (1984; Table 2).

245 An adjusted z-score method, using Student's t inverse distribution (Maureille et al., 2001),
246 was employed to compare each of the La Cotte measurements with the means and standard
247 deviations of comparative groups. The formula applied was:

$$\frac{\text{La Cotte dimension} - X}{\text{Inv}t_{0,975; n-1} * SD}$$

250 where X, SD and n represent the mean, sample standard deviation and sample size
251 respectively of the comparative sample. The interval between -1 and +1 comprises 95% of
252 the variation in the comparative sample. A value of zero denotes that the La Cotte dimension
253 equals the mean of the comparative sample. A positive adjusted Z score indicates a La Cotte
254 dimension above the mean value and vice versa. All measurements and observations on the
255 La Cotte teeth were repeated by the same observer after an interval of one month.

256

257 3. Results

258 3.1. Descriptions

259 The tooth crown and roots appear to not have undergone any erosive taphonomic
260 processes. However, cracking and areas of taphonomic reworking of the dentine are evident
261 in the CT scans. Layers of cementum are apparent on the apical half of the root surfaces, with
262 the exception of SJMJ2459 (right M³), but hypercementosis is not present. The pulp
263 chambers of the teeth exhibit what appears to be demineralisation and subsequent desiccation
264 ~~taphonomic alteration~~ of the circumpulpal primary dentine, leading to it having a 'feathered'
265 appearance (C. Dean, pers. comm.). There are deposits of secondary dentine in the molar
266 pulp chambers. All the teeth show some wear and this is generally flat and near horizontal.
267 Most tooth crowns have dentine exposed on individual cusps, and the surface morphology
268 has largely been obliterated.

269 Our identifications of tooth type are in agreement with those given by Keith and Knowles
270 (1912). Traits are described using the ASUDAS grades (Turner et al., 1991) unless otherwise

271 stated. X-ray photographs of the teeth are shown in SOM Figures S2 and S3. Discrete
272 morphological traits of the teeth, along with comparative data, are reported in Tables 3–7.

273 Lower left permanent canine (SJMJ2463) See Figure 4. The crown is complete, but the apex
274 of the root is missing. Severe cracking is evident on the buccal surface of the root below the
275 cervix and running down the distal surface from this point to the apex. This is also evident in
276 the buccolingual CT slice (Fig. 4h).

277 There is moderate (grade 2) shoveling (Fig. 4a), trace (grade 1) double shoveling (Fig. 4a),
278 a grade 4 distal accessory ridge (Fig. 4g), and a mesiobuccal bulge viewed occlusally.
279 Lingually, a tuberculum dentale is present as a mild medially placed bulge without a free
280 apex and there is a faint, wide but low, lingual medial ridge (Fig. 4g). The root is
281 labiolingually wide, with deep mesial and distal longitudinal grooves. The mesial groove is
282 particularly marked. The pulp canal is single and ovoid throughout the root, wide viewed
283 distally, and mesiodistally flattened (Fig. 4h, i). There is distinct vertical convex curvature of
284 the buccal aspect of the root, particularly towards the apex, and vertical convexity of the
285 lingual aspect.

286 Upper left fourth premolar (SJMJ2457) See Figure 5. The preserved morphology (narrow and
287 ovoid, rather than a more triangular crown shape) is consistent with a P⁴. The tooth has
288 matching occlusion (facets, wear shape and level of wear) with the left P₄ (SJMJ2465). The
289 crown has a postmortem chip on the distolingual corner of the occlusal rim, at the edge of a
290 large double fracture, and the root apices are missing. The distal aspect of the crown must
291 have broken off in life, since there is rounding and vertical striations on the occlusal edge of
292 the fracture.

293 The buccal surface of the crown is swollen, viewed mesially. The sagittal sulcus is visible
294 at the OES, curved lingually at the distal end (Fig. 5d) and, from the EDJ, it can be seen that
295 it terminates at the mesial margin (Fig. 5g). The EDJ reveals a small mesial accessory crest

296 (Fig. 5g), that likely delineated a small mesial fovea in the unworn tooth. A small pit is still
297 visible in this location on the worn occlusal surface (Fig. 5d). There are two robust roots,
298 with separate root canals, linked mesially by a radicular plate, creating a deep groove on the
299 distal root surface (cross-section in Fig. 5i). The buccal root is vertically convex. The pulp
300 chamber is taurodont, extending to the root furcation. It is mildly ovoid in distal and buccal
301 views (Fig. 5h; SOM Fig. S4).

302 Lower left third premolar (SJMJ2464) See Figure 6. The large size of the buccal cusp, and its
303 more lingual placement than in SJMJ2465 (left P₄), and our analysis of cervix shape (SOM
304 Fig. S5) indicate a P₃. Additionally, a buccal cingulum is present at the EDJ, which occurs
305 only on the P₃ in the comparative samples. The crown is complete, but the root apices are
306 missing.

307 The occlusal crown outline is buccolingually oblong, with slight mesiolingual truncation
308 (insufficient to score tooth as asymmetric) and the mesiodistal dimension greatest buccally.
309 Viewed mesially, the upper part of the buccal surface is curved sharply lingually and the
310 lingual surface is swollen. The bulbous metaconid is mesially placed, and there are two
311 smaller distolingual cusps observable at the OES (Fig. 6a). The Y-shaped mesiobuccally
312 slanted sagittal sulcus is not interrupted (Fig. 6a). It is narrow and the two foveae are
313 insignificant, the distal being the deepest. Traces of mesial and distal accessory ridges can be
314 seen on the buccal cusp at the OES, and are clearly visible at the EDJ (Fig. 6d, g). A faint
315 distolingual groove is present at the OES (Fig. 6a, d), but the lingual margin is uninterrupted
316 at the EDJ (Fig. 6g; Davies et al., 2019). The mesial and distal margins also both appear to
317 have been uninterrupted (there is no evidence of interruption at the EDJ). Examination of the
318 EDJ (Fig. 6g) indicates no evidence of a transverse crest. Small dentine horns underlie the
319 two accessory cusps distal to the metaconid (Fig 6g). Although not visible at the enamel

320 surface, there is a faint buccal cingulum at the EDJ, consisting of a mesially placed horizontal
321 ridge continuing from a slight mesial vertical groove/ridge (not shown).

322 There is a grade 4 Tomes' root (cross-section in Fig. 6i), with partial division into two
323 roots, each with a single root canal. In the mesiobuccal root there is a vertical mesial groove
324 and a prominent buccal groove. The buccal aspect of this root is vertically convex. The
325 taurodont pulp chamber extends to the root furcation and is mildly ovoid in lingual view
326 (SOM Fig. S6). In distal view it is convex lingually on the lingual side at the cervix, and is
327 hourglass shaped below this. The root canal in the buccal root is enlarged buccolingually
328 (Fig. 6h, i).

329 Lower left fourth premolar (SJM2465) See Figure 7. Morphological identification as a P₄ is
330 confirmed by analysis of cervix shape (SOM Fig. S5). The tooth cannot be a metamere of
331 SJMJ2464 (left P₃) because the interproximal facets do not match. The tooth is complete
332 apart from the apex of the root, which is chipped. Severe cracking can be seen on the lingual
333 side of the root in the buccolingual CT slice (Fig. 7h).

334 The occlusal outline is oblong, with very slight mesiolingual truncation. The worn down
335 buccal surface of the crown lacks the convexity and lingual inclination observed in
336 SJMJ2464 (left P₃), and the lingual face is less swollen. The narrow sagittal sulcus has a
337 small bridge of enamel centrally (Fig 7d). However, examination of the EDJ reveals no
338 evidence of a transverse crest (Fig. 7g). As with SJMJ2464 (left P₃), the mesial and distal
339 foveae (distal deepest) do not appear to have been large. The sagittal sulcus does not interrupt
340 either margin at the OES at this level of wear (Fig. 7d); and neither margin is interrupted at
341 the EDJ. The EDJ reveals a distolingual cusp, in addition to the metaconid, as well as a small
342 dentine horn on the mesial marginal ridge, and confirms the presence of a distal accessory
343 ridge on the buccal cusp (Fig. 7g).

344 There is a single straight-sided root, mesially convex viewed apically, with a longitudinal
345 groove in the apical half of the distal surface. The root is taurodont, with the pulp chamber
346 extending to the apex (SOM Fig. S6). In distal view it can be seen that there has been
347 considerable taphonomic alteration of the dentine towards the centre of the root, so that it is
348 difficult to determine the original shape of the pulp chamber but, as with the left P₃
349 (SJMJ2464), the lingual side appears to be convex at the cervix (Fig. 7h; SOM Fig. S6).

350 Molars The molar buccal and lingual faces are mildly convex viewed mesially. The buccal
351 surface grooves on upper molars are weak, and they are absent on lower molars. The loss of
352 occlusal surface morphology on the molars, despite a relatively low level of wear, suggests
353 that the unworn cusps were low. All the molar roots exhibit supraradicular taurodontism
354 (Kallay, 1970), where the pulp chamber is enlarged before the furcation of the roots.

355 Upper right permanent first molar (SJMJ2456) See Figure 8. The low crown index value
356 (equal mesiodistal and buccolingual measurements), particularly in relation to the other upper
357 molars in the comparative samples, and our analysis of cervix shape among Neanderthal and
358 *H. sapiens* M¹–M³, indicate an M¹ (SOM Fig. S7). Additionally, the oblique ridge at the EDJ
359 is type 1, running from the metacone dentine horn tip to the lingual marginal ridge distal to
360 the protocone. Type 1 is typical of M¹, but not of M² and M³ (Martin et al., 2017). The crown
361 is complete, but the roots are missing above the trunk. Part of the distal margin of the crown
362 broke off antemortem, as indicated by the presence of regular minor chipping along the
363 occlusal edge of the fracture.

364 The occlusal shape is a rounded and slightly skewed rhomboid, with a metacone that is
365 mesiolingually placed, resulting in distobuccal truncation, and a buccally protruding paracone
366 (Fig. 8a). Taking into account corrections for the missing fractured areas, the metacone and
367 hypocone are of similar size. Although worn, there appears to be a grade 2 metaconule (Fig.
368 8a; mesial and distal enamel protrusions from the uninterrupted oblique ridge: Reid and Van

369 Reenen, 1995). Examination of the EDJ (Fig. 8g) indicates no cusp 5 (hypoconule), two small
370 accessory dentine horns on the mesial marginal ridge, and a grade 3 post-paracone tubercle
371 (Ortiz et al., 2017) that cannot be detected at the enamel surface due to wear. The root is
372 hypertaurodont. The lingual aspect of the root trunk is flared lingually, and there is a vertical
373 groove reaching the cervix. At the broken root surface there is no evidence of separated roots
374 buccally or mesially, but the base of the trunk is visible distally. Due to taphonomic alteration
375 of the dentine it is difficult to determine the original shape of the pulp chamber.

376 Upper left permanent second molar (SJMJ2458) See Figure 9. The distal reduction in the
377 crown and presence of a distal interproximal facet indicate an M². This tooth occludes with
378 the left M₂ (SJMJ2455; Keith and Knowles, 1912). The tooth is complete apart from the root
379 apices.

380 The occlusal outline is near triangular, convex mesially and distally, and flattened
381 buccally. The tooth has a deep central fossa and no oblique ridge (Fig. 9a). No hypocone is
382 visible on the worn OES. There is a hypocone dentine horn at the EDJ (Fig. 9g), which is
383 likely to have been below grade 3 (reduced) on the original enamel surface due to its small
384 size. The presence of a cusp 5 is indicated by dentine exposure on the distal margin of the
385 OES (Fig. 9a). ~~There is a~~ grade 2 post-paracone tubercle (Ortiz et al., 2017) ~~visible at the~~
386 ~~EDJ (Fig. 9g),~~ and a mesial marginal ridge accessory tubercle are visible at the EDJ (Fig. 9g).
387 The root is hypertaurodont. The individual roots are furcated mesially at the level at which
388 they are preserved, but with both buccal and distal radicular plates (cross-section in Fig. 9i).
389 Three individual root canals are evident. The roots curve inwards in the apical half viewed
390 distally (Fig. 9b), and both root trunk and individual roots have a pronounced distal
391 inclination. Though taphonomically altered buccally, the pulp chamber appears to have been
392 hour glass shaped in distal view (Fig. 9h).

393 Upper right third molar (SJM2459) See Figure 10. The diminutive distal portion of the
394 crown, and the lack of a distal interproximal facet despite the presence of substantial occlusal
395 wear, indicate an M³. The crown is complete, but the lingual root has been broken off at the
396 trunk, and the buccal roots are missing above the trunk.

397 Viewed occlusally, the mesial aspect of the tooth, including the root trunk, is markedly
398 concave, and the remainder of the tooth is near circular (Fig. 10a). Most surface morphology
399 has been obliterated due to wear. It is unclear which cusps were present in the large distal
400 area of dentine exposure, even at the EDJ (Fig. 10g). There are two dentine horns evident at
401 the EDJ between this area and the protocone (Fig 10g). If one of these is the hypocone, it is
402 most likely to be the more distally placed of the two, both from its position and its larger size.
403 If this is the case, it implies the presence of multiple lingual cusps along the distal rim of the
404 unworn tooth in addition to metacone, hypocone and cusp 5. No oblique ridge is evident at
405 the EDJ. There is a faint horizontal ridge on the buccal OES of the paracone (Fig. 10a), not
406 seen at the EDJ. The root is mesotaurodont. The lingual root is separated from the buccal root
407 mesially and distally just below the fragmented root surface. The buccal root is not bifurcated
408 at this level, though separate root canals are apparent.

409 Upper left third molar (SJM2467, cast) See Figure 11. The description is based on the 1911
410 Natural History Museum cast, and published details (Keith and Knowles, 1912; see SOM Fig.
411 S8B). The crown appears to have been complete. Only part of the root trunk is present in the
412 cast, but the root appears to have been complete in the original tooth according to the
413 photograph in Keith and Knowles (1912; Fig. 11e).

414 Viewed occlusally, the crown is strongly tapered distally, and flattened mesially. Details
415 of morphology are not clear due to the poor quality of the cast. There is a deep central fossa
416 and no oblique ridge (Fig. 11a). Keith and Knowles (1912) described the tooth as three-
417 cusped, lacking the hypocone. There is no evidence of a cusp 5 (Fig. 11e). The roots were

418 described as more compressed together than in the left M^2 , but otherwise similar in form to
419 those of the molars found previously (Keith and Knowles, 1911, 1912). The roots appear to
420 have been hypertaurodont, with a greater degree of taurodontism than the other La Cotte
421 molars (Fig. 11e).

422 Lower right permanent second molar (SJMJ2461) See Figure 12. This tooth is identified as
423 an antimere of SJMJ2455 (left M_2). It has a distal interproximal facet, which is located
424 lingually, implying lingual displacement of the adjacent tooth. Displacement of this nature is
425 more likely to occur in an M_3 than in an M_2 . The tooth is complete apart from the root apices.

426 The occlusal shape is rectangular, wider distally than mesially. It has rounded buccal and
427 distal aspects (mesial worn), and partial flattening lingually. There is a 'Y' groove pattern,
428 and a large (grade 5) distally oriented hypoconulid (cusp 5) visible at the OES (Fig. 12a). A
429 small dentine horn at the EDJ indicates that a cusp 6 (entoconulid) was present (Fig. 12g).
430 The sagittal sulcus is uninterrupted at the OES and no mid-trigonid crest is evident. It is
431 absent also at the EDJ, with only a weak crest on the protoconid (grade 0: Bailey et al., 2011).
432 Traces of a wide mesial fovea (trait referred to as an anterior fovea in the ASUDAS: Turner
433 et al., 1991; Scott and Turner, 1997; Scott and Irish, 2017; Scott et al., 2018) can be identified
434 at the OES and it is present as a linear depression at the EDJ. The entoconid dentine horn tip
435 is positioned on the margin of the tooth (Martin et al., 2017; Fig. 12g). There is a pit (grade 1)
436 protostylid at the OES (Fig. 12a), with a corresponding horizontal cingular crest at the EDJ
437 (Fig. 12g).

438 The mesial root is rectangular in shape and bifurcated at the apex, but fused to the distal
439 root buccally. The lingual furcation of the mesial root is convex mesially. The buccal sides of
440 both roots curve lingually. Marginal ridges are present mesially and distally on the mesial
441 root, and mesially on the distal root. The root is classed as hypertaurodont using Shifman and
442 Chananel's (1978) method but, with an estimated root length of 14.9 mm, Keene's (1966)

443 method gives a figure of 37%, which is classed as hypotaurodont (25–49.9%). The pulp
444 chamber is barrel shaped, viewed lingually, and widening of the mesial root canals is evident
445 in the mesiodistal CT slices (Fig. 12h; SOM Fig. S9).

446 Lower left permanent second molar (SJMJ2455) See Figure 13. This tooth occludes with the
447 left M² (SJMJ2458; Fig. 13i). It has mesial and distal interproximal wear facets, and, as with
448 SJMJ2461 (right M₂), the distal interproximal facet is located lingually. Based on a similar
449 degree of wear, similar dimensions and crown morphology, and the description of the
450 original root morphology (Keith and Knowles, 1912), this is likely to be the antimere to
451 SJMJ2461 (right M₂). The crown is complete, but Keith and Knowles (1912) sectioned the
452 root just below, and parallel to, the cervix (line visible in Fig. 13b). Part of the root has been
453 restored with filler. Only 9 mm of the trunk remains and the apical part of the root has been
454 lost. The tooth was described by Keith and Knowles (1912) as having roots of the same form
455 as the right M₂, fused buccally but not lingually, inclined distally and lingually, and having a
456 trunk length of 7 mm.

457 The occlusal shape is rectangular, with rounded margins (mesial worn), and partially
458 flattened lingually. As with the right M₂, there is a ‘Y’ groove pattern, and a large (grade 5)
459 distally placed hypoconulid is present (Fig. 13a, d). Unlike the right M₂ there is no cusp 6
460 dentine horn and no protostylid crest at the EDJ, though a trace protostylid is present on the
461 hypoconid (Fig. 13g). However, as with the right M₂, there is no mid-trigonid crest at the EDJ
462 (site worn at the OES; grade 0: Bailey et al., 2011) and only a weak crest evident on the
463 protoconid. The entoconid dentine horn tip is positioned on the margin of the tooth (Martin et
464 al., 2017).

465 Lower right third molar (SJMJ2460) See Figure 14. This tooth lacks a distal interproximal
466 facet despite the presence of dentine exposure. This, together with its shape and the presence
467 of a large number of accessory crests, indicates an M₃. The interproximal wear facet matches

468 with that of the right M₂ (SJM2461) (Fig. 14i) and it is likely the teeth are metamerous. Only
469 the crown and less than one-quarter of the root are present. A portion of the mesial margin of
470 the crown has broken off postmortem. A lingual crack can be seen in the CT slice (Fig. 14h).

471 The overall occlusal shape of the crown is near circular. The unworn lingual half of the
472 tooth is very wrinkled, with multiple cusps present at the OES (Fig. 14a, d). There is an 'X'
473 groove pattern (Fig. 14a). There are three crests running from the mesial margin into, and
474 filling, the mesial (anterior) fovea at the OES, but the presence of any associated mesial
475 marginal ridge tubercles cannot be assessed because the mesial face of the tooth is missing
476 (Fig. 14a). There is no mid-trigonid crest (grade 0 at the EDJ: Bailey et al., 2011). There is a
477 single mesiodistal groove at the OES on the buccal slope of the hypoconid, and lingual to the
478 dentine exposure, that delineates the large protostylid cingular crest seen at the EDJ (Fig.
479 14d, g). Examination of the EDJ (Fig. 14g) reveals the presence of numerous primary and
480 accessory dentine horns. Some of these can be reasonably identified as cusps, while others
481 reflect repeated enamel knot initiation (Martin et al., 2017). Moving distally from the
482 metaconid dentine horn, there is a small (grade 3) cusp 7, the entoconid, an undulating ridge
483 that potentially exhibits incipient dentine horns, a cusp 6, and then one additional dentine
484 horn lingual to the grade 4 hypoconulid. Additionally, there is a small dentine horn on the
485 protostylid ridge on the buccal aspect of the hypoconulid. The degree of internal placement of
486 the hypoconid relative to the protostylid cingulum is uncommon (not seen in any of the CT-
487 scan comparative samples), and may further reflect a general perturbation of the development
488 of this tooth. The metaconid and entoconid dentine horn tips are positioned on the margin of
489 the tooth (Martin et al., 2017).

490 Occipital fragment (SJM2452) See Figure 15. The occipital fragment comprises a small part
491 of a left squamous, measuring 53 mm between the broken anterior and posterior edges, and
492 37 mm from the asterion to the broken medial edge. The endocranial and exocranial surfaces

493 are weathered and marked by superficial cracks and abraded areas. One edge of the piece is
494 defined by the lambdoid suture, which extends 45 mm from the asterion. All the other edges
495 are defined by natural breaks. The thickness of the bone, and weak markings on the external
496 surface, are consistent with an immature age at death. The lambdoid suture has several
497 abraded patches but appears to be mostly open. An area of interdigitated bone, visible on the
498 external surface located 35 mm from the asterion, may represent an early stage of fusion at
499 the lambdoid suture. A finger of bone projecting inwards from the lambdoid suture, situated 6
500 mm from the asterion, and measuring 6.2 by 2.6 mm, appears to be a small wormian bone.
501 The endocranial surface has a well demarcated transverse sulcus that extends 35 mm from
502 just below the asterion to the broken medial edge along the lower border, and 32 mm from
503 the lambdoid suture to the broken medial edge along the upper border. The transverse sulcus
504 passes directly across the asterion and would have crossed the posteroinferior (mastoid)
505 corner of the parietal bone before reaching the temporal bone, instead of crossing directly
506 onto the temporal bone (Fig. 15B, indicated by dotted lines). Taken together, the size and
507 morphology of the occipital fragment are consistent with an immature individual who died in
508 late childhood or adolescence.

509

510 3.2. *Qualitative morphological comparisons*

511 Trait frequencies for the tooth types found in the La Cotte material, and in comparative
512 samples of Late Pleistocene hominins, are reported in Tables 3–7. Traits that show a
513 significant difference between Neanderthal and fossil *H. sapiens* are identified: (1) where the
514 95% confidence interval for the difference between the proportions for the two samples is
515 entirely above or below zero, i.e., does not include 0% difference; (2) where the 95%
516 confidence intervals for the two sample proportions do not overlap (SOM S3). These are the
517 traits principally discussed.

518 Lower canine (SJM2463) The characteristics of this tooth support a Neanderthal affinity.
519 Shoveling is present in the entire Neanderthal comparative sample and most (88%) of the
520 fossil *H. sapiens* sample (Table 3). The distal accessory ridge is more common in
521 Neanderthals (78%) than fossil *H. sapiens* (42%; Table 3). It tends to be more strongly
522 expressed in Neanderthals, as it is at La Cotte, than in fossil *H. sapiens* (50% compared to 8%
523 at their grade 2 in Martín-Torres et al.'s [2012: Table 17] samples). The mild expressions
524 of the tuberculum dentale and lingual medial ridge in SJM2463 (C₁) are the forms frequently
525 found in both comparative samples (Martín-Torres et al., 2012).

526 The buccal curvature of the root is typical of Neanderthals, but not of *H. sapiens*
527 (Bilsborough and Thompson, 2005; Le Cabec et al., 2013), as is the convex buccal contour of
528 crown and root together, known as 'cyrtodonty' (Patte, 1962; Brabant and Sahly, 1964). The
529 wide root canal, as viewed distally, is unlike the narrow straight sided canals found in recent
530 human teeth (van Beek, 1983).

531 Upper fourth premolar (SJM2457) The morphological traits of this tooth support a
532 Neanderthal affinity. The swollen buccal surface, viewed mesially, and sharp lingual
533 inclination from the point of maximum curvature, is typical of Neanderthals, and more
534 pronounced than is generally found in *H. sapiens* (TC, personal observation). The absence of
535 a buccal mesial accessory ridge is also typical of Neanderthals (83%) and less common in
536 fossil *H. sapiens* (40%; Table 4).

537 The roots are robust compared to *H. sapiens*. The two-rooted form present is the most
538 common type in Neanderthals (Maureille et al., 2008). The taurodontism, and a relatively
539 longer root trunk before furcation of the roots than in recent humans, are also seen in some
540 Neanderthal P⁴ (Kallay, 1963).

541 Lower third (SJM2464) and fourth (SJM2465) premolars The characteristics of both
542 premolars give an ambiguous picture. For the P₃ (SJM2464) the Neanderthal features are the

543 large lingually placed buccal cusp (Gómez-Robles et al., 2008), and the presence of a buccal
544 cingulum at the EDJ, which occurs frequently in the Neanderthal sample but is not seen in the
545 recent human sample. For the P₄ (SJMJ2465) the Neanderthal features are the presence of
546 multiple lingual cusps (94%), a mesially placed metaconid (97%), and a buccal distal
547 accessory ridge (88%; Table 4). The corresponding figures for fossil *H. sapiens* are
548 significantly lower (Table 4). The cusp on the mesial margin, represented by a dentine horn at
549 the EDJ, found on SJMJ2465 (left P₄), also occurs on three Krapina P₄ (Compton and
550 Stringer, 2012). Three or more lingual cusps on P₄ (three at La Cotte) are present in 89% of
551 Neanderthals but only 20% of fossil *H. sapiens* (Martinón-Torres et al 2012: Table 19).

552 In contrast, the absence of a transverse crest, and a symmetrical shape, found on both
553 premolars, are rare in Neanderthal P₃ (3% and 6% respectively) and P₄ (both at 6%; Table 4).
554 Additionally, Davies et al. (2019) recorded the presence of a transverse crest in their entire
555 Neanderthal P₃ sample. Martinón-Torres et al. (2012: Tables 18 and 19), however, reported
556 absence of a transverse crest in 15% of P₃ and 19% of P₄ in their Neanderthal sample. The
557 absence of a transverse crest, and a symmetrical shape, are more frequently observed for P₃
558 and P₄ in fossil *H. sapiens* (Table 4). Bailey (2002) looked at the combination of three
559 characteristics (well-developed metaconid, transverse crest and asymmetry) in P₄ and found
560 that 98% of modern humans had only one of these traits, as at La Cotte, compared to only 6%
561 of Neanderthals.

562 The robust roots of SJMJ2464 (left P₃) are more typical of Neanderthals than of *H.*
563 *sapiens*. Interestingly, grade 4–5 Tomes' root, present on the P₃, occurs less frequently in the
564 P₃ (12%) than in the P₄ (25%) in Neanderthals, the reverse of that found in fossil *H. sapiens*
565 (38% and 23% respectively; Table 4) and recent humans. Tomes' root occurs less frequently
566 in recent humans than in fossil *H. sapiens* (12.5% and 2.5% respectively for P₃ and P₄ in a
567 large mixed sample; Shields, 2005). The wide root canal observed in SJMJ2465 (left P₄) is

568 typical of Neanderthal P₄ but uncommon in recent humans (Prado-Simón et al., 2012). The
569 extended taurodont pulp chambers in SJMJ2464 (left P₃) and SJMJ2465 (left P₄) are apparent
570 as widening in both buccolingual and mesiodistal directions (SOM Fig. S6). In some teeth, in
571 both comparative samples (Table 4), extension of the pulp chamber into the root is only
572 apparent as widening in a buccolingual direction. Considering the small samples involved
573 (Table 4), the frequency of taurodontism is similar between P₃ and P₄ and between
574 Neanderthals and fossil *H. sapiens*. Taken overall, widening in a buccolingual direction, with
575 or without mesiodistal widening, occurs at approximately twice the frequency as widening in
576 both directions together (51% against 23%; Table 4).

577 Molars The upper molar cusps are internally placed, as is often observed in Neanderthals.
578 Carabelli's trait is absent in the upper molars. This was previously thought to be unusual in
579 Neanderthals (McCown and Keith, 1939; Smith, 1989). More recently Martín-Torres et al.
580 (2012) reported 20% absence for M¹, 42% for M² and 80% for M³, in their Neanderthal
581 sample. The post-paracone dentine horn, which is present at the EDJ in SJMJ2456 (right M¹)
582 and SJMJ2458 (left M²) and could not be scored in SJMJ2459 (right M³), was ubiquitous in a
583 sample of Neanderthal maxillary molars and present in 86% of a recent human sample
584 (Martin et al., 2017: Table 10). In contrast, Ortiz et al. (2017: Table 4) reported the presence
585 of post-paracone dentine horns in 98% of a Neanderthal sample but only 25% of a recent
586 human sample. Taurodontism is particularly associated with Neanderthals, but it is also found
587 in fossil *H. sapiens* from Skhūl and Qafzeh (McCown and Keith, 1939; Vandermeersch,
588 1981) and in Aterians (Kupczik and Hublin, 2010). Kupczik et al. (2019: Table S1) found
589 taurodontism (grades III and IV of their bifurcation index) in 88% (14 of 16) of their sample
590 of Neanderthal M₂. Studies of recent Europeans have shown taurodontism is present in less
591 than 10% of molars (Jafarzadeh et al., 2008: Table 3). The absence of enamel extensions

592 above trace level on any of the molars is also typical of Neanderthals, and most *H. sapiens*
593 outside Asia (Bailey, 2006b).

594 Upper first molar (SJMJ2456) The Neanderthal M¹ crown has a distinct shape (Bailey, 2004;
595 Gómez-Robles et al., 2007; Martín-Torres et al., 2013): The main cusp tips are more
596 internally placed, leading to a relatively smaller occlusal polygon (formed by linking the tips
597 of the four principal cusps) compared to the total occlusal area (Table 5). There is a
598 statistically significant difference at $p \leq 0.01$ between Neanderthal and *H. sapiens* for this
599 percentage figure (Martín-Torres et al., 2013). The occlusal shape is skewed and there is a
600 large distally projected and swollen hypocone, leading to a narrow hypocone angle (Table 5;
601 Fig. 16). The metacone is relatively smaller than the hypocone and mesiolingually oriented,
602 leading to distobuccal truncation of the occlusal outline and a wide metacone angle (Table 5;
603 Fig. 16). The hypocone is larger than the metacone in 14/16 molars in Bailey's (2004)
604 Neanderthal sample. The occlusal polygon is narrower distally than mesially (Fig. 16).

605 The M¹ (SJMJ2456) shows clear Neanderthal affinities (see Table 5; Fig. 16). It has a
606 relatively small occlusal polygon (24%), a mesiolingually placed metacone, along with a
607 large metacone angle (116°), and an occlusal polygon that is narrower distally than mesially.

608 However, in contrast, the crown has only a mildly skewed appearance, with a small
609 protocone angle (100°) compared to the means of both the comparative samples (106°). The
610 relative size of the hypocone compared to total occlusal area (19%) is small in comparison to
611 the Neanderthal sample mean (23.7%) and smaller than the metacone (21%), and the
612 hypocone angle (76°) is large. While being within the Neanderthal range of variation, both of
613 these features are more similar to the fossil *H. sapiens* sample. Additionally, the protocone is
614 relatively large (33%) compared to Neanderthal (29.9%).

615 Upper second molar (SJMJ2458) The presence of a cusp 5 is common in Neanderthals
616 (68%), and the presence of a mesial accessory cusp is ubiquitous. Both are less frequent in

617 fossil *H. sapiens* (39% and 13% respectively; Table 6). The reduced hypocone is unusual,
618 though, in both Neanderthals and fossil *H. sapiens*, occurring at frequencies of only 6% and
619 15% respectively (Table 6). It is, however, common in the pre-Neanderthal Atapuerca-SH
620 sample (Martinón-Torres et al., 2012).

621 Upper third molars (SJMJ2459 and SJMJ2467) The concave mesial aspect, viewed
622 occlusally, of SJMJ2459 (right M³) is distinctly unusual. The presence of multiple cusps
623 along the distal rim (i.e., in excess of metacone, hypocone and a single cusp 5), as inferred for
624 SJMJ2459 (right M³), has been reported in Krapina M³ (Compton and Stringer, 2012); and
625 Martin et al. (2017) found considerable variation in distal cusp pattern in Neanderthal M³.
626 Multiple distal cusps and split hypocones occur in Aterian teeth (Bailey et al., 2017), and split
627 hypocones have been reported in recent humans (Greene et al., 1967; Bermúdez de Castro
628 and Martínez, 1986), but mention of multiple distal cusps in recent humans is rare in the
629 literature. Ortiz et al. (2017: Table S3) found multiple cusp 5 at the EDJ in ~20% of
630 Neanderthals but only in ~1% of recent humans.

631 Lower molars (SJMJ2455 and SJMJ2461 M₂; SJMJ2460 M₃) We did not observe the
632 protostylid forms seen at the EDJ on SJMJ2461 (right M₂) and SJMJ2460 (right M₃) in our
633 comparative samples. The hypoconulid expression in the M₂ (SJMJ2455 and SJMJ2461) is
634 particularly large. Martinón-Torres et al. (2012: Table 21) found only 16.6% of Neanderthal
635 and 4% of fossil *H. sapiens* M₂ with grade 5 hypoconulids. The characteristics of the La
636 Cotte lower molars give an ambiguous picture. Neanderthal characteristics include the
637 presence of a hypoconulid (found in the entire Neanderthal sample), a wide mesial (anterior)
638 fovea (89% of M₂ and 93% of M₃), and a ‘Y’ groove pattern in M₂ (75%; Table 7). The
639 corresponding figures for fossil *H. sapiens* are significantly lower (Table 7). Additionally, the
640 multiple cusps and accessory crests found on SJMJ2460 (right M₃) have been observed in

641 Neanderthals (McCown and Keith, 1939; Radovčić et al., 1988; Bailey and Hublin, 2006), as
642 has the repeated enamel knot initiation seen at the EDJ (Martin et al., 2017).

643 In contrast, the absence of a mid-trigonid crest at the OES, observed in SJMJ2461 (right
644 M₂) and SJMJ2460 (right M₃), is rare in Neanderthal M₂ and M₃ (4% and 7% respectively),
645 but almost ubiquitous in the fossil *H. sapiens* sample, at 96% and 100% respectively (Table
646 7). At the EDJ, Bailey et al. (2011: Table 3) recorded the presence of a continuous mid-
647 trigonid crest in their entire Neanderthal M₂ and M₃ sample (absent at La Cotte), but only
648 35.5% and 14.3% respectively of a recent European sample. Furthermore, the position of the
649 metaconid dentine horn tip on the occlusal margin of SJMJ2460 (right M₃) is rare in
650 Neanderthals. The metaconid dentine horn was centrally placed in 95% of a late Neanderthal
651 sample but only 36% of a recent human sample (Martin et al., 2017: Table 9).

652 The non-tapering shape and bifurcation of the mesial root, and the presence of longitudinal
653 marginal ridges on mesial and distal roots, observed in SJMJ2461 (right M₂), are typical of
654 Neanderthal M₂ (Compton and Stringer, 2015).

655 Occipital fragment (SJMJ2452) The occipital lacks any diagnostic Neanderthal anatomical
656 features. The transverse sulcus pathway is typical of recent humans, and differs from the
657 pathway observed in some Neanderthals, in which the transverse sulcus passes directly from
658 the occipital to the temporal without crossing the parietal bone (Arsuaga et al., 2002).

659

660 3.3. Geometric morphometric analysis of cervix shape

661 Figures 17–23 illustrate PCAs of cervix morphology in shape and form (form including
662 the log of centroid size as a variable) space for upper and lower molars and premolars.

663 The P⁴ (SJMJ2457) falls closer to the *H. sapiens* samples (fossil and recent humans) in
664 shape space but with the Neanderthals in form space, reflecting its large size (Fig. 17a, b). It
665 differs from the mean Neanderthal cervix shape in being somewhat compressed

666 mesiolingually and distobuccally (Fig. 17c, d). Using 11 shape PCs, attribution accuracy of
667 the comparative P⁴ sample is ~65% (i.e., the proportion of specimens of known taxonomic
668 affiliation that are attributed correctly using cross-validated canonical variate analysis) and
669 posterior probabilities of discriminant analysis consistently assign SJMJ2457 (P⁴) to *H.*
670 *sapiens* rather than Neanderthal.

671 The identification of SJMJ2464 as a P₃ and SJMJ2465 as a P₄ is supported by their cervix
672 shape that groups them with the *H. sapiens* (fossil and recent humans) P₃ and P₄ samples
673 (SOM Fig. S5). The P₃ falls with the *H. sapiens* samples in shape space but closer to the
674 Neanderthal sample in form space due to its large size (Fig 18a, b). Wireframe models
675 indicate Neanderthals have a distally expanded cervix compared to the *H. sapiens* samples
676 and SJMJ2464 (P₃; Fig. 18c, d). Using 11 shape PCs, attribution accuracy of the comparative
677 P₃ sample is ~70% (with cross-validation), and posterior probabilities consistently assign
678 SJMJ2464 (P₃) to *H. sapiens*. The P₄ falls with the *H. sapiens* samples in both shape and
679 form space (Fig. 19a, b), sharing a buccolingually expanded cervix with both *H. sapiens*
680 samples (Fig. 19c, d) but being more similar in size to the earlier sample. Using 9 shape PCs,
681 attribution accuracy of the P₄ sample is ~90% (with cross-validation) and posterior
682 probabilities consistently assign SJMJ2465 (P₄) to *H. sapiens*.

683 The SJMJ2456 M¹ plots with Neanderthals in both shape space and form space (Fig. 20a,
684 b). It shares a distolingual expansion of the cervix with Neanderthals although it is not as
685 marked as the average Neanderthal M¹ wireframe (Fig. 20c, d). Using 11 shape PCs,
686 attribution accuracy of the comparative M¹ sample is ~90% (with cross-validation) and
687 posterior probabilities consistently assign SJMJ2456 (M¹) to Neanderthals.

688 The SJMJ2458 M² falls on the margin of the overlapping distributions of the *H. sapiens*
689 and Neanderthal samples in shape space, and the form analysis demonstrates it is larger than
690 most of the *H. sapiens* comparative sample and of average size for a Neanderthal (Fig. 21a,

691 b). The wireframe model highlights the unusually small hypocone of SJMJ2458 (M^2)
692 compared to the mean *H. sapiens* and Neanderthal cervix shapes (Fig. 21c, d). Using 13
693 shape PCs, attribution accuracy of the comparative M^2 sample is ~70% (with cross-
694 validation) and SJMJ2458 (M^2) assigns with near equal frequency as either a Neanderthal or
695 *H. sapiens* (i.e., its taxonomic attribution cannot be determined based on cervix shape).

696 The SJMJ2459 M^3 falls well outside of both Neanderthal and *H. sapiens* ranges and it is
697 considerably larger than the largest Neanderthals in this analysis (Fig 22a, b). As with the
698 SJMJ2458 M^2 , the wireframe comparisons of mean shape illustrate the particularly strange
699 contour of the SJMJ2459 M^3 (Fig. 22c, d). Using 9 shape PCs, attribution accuracy of the
700 comparative M^3 sample is ~70% (with cross-validation) and SJMJ2459 (M^3) is consistently
701 assigned to Neanderthals.

702 The two M_2 (SJMJ2455 and SJMJ2461) fall in an intermediate position between the
703 Neanderthals and *H. sapiens* in shape space but fall closer to the fossil *H. sapiens* and
704 Neanderthal samples when size is included (Fig. 23a, b). The M_2 s are similar to the
705 Neanderthal sample in having a buccally expanded cervix without the buccal pinching distal
706 to the protoconid present in the *H. sapiens* samples (Fig. 23c, d). Using 14 shape PCs,
707 attribution accuracy of the comparative sample is ~85% (with cross-validation) and posterior
708 probabilities consistently assign both SJMJ2455 and SJMJ2461 (M_2) to Neanderthals.

709 Cervix shape alone tends to perform less well at taxonomic discrimination than analyzes
710 that also incorporate the EDJ marginal ridge (Martin et al., 2017) and, at a number of tooth
711 positions, attribution accuracy of the comparative sample (in which taxonomic affiliation is
712 known) ranges between 60–90%. In summary, the P_3 , P_4 and P^4 are consistently assigned as
713 *H. sapiens*, while the two M_2 , the M^1 and the M^3 are consistently assigned as Neanderthals.
714 Attribution of the M^2 is less consistent and cervix shape cannot contribute strongly to its
715 taxonomic assessment.

716

717 *3.4. Metrical comparisons*

718 Comparative data for crown dimensions are presented in SOM Tables S7 and S8, and
719 adjusted Z scores for crown dimensions are illustrated in Figures 24 and 25.

720 Crown area See Figure 24. The crown areas of the La Cotte teeth are all close to or above the
721 late Neanderthal comparative sample means, with associated adjusted Z scores under ± 0.5 ,
722 except for SJMJ2463 (left C₁) and SJMJ2464 (left P₃), which are particularly large. The C₁
723 crown area is above the range of the late Neanderthal comparative sample, and its
724 buccolingual dimension is only exceeded by Kebara 2 (10.2 mm). The buccolingual
725 dimension of the P₃ is only exceeded by La Quina 9 (11.0 mm), and this is the only tooth in
726 the late Neanderthal comparative sample with a larger crown area (99 sq mm). With the
727 exception of these two teeth, the crown areas of the La Cotte teeth are all within the ranges of
728 the other comparative samples, with associated adjusted Z scores up to ± 0.7 (-0.8 for the
729 Krapina P₄). In contrast, the adjusted Z scores for SJMJ2463 (left C₁) and SJMJ2464 (left P₃)
730 are 0.8 and 0.7 respectively in relation to late Neanderthals, and 1.0 and 1.4 in relation to
731 fossil *H. sapiens*.

732 Crown index See Figure 25. The crown indices of the La Cotte teeth all have adjusted Z
733 scores under ± 0.5 in relation to the late Neanderthal comparative sample except for the left
734 M³ SJMJ2467 (-0.7). The La Cotte M¹, M² and M³ have crown indices below the means of all
735 the comparative samples (SOM Table S7; with the lone exception of the right M³ SJMJ2459
736 in relation to Krapina), indicating that they are squarer; and C₁, P₃ and P₄ have crown indices
737 above the means of the comparative samples (SOM Table S8), indicating that they are
738 relatively buccolingually expanded. Two large differences in the comparative samples stand
739 out. The fossil *H. sapiens* M¹ has an adjusted Z score of -1.3, reflecting the more rectangular
740 shape of these teeth compared to Neanderthals. The Krapina P₃ has an adjusted Z score of 2.2

741 due to the lower crown indices of these teeth and this is also apparent in the Krapina lower
742 molars.

743 Cervical dimensions See Table 8. In all but one case (SJM2461, right M₂) the La Cotte
744 dimensions are above the Neanderthal comparative sample means. The mesiodistal
745 dimensions of SJMJ2463 (left C₁) and SJMJ2464 (left P₃), and the buccolingual dimension of
746 SJMJ2457 (left P⁴), at the cervix are either above or at the upper end of the Neanderthal
747 ranges. SJMJ2464 (left P₃) has adjusted Z scores for Neanderthal of 1.5 for the mesiodistal
748 dimension and 1.0 for the buccolingual dimension. Keith and Knowles (1912) noted the large
749 cervical dimensions; and the particularly high cervical dimensions of the La Cotte canine and
750 premolars, other than SJMJ2465 (left P₄), is very distinctive. Fossil *H. sapiens* have smaller
751 cervical dimensions than Neanderthals, and this difference is most pronounced in the P₄, M²
752 and M₂. The fossil *H. sapiens* adjusted Z scores for SJMJ2463 (left C₁) and SJMJ2464 (left
753 P₃) in both mesiodistal and buccolingual dimensions, and for SJMJ2458 (left M²) in the
754 mesiodistal dimension, are all at 1.0 or above.

755 Root length The only La Cotte tooth with a complete root is SJMJ2467 (LM³), for which only
756 a cast is now available (Keith and Knowles, 1912: preface). It has a length of 16.0 mm, which
757 is within the Neanderthal range (13.5–16.7 mm, mean 15.2 mm; Bailey, 2005), and above the
758 ranges for Předmostí (11.0–14.0 mm; Matiegka, 1934) and contemporary humans (8.0–15.0
759 mm; Black, 1902).

760

761 3.5. *Number of individuals*

762 Since all the teeth from La Cotte were found in one place, and are broadly similar in their
763 degree of development and wear, the ‘null hypothesis’ would be that they all come from the
764 same individual (Keith and Knowles, 1912). Our observations demonstrate that the eleven

765 teeth from La Cotte represent a maximum of six individuals, made up of three groups of teeth
766 that can be confidently associated with one another and three isolated teeth:

- 767 i) The largest group of unambiguously associated teeth comprises four molars, SJMJ
768 2455, 2458, 2460 and 2461 (referred to hereafter as individual A-1). SJMJ2455 (left
769 M₂) and SJMJ2458 (left M²) occlude (Fig. 13i). SJMJ2455 (left M₂) and SJMJ2461
770 (right M₂) are likely to be antimeres, due to the similarities of morphology and size,
771 and the shared presence of lingually placed distal interproximal facets, a highly
772 unusual pattern of distal wear (Fig. 12a, marked 'a') and unusually lingually inclined
773 roots. SJMJ2461 (right M₂) and SJMJ2460 (right M₃) are likely metamerer. The
774 lingual placement of the interproximal facet on SJMJ2461 suggests lingual
775 displacement of the adjacent M₃, and the form of wear on SJMJ2460 is consistent
776 with this (Fig. 14i). SJMJ2460 (right M₃) also has a prominent form of the protostylid,
777 similar to, although larger than, that seen on SJMJ2461.
- 778 ii) The matching interproximal wear between SJMJ2463 (left C₁) and SJMJ2464 (left
779 P₃), and their unusually large size, demonstrates that they are metamerer (A-2)
- 780 iii) SJMJ2456, right M¹ (A-3)
- 781 iv) SJMJ2467, left M³ (A-4)
- 782 v) SJMJ2457 (left P⁴) and SJMJ2465 (left P₄) occlude (B-1)
- 783 vi) SJMJ2459, right M³ (B-2).

784 The minimum number of individuals (MNI) represented by these eleven teeth is two,
785 referred to as Individuals A and B. This can be confidently inferred from the fact that some of
786 the groupings identified above cannot belong to the same dentition. Firstly, SJMJ2459 (right
787 M³; B-2) does not occlude with either the right M₂ or the right M₃ from A-1. Secondly,
788 premolars SJMJ2464 (left P₃; A-2) and SJMJ2465 (left P₄; B-1) are not metamerer, since the

789 interproximal facets do not match, and their large difference in size is inconsistent with a
790 single dentition.

791 Teeth from individual B (SJMJ2457 [left P⁴; B-1] and SJMJ2465 [left P₄; B-1] and
792 SJMJ2459 [right M³; B-2]) exhibit a similar degree of wear that is proportionally greater than
793 that of the other teeth and consistent with a single individual. The remaining four teeth, SJMJ
794 2456, 2467, 2463 and 2464, cannot with complete confidence be associated with either
795 Individual A or B, but are tentatively included with Individual A on the basis of dental
796 metrics. SJMJ2456 (right M¹; A-3), SJMJ2467 (left M³; A-4) and SJMJ2458 (left M²; A-1)
797 have similar crown area and crown index values in relation to the Neanderthal means.
798 Likewise, the relationship of crown area to the Neanderthal mean in SJMJ2463 (left C₁) and
799 SJMJ2464 (left P₃; A-2) is similar to that in M₂ SJMJ2461 and SJMJ2455 (A-1).

800 In summary, Individual A is represented by four teeth that are unambiguously associated
801 and another four teeth that could belong to this individual, and Individual B is represented by
802 three teeth. Based on the level of wear and the fact that there is dentine exposure on third
803 molars in both individuals, it is likely that Individuals A and B were (young) adults. Trinkaus
804 (1995) found a uniform pattern of wear in a sample of Neanderthals and noted that there was
805 slight dentine exposure on first molars, as at La Cotte, in the third decade of life. However,
806 the accumulation of cementum on the apical two thirds of the roots and the amount of
807 secondary dentine in the pulp chambers of the molars, from both individuals, could indicate a
808 greater age at death, as these are age related processes (Hillson, 1996; Guatelli-Steinberg and
809 Huffman, 2012). The teeth found in the first season (1910) clearly did not all come from a
810 right mandible as stated by Nicolle and Sinel (1910), but the fact that the teeth were in a row
811 suggests that those from Individual A, at least, might have been originally deposited in
812 anatomical association.

813 The occipital fragment came from an individual who died in late childhood or
814 adolescence. It can therefore be concluded, from the degree of root development and wear on
815 the teeth, that this fragment is not associated with the dental remains and therefore comes
816 from a third individual.

817

818 **4. Discussion**

819 Individually, all of the La Cotte teeth have diagnostically Neanderthal characteristics and
820 seven teeth also have *H. sapiens* characteristics. The teeth that lack *H. sapiens* characteristics
821 are SJMJ2463 (left C₁), SJMJ2458 (left M²), and the upper third molars, SJMJ2459 (right
822 M³) and SJMJ2467 (left M³). Table 9 summarizes the mix of Neanderthal and *H. sapiens*
823 characteristics within the individual teeth, grouped according to the maximum number of six
824 individuals (A-1, A-2, A-3, A-4, B-1 and B-2) and minimum number of two individuals (A
825 and B).

826 Within A-1 (SJMJ2458, left M²; SJMJ2461, right M₂; SJMJ2455, left M₂; SJMJ2460,
827 right M₃), the M² has no *H. sapiens* characteristics and the other three molars have a mixture
828 of characteristics. Within A-2 (SJMJ2463, left C₁; SJMJ2464, left P₃), the canine has entirely
829 Neanderthal diagnostic characteristics but those of the premolar are mixed. A-3 (SJMJ2456,
830 right M¹) has mixed characteristics. A-4 (SJMJ2467, left M³) only has Neanderthal
831 characteristics. Within B1, both premolars (SJMJ2457, left P⁴; SJMJ2465, left P₄) have a
832 mixture of characteristics. B-2 (SJMJ2459, right M³) only has Neanderthal characteristics.

833 Traits that are specific to one of these six groups include absence of mid-trigonid crest in
834 lower molars (A-1), and particularly large teeth compared to Neanderthal and *H. sapiens* (A-
835 2). Traits that occur in more than one group include absence of transverse crest and
836 mesiolingual truncation in lower premolars, and cervix shape of *H. sapiens* form (A-2 and B-
837 1). It is notable that for teeth with multiple crown traits that show a significant difference in

838 prevalence between Neanderthals and fossil *H. sapiens* (P₄, M₂, M₃) there is an ambiguous
839 picture.

840 Four of the maximum of six individuals have a mixture of diagnostic Neanderthal, and *H.*
841 *sapiens*, characteristics. Three of these sets of teeth could belong to the same dentition
842 (Individual A) but the fourth belongs to a second dentition (Individual B). This suggests that
843 the occurrence of mixed characteristics relates to a group of individuals, rather than being
844 specific to one individual. The *H. sapiens* characteristics occur principally in the lower
845 premolars, are less common in the P⁴, M¹ and lower molars, and are reflected in cervix shape
846 and crown morphological traits. The analysis of cervix shape gives a varied picture. The
847 molars (other than M²) are assigned to Neanderthals, while the premolars are assigned to *H.*
848 *sapiens*. The root forms and the tooth dimensions are entirely compatible with Neanderthals.
849 Several traits that are considered to be particularly typical of Neanderthals (Bailey, 2002,
850 2004, 2006a; Martin et al., 2017) are absent in the La Cotte teeth. These are the presence of a
851 transverse crest, and mesiolingual truncation in lower premolars; the presence of a mid-
852 trigonid crest, and metaconid central dentine horn tip placement in lower molars; and
853 peculiarities of the occlusal shape of M¹. The first four of these traits are not diagnostic of
854 either Neanderthals or *H. sapiens*, but they are consistently present in Neanderthals and less
855 common in *H. sapiens*. The small occlusal polygon of the M¹ from La Cotte is diagnostically
856 Neanderthal, but other aspects of the M¹ morphology are more ambiguous.

857 Three aspects of the morphology of the La Cotte teeth are unusual in both Neanderthals
858 and fossil *H. sapiens*. These are the reduced hypocone on SJMJ2458 (left M²); the concave
859 mesial surface and unusual cervical shape of SJMJ2459 (right M³); and the protostylid form
860 on SJMJ2461 (right M₂) and SJMJ2460 (right M₃). The protostylid form of SJMJ2461 (right
861 M₂) is superficially similar to that observed in *Paranthropus robustus* (Skinner et al., 2009),
862 although not identical. We consider the SJMJ2460 (right M₃) protostylid form to reflect

863 abnormal development of the distal part of the crown and thus not useful for its taxonomic
864 assessment.

865 With the exception of the possibly early form of the protostylid, there are no traits relating
866 to earlier hominins in the La Cotte teeth. Traits that are only seen in *Homo heidelbergensis*,
867 pre-Neanderthals or early Neanderthals (Compton and Stringer, 2015) are absent. These
868 include a buccal cingulum at the enamel surface on P₃ (*H. heidelbergensis*); a distal
869 occlusolingual cleft on P₃ (*H. heidelbergensis* and pre-Neanderthal); mesiobuccal swelling
870 (viewed occlusally) of P₄ (*H. heidelbergensis*, pre-Neanderthal and early Neanderthal); and
871 grade 2 buccal vertical grooves/cingula on lower molars (*H. heidelbergensis*, pre-Neanderthal
872 and early Neanderthal). Multiple lingual cusps on the P₃ (present at La Cotte) are not found in
873 *H. heidelbergensis* (Compton and Stringer, 2015; M. Bermúdez de Castro, pers. comm.
874 regarding Arago),

875 The dental morphology of at least two dental individuals from La Cotte therefore displays
876 a mixture of Neanderthal and *H. sapiens* characteristics, with Neanderthal features more
877 strongly represented, and is clearly distinct from earlier hominins. Since there is more than
878 one individual involved, abnormality of development can be dismissed as a likely cause. This
879 mix of features could suggest shared ancestry or, alternatively, a need to extend the
880 phenotype of one or other species to accommodate this variation. If this combination of
881 features is not the result of introgression, it could be due to genetic drift as a consequence of
882 isolation, but this does not seem probable since, at the likely date of these fossils (<48 ka),
883 sea levels were lower and Jersey was connected to mainland Europe. Another possibility is
884 short term evolutionary pressures, although it is difficult to see what advantage would be
885 conveyed by these minor morphological differences. The small sample of teeth from La Cotte
886 does not enable us to determine which of these scenarios is more likely. Attempts to extract
887 DNA and resolve the issue through genetic analysis have thus far proved unsuccessful.

888 The site of Palomas in southern Spain has hominin dental material from secure
889 stratigraphic contexts dated to ~45–38 ka cal BP (Walker et al., 2017), which shows a
890 comparable mix of dental features to those found at La Cotte. The traits of the Palomas teeth
891 are primarily Neanderthal, but not all the P₄ exhibit asymmetry and a transverse crest (present
892 in 50% and 75% respectively); only one of the eight lower molars has a mid-trigonid crest at
893 the OES, and fewer than half (43%) have a mesial (anterior) fovea of grade >1 (Zapata et al.,
894 2017). However, unlike La Cotte, the crown breadths of some of the anterior teeth, and crown
895 areas of some of the lower molars, are more than two standard deviations below the
896 Neanderthal mean (Pinilla and Trinkaus, 2017). Trinkaus (2017) concluded that the Palomas
897 remains were Neanderthals, but acknowledged that the Neanderthal range of variation would
898 need to be extended to accommodate this group within Neanderthals because of differences
899 in dental traits, their small size, and other aspects of their skeletal morphology. DNA analysis
900 might help resolve the taxonomic ambiguity, but to date none has been reported.

901 Trinkaus (2007) identified distinct Neanderthal dental characteristics that appear in
902 European Late Pleistocene *H. sapiens* dated earlier than 33 ka, and considered these to be due
903 to the assimilation of Neanderthals into these populations. The characteristics listed involve:
904 (1) morphological traits in I¹, C¹ and P₄ (multiple lingual cusps, mesially placed metaconid,
905 and asymmetry for P₄) that are present in the earlier material and generally absent in later,
906 post 33 ka, material; (2) relatively large anterior teeth; and (3) megadont distal molars. The
907 only *H. sapiens* specimen known to have with a high level of Neanderthal ancestry is the Oase
908 1 mandible and, by association, the Oase 2 cranium (Fu et al., 2015). Between 6 and 9% of its
909 genome was derived from Neanderthals and it was concluded that there had been a
910 Neanderthal ancestor 4–6 generations back (Fu et al., 2015). However, the Oase teeth
911 (molars) do not exhibit any Neanderthal features. The lower molar mesial (anterior) foveae
912 are small and there are no mid-trigonid crests; the M¹ is of *H. sapiens* form; and the teeth are

913 non-taurodont. The complex crown morphology of the M³ was considered unique (Trinkaus
914 et al., 2012). The teeth, however, are very large, particularly the second and third molars. A
915 discriminant function analysis of the lower molar crown dimensions plotted them with
916 Neanderthals (Trinkaus et al., 2003).

917 There is no evidence of transitional or Upper Paleolithic characteristics in the stone
918 artifacts retained from the excavations at La Cotte. However, the degree of association
919 between the teeth and the Mousterian artifacts in the occupation level is uncertain because the
920 teeth were found on a ledge above the occupation level (though clearly accessible). The stone
921 artifacts recovered at Palomas are similarly described as Mousterian (Walker et al., 2017).

922 The supraradicular taurodontism found in the La Cotte molars is the type generally found
923 in Neanderthals. The more extreme radicular or total taurodontism, where the pulp chamber
924 extends to the tip of a single root, is only found at a few sites, e.g., Krapina (Smith, 1976);
925 Fondo Cattíe (Tarli, 1983); Palomas (Walker et al., 2008). Pyramidal roots, defined by
926 Kupczik and Hublin (2010) as fused roots that can have apical root canal branches in addition
927 to radicular or total taurodontism, are found at Regourdou, Kebara and La Quina (Kupczik
928 and Hublin, 2010) and Aubesier (Lebel et al., 2001). The description of SJMJ2461 (M₂),
929 where both Shifman and Chananel's (1978) and Keene's (1966) methods are used to measure
930 the degree of taurodontism, demonstrates that different methods can give very different
931 results. The degree of taurodontism in the La Cotte premolars is particularly notable. The
932 extent of taurodontism in molars can be identified by the type, the height of the pulp
933 chamber, and its shape—hourglass or barrel. In the comparative samples of Neanderthal P₃
934 and P₄ there is considerably greater variation of form than is found in molars. There is
935 variation in the degrees of buccolingual and mesiodistal widening, and in the overall shape
936 and the degree of tapering, in addition to the extent to which the pulp chamber expands
937 towards the root apex. Consideration is needed as to how this should be measured. A point of

938 interest is that P₃ and P₄ show a similar degree and shape of the taurodontism when both teeth
939 are present in a specimen in the comparative samples in six of nine cases, and the P₄ has a
940 slightly greater level of taurodontism in the remainder. This contrasts with the situation in
941 molars, where the degree of taurodontism frequently increases from first to third (Dumančić
942 et al., 2001).

943

944 **5. Conclusions**

945 The crown and root dimensions for the La Cotte teeth fit well with the Neanderthal
946 comparative samples, and the morphology of the crowns and roots are, in most aspects,
947 typical of Neanderthals. However, there are also *H. sapiens* characteristics, specifically the
948 lack of asymmetry and absence of transverse crests in the lower premolars; the mixture of
949 characteristics in the M¹; and the absence of mid-trigonid crests, and the marginal position of
950 the metaconid dentine horn tip, in the lower molars. Furthermore, the cervix shape of molars
951 and premolars gives a mixed picture, Neanderthal for molars and *H. sapiens* for premolars.
952 The taxonomic attribution of the teeth is therefore ambiguous. Neanderthal characteristics are
953 present in all eleven teeth, but seven of the teeth also have *H. sapiens* characteristics. *Homo*
954 *sapiens* characteristics occur in teeth from both the minimum of two adult individuals
955 identified, suggesting a group or kin with these characteristics. Also of note is the unusual
956 form of the protostylids found at the EDJ on lower molars, which has not previously been
957 observed in Neanderthal or *H. sapiens* teeth.

958 The occipital fragment, which was found in a stratigraphically higher archaeological
959 horizon, is likely to be from an immature individual who died in late childhood or
960 adolescence. Its taxonomic status cannot be determined with certainty, but there are no
961 anatomical features preserved in the bone that clearly indicate a Neanderthal affinity.

962 Of the various scenarios that can be considered to explain the mix of features in the La
963 Cotte teeth, we favor shared Neanderthal and *H. sapiens* ancestry. The likely dating of the
964 fossils during a period of temporal overlap between these groups is consistent with this
965 interpretation.

966

967 **References**

968 Altman, D.G., Machin, D., Bryant, T.N., Gardner, M.J., 2000. Statistics with Confidence:
969 Confidence Intervals and Statistical Guidelines, 2nd ed. BMJ Books, London.

970 Angel, J.L., Coon, C.S., 1954. La Cotte de St. Brelade II: Present status. *Man* 54, 53–55.

971 Arsuaga, J.L., Villaverde, V., Quam, R., Gracia, A., Lorenzo, C., Martínez, I., Carretero,
972 J.M., 2002. The Gravettian occipital bone from the site of Malladetes (Barx, Valencia,
973 Spain). *Journal of Human Evolution* 43, 381–393.

974 Auguste, P., 2009. Évolution des peuplements mammaliens en Europe du Nord-Ouest durant
975 le Pléistocène moyen et supérieur. Le cas de la France septentrionale. *Quaternaire. Revue*
976 *de l'Association Française pour l'étude du Quaternaire* 20, 527–550.

977 Bailey, S.E., 2002. A closer look at Neanderthal postcanine dental morphology. I. The
978 mandibular dentition. *Anatomical Record* 269, 148–156.

979 Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle–Late
980 Pleistocene hominins. *Journal of Human Evolution* 47, 183–198.

981 Bailey, S.E., 2005. Diagnostic dental differences between Neandertals and Upper Paleolithic
982 modern humans: Getting to the root of the matter. In: Zadzinska, E. (Ed.), *Current Trends*
983 *in Dental Morphology Research*. University of Lodz Press, Lodz, pp. 201–210.

984 Bailey, S.E., 2006a. Beyond shovel-shaped incisors: Neandertal dental morphology in a
985 comparative context. *Periodicum Biologorum* 108, 253–267.

- 986 Bailey, S.E., 2006b. The evolution of non-metric dental variation in Europe. *Mitteilungen der*
987 *Gesellschaft für Urgeschichte* 15, 9–30.
- 988 Bailey, S.E., Hublin, J.J., 2006. Dental remains from the Grotte du Renne at Arcy-sur-Cure
989 (Yonne). *Journal of Human Evolution* 50, 485–508.
- 990 Bailey, S.E., Glantz, M., Weaver, T.D., Viola, B., 2008. The affinity of the dental remains
991 from Obi-Rakhmat Grotto, Uzbekistan. *Journal of Human Evolution* 55, 238–248.
- 992 Bailey, S.E., Skinner, M.M., Hublin, J.J., 2011. What lies beneath? An evaluation of lower
993 molar trigonid crest patterns based on both dentine and enamel expression. *American*
994 *Journal of Physical Anthropology* 145, 505–518.
- 995 Bailey, S.E., Weaver, T.D., Hublin, J.J., 2017. The dentition of the earliest modern humans:
996 How ‘modern’ are they? In: Marom, A., Hovers, E. (Eds), *Human Paleontology and*
997 *Prehistory*. Springer, Cham, pp. 215–232.
- 998 Bates, M., Pope, M., Shaw, A., Scott, B., Schwenninger, J.L., 2013. Late Neanderthal
999 occupation in North-West Europe: rediscovery, investigation and dating of a last glacial
1000 sediment sequence at the site of La Cotte de Saint Brelade, Jersey. *Journal of Quaternary*
1001 *Science* 28, 647–652.
- 1002 Becam, G., Verna, C., Gómez-Robles, A., Gómez-Olivencia, A., Albessard, L., Arnaud, J.,
1003 Frelat, M.A., Madelaine, S., Schwab, C., Souday, C., Turq, A., 2019. Isolated teeth from
1004 La Ferrassie: Reassessment of the old collections, new remains, and their implications.
1005 *American Journal of Physical Anthropology* 169, 132–142.
- 1006 Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni,
1007 F., Bayle, P., Coquerelle, M., Condemi, S., 2011. Early dispersal of modern humans in
1008 Europe and implications for Neanderthal behaviour. *Nature* 479, 525–528.

- 1009 Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta,
1010 D., Vicino, G., Starnini, E., Mannino, M.A., 2015. The makers of the Protoaurignacian
1011 and implications for Neandertal extinction. *Science* 348, 793–796.
- 1012 Bermúdez de Castro, J.M., Martínez, I., 1986. Hypocone and metaconule: identification and
1013 variability on human molars. *International Journal of Anthropology* 1, 165–168.
- 1014 Bilsborough, A., Thompson, J.L., 2005. The dentition of the Le Moustier 1 Neandertal. In:
1015 Ullrich, H. (Ed.), *The Neandertal Adolescent Le Moustier 1 – New Aspects, New Results*.
1016 Staatliche Museum, Berlin, pp. 157–186.
- 1017 Black, G.V., 1902. *Descriptive Anatomy of the Human Teeth*, 4th ed. S White Dental
1018 Manufacturing Co., Philadelphia.
- 1019 Brabant, H., Sahly, A., 1964. Étude des dents Néandertaliennes découvertes dans la Grotte du
1020 Portel, en Ariège (France). *Bulletin du Groupement International pour la Recherche*
1021 *Scientifique en Stomatologie & Odontologie* 7, 237–254.
- 1022 Burdo, C., 1960. *La Cotte-de-Saint-Brelade, Jersey, British Channel Islands: Excavation of a*
1023 *Pre-Mousterian Horizon, 1950-1958*. Société Jersiaise, St. Helier.
- 1024 Callow, P., 1986a. Appendix B: Artefacts from the Weichselian deposits. In: Callow, P.,
1025 Cornford, J.M. (Eds.), *La Cotte de St. Brelade 1961–1978. Excavations by C.B.M.*
1026 *McBurney*. Geobooks, Norwich, pp. 397–408.
- 1027 Callow, P., 1986b. Appendix F: Fauna from deposits of the last cold stage at La Cotte de St
1028 Brelade. In: Callow, P., Cornford, J.M. (Eds.), *La Cotte de St. Brelade 1961–1978.*
1029 *Excavations by C.B.M. McBurney*. Geobooks, Norwich, microfiche bound with book.
- 1030 Callow, P., 1986c. Interpreting the La Cotte sequence. In: Callow, P., Cornford, J.M. (Eds.),
1031 *La Cotte de St. Brelade 1961–1978. Excavations by C.B.M. McBurney*. Geobooks,
1032 Norwich, pp. 73–82.

- 1033 Compton, T., Stringer, C.B., 2012. The human remains. In: Aldhouse-Green, S., Peterson, R.,
1034 Walker, E.A. (Eds.), *Neanderthals in Wales: Pontnewydd and the Elwy Valley Caves*.
1035 Oxbow Books, Oxford, pp. 118–230.
- 1036 Compton, T., Stringer, C., 2015. The morphological affinities of the Middle Pleistocene
1037 hominin teeth from Pontnewydd Cave, Wales. *Journal of Quaternary Science* 30, 713–730.
- 1038 Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.J., Skinner, M.M., 2019. Endostructural
1039 morphology in hominoid mandibular third premolars: Discrete traits at the enamel-dentine
1040 junction. *Journal of Human Evolution* 136, 102670.
- 1041 Dean, D., Hublin, J.-J., Holloway, R., Ziegler, R., 1998. On the phylogenetic position of the
1042 pre-Neandertal specimen from Reilingen, Germany. *Journal of Human Evolution* 34, 485–
1043 508.
- 1044 Dumančić, J., Kaić, Z., Petrovečki, M., 2001. Evaluation of taurodontism in Krapina
1045 Neanderthals. In: Brook, A. (Ed.), *Dental Morphology 2001*. Sheffield Academic Press,
1046 Sheffield, pp. 111–121.
- 1047 Fewlass, H., Talamo, S., Wacker, L., Kromer, B., Tuna, T., Fagault, Y., Bard, E., McPherron,
1048 S.P., Aldeias, V., Maria, R., Martisius, N.L., 2020. A ¹⁴C chronology for the Middle to
1049 Upper Palaeolithic transition at Bacho Kiro Cave, Bulgaria. *Nature Ecology & Evolution*
1050 4, 794–801.
- 1051 Fu, Q., Hajdinjak, M., Moldovan, O.T., Constantin, S., Mallick, S., Skoglund, P., Patterson,
1052 N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J.,
1053 Reich, D., Pääbo, S., 2015. An early modern human from Romania with a recent
1054 Neanderthal ancestor. *Nature* 524, 216–219.
- 1055 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A.,
1056 Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., Martínez, L.M., 2007. A

1057 geometric morphometric analysis of hominin upper first molar shape. *Journal of Human*
1058 *Evolution* 53, 272–285.

1059 Gómez-Robles, A., Martínón-Torres, M., de Castro, J.M.B., Prado, L., Sarmiento, S.,
1060 Arsuaga, J.L., 2008. Geometric morphometric analysis of the crown morphology of the
1061 lower first premolar of hominins, with special attention to Pleistocene *Homo*. *Journal of*
1062 *Human Evolution* 55, 627–638.

1063 Greene, D.L., Ewing, G.H., Armelagos, G.J., 1967. Dentition of a Mesolithic population from
1064 Wadi Halfa, Sudan. *American Journal of Physical Anthropology* 27, 41–55.

1065 Guatelli-Steinberg, D., Huffman, M., 2012. Histological features of dental hard tissues and
1066 their utility in forensic anthropology. In: Crowder, C., Stout, S.D. (Eds.), *Bone Histology.*
1067 *An Anthropological Perspective*. CRC Press, Boca Raton, pp. 91–107.

1068 Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and
1069 surfaces. *Hystrix* 24, 103–109.

1070 Guy, F., Lazzari, V., Gilissen, E., Thiery, G., 2015. To what extent is primate second molar
1071 enamel occlusal morphology shaped by the enamel-dentine junction? *PLoS One* 10,
1072 e0138802.

1073 Hajdinjak, M., Fu, Q., Hübner, A., Petr, M., Mafessoni, F., Grote, S., Skoglund, P.,
1074 Narasimham, V., Rougier, H., Crevecoeur, I., Semal, P., 2018. Reconstructing the genetic
1075 history of late Neanderthals. *Nature* 555, 652–656.

1076 Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C., Karkanas,
1077 P., Thompson, N.C., Koutoulidis, V., Mouloupoulos, L.A., Gorgoulis, V.G., 2019. Apidima
1078 Cave fossils provide earliest evidence of *Homo sapiens* in Eurasia. *Nature* 571, 500–504.

1079 Higham, T., Douka, K., Wood, R., Ramsey, C.B., Brock, F., Basell, L., Camps, M.,
1080 Arrizabalaga, A., Baena, J., Barroso-Ruíz, C., Bergman, C., 2014. The timing and
1081 spatiotemporal patterning of Neanderthal disappearance. *Nature* 512, 306–309.

- 1082 Hillson, S., 1996. *Dental Anthropology*. Cambridge University Press, Cambridge.
- 1083 Hoffecker, J.F., 2009. The spread of modern humans in Europe. *Proceedings of the National*
1084 *Academy of Sciences USA* 106, 16040–16045.
- 1085 Hublin, J.J., 2015. The modern human colonization of western Eurasia: when and where?
1086 *Quaternary Science Reviews* 118, 194–210.
- 1087 Hublin, J.-J., Roebroeks, W., 2009. Ebb and flow or regional extinctions? On the character of
1088 Neandertal occupation of northern environments. *Comptes Rendus Palevol* 8, 503–509.
- 1089 Hublin, J.J., Talamo, S., Julien, M., David, F., Connet, N., Bodu, P., Vandermeersch, B.,
1090 Richards, M.P., 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire
1091 support a Neandertal origin for the Châtelperronian. *Proceedings of the National Academy*
1092 *of Sciences USA* 109, 18743–18748.
- 1093 Hublin, J.J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E.,
1094 Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., 2020. Initial Upper Palaeolithic
1095 *Homo sapiens* from Bacho Kiro Cave, Bulgaria. *Nature* 581, 299–302.
- 1096 Jafarzadeh, H., Azarpazhooh, A., Mayhall, J.T., 2008. Taurodontism: a review of the
1097 condition and endodontic treatment challenges. *International Endodontic Journal* 41,
1098 375–388.
- 1099 Kallay, J., 1963. A radiographic study of the Neanderthal teeth from Krapina, Croatia. In:
1100 Brothwell, D.R. (Ed.), *Dental Anthropology*. Pergamon Press, Oxford, pp. 75–86.
- 1101 Kallay, J., 1970. A new classification of the taurodont teeth of the Krapina Neanderthal man.
1102 *Bulletin Scientifique (Yugoslavie)* 15, 2–3.
- 1103 Keene, H., 1966. A morphologic and biometric study of taurodontism in a contemporary
1104 population. *American Journal of Physical Anthropology* 25, 208–209.
- 1105 Keith, A., 1913. Problems relating to the teeth of the earlier forms of prehistoric man.
1106 *Proceedings of the Royal Society of Medicine* 6, 103–124.

- 1107 Keith, A., Knowles, F.H., 1911. A description of teeth of Palaeolithic man from Jersey.
1108 Journal of Anatomy and Physiology 46, 12–27.
- 1109 Keith, A., Knowles, F.H., 1912. A description of teeth of Palaeolithic man from Jersey.
1110 Bulletin Société Jersiaise 37, 222–240.
- 1111 Krenn, V.A., Fornai, C., Wurm, L., Bookstein, F.L., Haeusler, M., Weber, G.W., 2019.
1112 Variation of 3D outer and inner crown morphology in modern human mandibular
1113 premolars. American Journal of Physical Anthropology 169, 646–663.
- 1114 Kupczik, K., Hublin, J.J., 2010. Mandibular molar root morphology in Neanderthals and Late
1115 Pleistocene and recent *Homo sapiens*. Journal of Human Evolution 59, 525–541.
- 1116 Kupczik, K., Delezene, L.K., Skinner, M.M., 2019. Mandibular molar root and pulp cavity
1117 morphology in *Homo naledi* and other Plio-Pleistocene hominins. Journal of Human
1118 Evolution 130, 83–95.
- 1119 Lebel, S., Trinkaus, E., Faure, M., Fernandez, P., Guérin, C., Richter, D., Mercier, N.,
1120 Valladas, H., Wagner, G.A., 2001. Comparative morphology and paleobiology of Middle
1121 Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France. Proceedings of
1122 the National Academy of Sciences USA 98, 11097–11102.
- 1123 Le Cabec, A., 2013. Anterior dental loading and root morphology in Neanderthals. Ph.D.
1124 Dissertation, Université Toulouse III-Paul Sabatier.
- 1125 Le Cabec, A., Gunz, P., Kupczik, K., Braga, J., Hublin, J.-J., 2013. Anterior tooth root
1126 morphology and size in Neanderthals: Taxonomic and functional implications. Journal of
1127 Human Evolution 64, 169–193.
- 1128 McCown, T.D., Keith, A., 1939. The Stone Age of Mount Carmel II. Clarendon Press,
1129 Oxford.
- 1130 Marett, R.R., 1911. XX.—Pleistocene man in Jersey. Archaeologia 62, 449–480.

- 1131 Marett, R.R., 1916. IV.—The site, fauna, and industry of La Cotte de St. Brelade, Jersey.
1132 *Archaeologia* 67, 75–118.
- 1133 Martin, R.M., Hublin, J.-J., Gunz, P., Skinner, M.M., 2017. The morphology of the enamel–
1134 dentine junction in Neanderthal molars: gross morphology, non-metric traits, and temporal
1135 trends. *Journal of Human Evolution* 103, 20–44.
- 1136 Martínón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L.,
1137 Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains
1138 from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution* 62, 7–58.
- 1139 Martínón-Torres, M., Spěváčková, P., Gracia-Téllez, A., Martínez, I., Bruner, E., Arsuaga,
1140 J.L., Bermúdez de Castro, J.M., 2013. Morphometric analysis of molars in a Middle
1141 Pleistocene population shows a mosaic of ‘modern’ and Neanderthal features. *Journal of*
1142 *Anatomy* 223, 353–363.
- 1143 Matiegka, J., 1934. *Homo předmostensis* – Fossilní Člověk z Předmostí Na Morarě I Lebký.
1144 Česká Akademie Věd a Umění, Prague.
- 1145 Maureille, B., Rougier, H., Houët, F., Vandermeersch, B., 2001. Les dents inférieures du
1146 Néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne):
1147 analyses métriques et comparatives. *Paléo* 13, 183–200.
- 1148 Maureille, B., Djindjian, F., Garralda, M.D., Mann, A., Vandermeersch, B., 2008. Les dents
1149 moustériennes de la grotte Bocard, lieu-dit Bas-de-Morant (commune de Créancey, Côte-
1150 d’Or, Bourgogne). *Bulletins et Mémoires de la Société d’Anthropologie de Paris* 20,
1151 59–78.
- 1152 Moorrees, C.F.A., 1957. *The Aleut Dentition*. Harvard University Press, Cambridge.
- 1153 NESPOS, 2013. NESPOS – Pleistocene People and Places.
1154 <https://www.nespos.org/display/openspace/Home> (last accessed on 20/12/2013).

- 1155 Nicolle, E.T., Sinel, J., 1910. 102. Report on the exploration of the Palaeolithic cave-dwelling
1156 known as La Cotte, St. Brelade, Jersey. *Man* 10, 185–188.
- 1157 Nicolle, E.T., Sinel, J., 1912. 88. Report on the resumed exploration of "La Cotte", St.
1158 Brelade, by the Societe Jersiaise. *Man* 12, 158–162.
- 1159 Oakley, K.P., Campbell, B.G., Molleson, T.I., 1975. Catalogue of Fossil Hominids (Vol. 2).
1160 British Museum (Natural History), London.
- 1161 Ortiz, A., Bailey, S.E., Hublin, J.J., Skinner, M.M., 2017. Homology, homoplasy and cusp
1162 variability at the enamel–dentine junction of hominoid molars. *Journal of Anatomy* 231,
1163 585–599.
- 1164 Patte, É., 1962. *La Dentition des Néanderthaliens*. Masson et Cie, Paris.
- 1165 Peter, B., 2019. Gene flow between hominins was common. *Proceedings of the European*
1166 *Society for the Study of Human Evolution* 8, 147.
- 1167 Pinilla, B., Trinkaus, E., 2017. The Palomas dental remains: Size and proportions. In:
1168 Trinkaus, E., Walker, M.J. (Eds.), *The People of Palomas: Neandertals from the Sima de*
1169 *las Palomas del Cabezo Gordo, Southeastern Spain*. Texas A&M University Press,
1170 College Station, pp. 89–104.
- 1171 Prado-Simón, L., Martín-Torres, M., Baca, P., Olejniczak, A.J., Gómez-Robles, A.,
1172 Lapresa, M., Arsuaga, J.L., Bermúdez de Castro, J.M., 2012. Three-dimensional
1173 evaluation of root canal morphology in lower second premolars of Early and Middle
1174 Pleistocene human populations from Atapuerca (Burgos, Spain). *American Journal of*
1175 *Physical Anthropology* 147, 452–461.
- 1176 Quam, R., Bailey, S., Wood, B., 2009. Evolution of M¹ crown size and cusp proportions in
1177 the genus *Homo*. *Journal of Anatomy* 214, 655–670.
- 1178 Radovčić, J., Smith, F.H., Trinkaus, E., Wolpoff, M.H., 1988. *The Krapina Hominids an*
1179 *Illustrated Catalog of Skeletal Collection*. Mladost, Zagreb.

1180 Rasband, W.S., 2008. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland,
1181 <http://rsb.info.nih.gov/ij/>.

1182 Reid, C., Reenen, J.F. Van, 1995. Remnants of the metaconule in recent man. In: Radlanski,
1183 R.J., Renz, H. (Eds.), Proceedings of the 10th International Symposium on Dental
1184 Morphology. C. and M. Brunne, Berlin, pp. 172–176.

1185 Scott, B., Bates, M., Bates, R., Conneller, C., Pope, M., Shaw, A., Smith, G., 2014. A new
1186 view from la Cotte de St Brelade, Jersey. *Antiquity* 88, 13–29.

1187 Scott, G.R., Turner II, C.G., 1997. *The Anthropology of Modern Human Teeth*. Cambridge
1188 Studies in Biological Anthropology, Cambridge University Press, Cambridge.

1189 Scott, G.R., Irish, J.D., 2017. *Human Tooth Crown and Root Morphology*. Cambridge
1190 University Press, Cambridge.

1191 Scott, G.R., Turner, C.G. II, Townsend, G.C., Martínón-Torres, M., 2018. *The Anthropology
1192 of Modern Human Teeth: Dental Morphology and its Variation in Recent and Fossil Homo
1193 sapiens*. 2nd ed. Cambridge University Press, Cambridge.

1194 Semal, P., Hauzeur, A., Rougier, H., Crevecoeur, I., Germonpré, M., Pirson, S., Haesaerts, P.,
1195 Jungels, C., Flas, D., Toussaint, M., Maureille, B., 2013. Radiocarbon dating of human
1196 remains and associated archaeological material. In: Rougier, H., Semal, P. (Eds), *Spy
1197 Cave: 125 Years of Multidisciplinary Research at the Betche Aux Rotches (Jemeppe-sur-
1198 Sambre, Province of Namur, Belgium)*. Société Royale Belge d'Anthropologie et de
1199 Préhistoire, Brussels, pp. 331–356.

1200 Shaw, A., Bates, M., Conneller, C., Gamble, C., Julien, M.A., McNabb, J., Pope, M., Scott,
1201 B., 2016. The archaeology of persistent places: the Palaeolithic case of La Cotte de St
1202 Brelade, Jersey. *Antiquity* 90, 1437–1453.

- 1203 Shields, E.D., 2005. Mandibular premolar and second molar root morphological variation in
1204 modern humans: What root number can tell us about tooth morphogenesis. *American*
1205 *Journal of Physical Anthropology* 128, 299–311.
- 1206 Shifman, A., Chananel, I., 1978. Prevalence of taurodontism found in radiographic dental
1207 examination of 1,200 young adult Israeli patients. *Community Dental Oral Epidemiology*
1208 6, 200–203.
- 1209 Skinner, M.M., Gunz, P., 2010. The presence of accessory cusps in chimpanzee lower molars
1210 is consistent with a patterning cascade model of development. *Journal of Anatomy* 217,
1211 245–253.
- 1212 Skinner, M.M., Wood, B.A., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M., Hublin,
1213 J.J., 2008. Dental trait expression at the enamel-dentine junction of lower molars in extant
1214 and fossil hominoids. *Journal of Human Evolution* 54, 173–186.
- 1215 Skinner, M.M., Wood, B.A., Hublin, J.-J., 2009. Protostylid expression at the enamel-dentine
1216 junction and enamel surface of mandibular molars of *Paranthropus robustus* and
1217 *Australopithecus africanus*. *Journal of Human Evolution* 56, 76–85.
- 1218 Skinner, M.M., Evans, A., Smith, T., Jernvall, J., Tafforeau, P., Kupczik, K., Olejniczak,
1219 A.J., Rosas, A., Radovčić, J., Thackeray, J.F., Toussaint, M., 2010. Brief communication:
1220 Contributions of enamel-dentine junction shape and enamel deposition to primate molar
1221 crown complexity. *American Journal of Physical Anthropology* 142, 157–163.
- 1222 Smith, B.H., 1984. Patterns of molar wear in hunter–gatherers and agriculturalists. *American*
1223 *Journal of Physical Anthropology* 63, 39–56.
- 1224 Smith, F.H., 1976. The Neandertal remains from Krapina: a descriptive and comparative
1225 study. Ph.D. Dissertation, University of Tennessee.

- 1226 Smith, P., 1989. Dental evidence for phylogenetic relationships of Middle Palaeolithic
1227 hominids. In: Vandermeersch, B. (Ed.), *L'Homme de Neandertal Vol 7. L'Extinction*.
1228 Université de Liège, pp. 111–120.
- 1229 Stringer, C.B., 2006. The Neanderthal-*H. sapiens* interface in Eurasia. In: Harvati, K.,
1230 Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer,
1231 Dordrecht, pp. 315–323.
- 1232 Stringer, C.B., Currant, A.P., 1986. Hominid specimens from La Cotte de St. Brelade. In:
1233 Callow, P., Cornford, J.M. (Eds.), *La Cotte de St. Brelade 1961–1978. Excavations by*
1234 *C.B.M. McBurney*. Geo Books, Norwich, pp. 155–158.
- 1235 Tarli, S.M.B., 1983. A Neanderthal lower molar from Fondo Cattie (Maglie, Lecce). *Journal*
1236 *of Human Evolution* 12, 383–401.
- 1237 Trinkaus, E., 1995. Neanderthal mortality patterns. *Journal of Archaeological Science* 22,
1238 121–142.
- 1239 Trinkaus, E., 2007. European early modern humans and the fate of the Neandertals.
1240 *Proceedings of the National Academy of Sciences USA* 104, 7367–7372.
- 1241 Trinkaus, E., 2017. The people of Palomas. In: Trinkaus, E., Walker, M.J. (Eds.), *The People*
1242 *of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern*
1243 *Spain*. Texas A&M University Press, College Station, pp. 245–247.
- 1244 Trinkaus, E., Moldovan, O., Bîlgăr, A., Sarcina, L., Athreya, S., Bailey, S.E., Rodrigo, R.,
1245 Mircea, G., Higham, T., Ramsey, C.B., van der Plicht, J., 2003. An early modern human
1246 from the Peștera cu Oase, Romania. *Proceedings of the National Academy of Sciences*
1247 *USA* 100, 11231–11236.
- 1248 Trinkaus, E., Bailey, S., Rougier, H., 2012. The dental and alveolar remains of Oase 1 and 2.
1249 In: Trinkaus, E., Constantin, S., Zilhão, J. (Eds.), *Life and Death at the Peștera cu Oase: A*

- 1250 Setting for Modern Human Emergence in Europe. Oxford University Press, New York,
1251 pp. 781–851.
- 1252 Turner, C.G., Nichol, C.R., Scott, G.R., 1991. Scoring procedures for key morphological
1253 traits of the permanent dentition. In: Kelley, M.A., Larsen, C.S. (Eds.), *Advances in*
1254 *Dental Anthropology*. Wiley-Liss, New York, pp. 13–31.
- 1255 Van Beek, G.C., 1983. *Dental Morphology: an Illustrated Guide*. Wright, Oxford.
- 1256 Vandermeersch, B., 1981. *Les Hommes Fossiles de Qafzeh (Israel)*. CNRS, Paris.
- 1257 Walker, M.J., Gibert, J., López, M.V., Lombardi, A.V., Pérez-Pérez, A., Zapata, J., Ortega,
1258 J., Higham, T., Pike, A., Schwenninger, J.L., Zilhão, J., 2008. Late Neandertals in
1259 southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. *Proceedings*
1260 *of the National Academy of Sciences USA* 105, 20631–20636.
- 1261 Walker, M.J., López, M.V., Haber, M., Trinkaus, E., 2017. The context of the Sima de las
1262 Palomas Neandertals. In: Trinkaus, E., Walker, M.J. (Eds.), *The People of Palomas:*
1263 *Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain*. Texas
1264 A&M University Press, College Station, pp. 4–18.
- 1265 Wollny, G., Kellman, P., Ledesma-Carbayo, M.J., Skinner, M.M., Hublin, J.-J., Hierl, T.,
1266 2013. MIA-A free and open source software for gray scale medical image analysis. *Source*
1267 *Code for Biology and Medicine* 8, 20.
- 1268 Wood, B.A., Abbott, S.A., 1983. Analysis of the dental morphology of Plio–Pleistocene
1269 hominids. I. Mandibular molars: crown area measurements and morphological traits.
1270 *Journal of Anatomy* 136, 197–219.
- 1271 Zapata, J., Bayle, P., Lombardi, A.V., Pérez-Pérez, A., Trinkaus, E., 2017. The Palomas
1272 dental remains: preservation, wear, and morphology. In: Trinkaus, E., Walker, M.J. (Eds.),
1273 *The People of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo,*
1274 *Southeastern Spain*. Texas A&M University Press, College Station, pp. 52–88.

1275 Zeuner, F.E., 1940. The age of Neanderthal man, with notes on the Cotte de St Brelade,
1276 Jersey, C.I. London University Institute of Archaeology, London.
1277 Zilhão, J., Trinkaus, E., Constantin, S., Milota, S., Gherase, M., Sacrina, L., Danciu, A.,
1278 Rougier, H., Quilès, J., Rodrigo, R., 2007. The Peștera cu Oase people, Europe's earliest
1279 modern humans. In: Mellars, P.M., Bar-Yosef, O., Stringer, C., Boyle, K.V. (Eds.),
1280 Rethinking the Human Revolution: New Behavioural and Biological Perspectives on the
1281 Origin and Dispersal of Modern Humans. McDonald Institute for Archaeological
1282 Research, Cambridge, pp. 249–262.

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1284 **Figure legends**

1285

1286 **Figure 1.** Location of La Cotte de St Brelade (from Shaw et al., 2016). A) Channel Islands
1287 within north-western Europe. B) Jersey in relation to other Channel Islands and the French
1288 coast, showing the ~7 m drop in sea level necessary to reconnect to the continent. C)
1289 simplified geological map of Jersey showing main sites. Based on an image supplied by John
1290 Renouf, with permission.

1291 **Figure 2.** Site plan (A) and cross-section (B) of La Cotte de St. Brelade.

1292 **Figure 3.** E.T. Nicolle shown standing on the level of the hearth, with what might be the
1293 ledge on which the teeth were found on the left-hand side. Photograph by R. Mollet.
1294 Reproduced with the kind permission of the Société Jersiaise.

1295 **Figure 4.** SJMJ2463, left C₁. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1296 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in lingual
1297 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1298 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1299 **Figure 5.** SJMJ2457, left P⁴. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1300 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1301 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1302 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1303 **Figure 6.** SJMJ2464, left P₃. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1304 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1305 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1306 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1307 **Figure 7.** SJMJ2465, left P₄. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1308 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1309 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1310 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1311 **Figure 8.** SJMJ2456, right M¹. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1312 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1313 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1314 shown in f). Occlusal polygon shape shown on occlusal photograph. Abbreviations: B =
1315 buccal; D = distal; L = lingual; M = mesial.

1316 **Figure 9.** SJMJ2458, left M². a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1317 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1318 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1319 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1320 **Figure 10.** SJMJ2459, right M³. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1321 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1322 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1323 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1324 **Figure 11.** Cast of SJMJ2467, left M³. a–f) Photographs in occlusal (a), mesial (b), buccal
1325 (c), apical (d), distal (e), lingual (f) views. Note that a black and white photo of the original
1326 tooth taken after casting is provided in distal view. Abbreviations: B = buccal; D = distal; L =
1327 lingual; M = mesial.

1328 **Figure 12.** SJMJ2461, right M₂. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1329 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1330 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1331 shown in f). Letters (a and b) on occlusal image denote mesiodistally concave/convex facets.
1332 Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1333 **Figure 13.** SJMJ2455, left M₂. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1334 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1335 view. h) CT cross-section (plane of section shown in d). i) occlusion of SJMJ2455 and
1336 SJMJ2458 (not to scale). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1337 **Figure 14.** SJMJ2460, right M₃. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1338 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1339 view showing numerous accessory dentine horns (*). h) CT cross-section (plane of section
1340 shown in d). i) articulation of SJMJ2460 and SJMJ2461 (not to scale). Abbreviations: B =
1341 buccal; D = distal; L = lingual; M = mesial.

1342 **Figure 15.** La Cotte SJMJ2452 occipital fragment (right) compared to a modern child aged
1343 about 6 years. A) ectocranial surface; B) endocranial surface, dotted lines indicating the
1344 pathway of the transverse sulcus, which passes directly across the asterion in both bones.

1345 **Figure 16.** Comparison of M¹ occlusal polygon shapes. Neanderthal: Krapina D161; La
1346 Cotte: SJMJ2456; fossil *H. sapiens*: La Madeleine. Abbreviations: B = buccal; D = distal; L =
1347 lingual; M = mesial.

1348 **Figure 17.** Results of the principal components analysis of cervix shape landmarks in P^4 in
1349 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1350 form (d) space. The percentage of variance depicted by each principal component (PC) is
1351 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1352 **Figure 18.** Results of the principal components analysis of cervix shape landmarks in P_3 in
1353 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1354 form (d) space. The percentage of variance depicted by each principal component (PC) is
1355 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1356 **Figure 19.** Results of the principal components analysis of cervix shape landmarks in P_4 in
1357 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1358 form (d) space. The percentage of variance depicted by each principal component (PC) is
1359 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1360 **Figure 20.** Results of the principal components analysis of cervix shape landmarks in M^1 in
1361 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1362 form (d) space. The percentage of variance depicted by each principal component (PC) is
1363 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1364 **Figure 21.** Results of the principal components analysis of cervix shape landmarks in M^2 in
1365 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1366 form (d) space. The percentage of variance depicted by each principal component (PC) is
1367 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1368 **Figure 22.** Results of the principal components analysis of cervix shape landmarks in M^3 in
1369 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1370 form (d) space. The percentage of variance depicted by each principal component (PC) is
1371 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1372 **Figure 23.** Results of the principal components analysis of cervix shape landmarks in M₂ in
1373 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1374 form (d) space. The percentage of variance depicted by each principal component (PC) is
1375 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1376 **Figure 24.** Crown area adjusted Z scores; distances of La Cotte dimensions from comparative
1377 sample means of late Neanderthal, fossil *Homo sapiens* and Krapina. Abbreviations: Hs = *H.*
1378 *sapiens*; U = upper; L = lower; C = canine; P = premolar; M = molar; UM3a = SJMJ2467;
1379 UM3b = SJMJ2459. P⁴: buccolingual dimension only.

1380 **Figure 25.** Crown index adjusted Z scores; distances of La Cotte dimensions from
1381 comparative sample means of late Neanderthal, fossil *Homo sapiens* and Krapina.
1382 Abbreviations: Hs = *H. sapiens*; U = upper; L = lower; C = canine; P = premolar; M = molar;
1383 UM3a = SJMJ2467; UM3b = SJMJ2459.

1384

Response to reviewers

A number of minor clarifications have been made to the ms, identified in the cover letter and the tracked version of the ms.

There are three minor factual corrections and some grammatical corrections, not tracked. The factual corrections are:

Line 43; 40.6 in place of 40.5

Line 616; '39% and 13%' in place of '13% and 39%'

Line 890; 'P₃ and' deleted.

Also, in Table 6, hypocone size for SJMJ2459 changed from (3.5) to (>2).

The morphology of the Late Pleistocene hominin remains from the site of La Cotte de St Brelade, Jersey (Channel Islands)

Tim Compton^{a,*}, Matthew M. Skinner^{b,c}, Louise Humphrey^a, Matthew Pope^d, Martin Bates^e, Thomas W. Davies^c, Simon A. Parfitt^{a,d}, William P. Plummer^b, Beccy Scott^f, Andrew Shaw^g, Chris Stringer^a

^a *Centre for Human Evolution Research, Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK*

^b *School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, UK*

^c *Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*

^d *UCL Institute of Archaeology, University College London, 31-34 Gordon Square, London WC1H 0PY, UK*

^e *Faculty of Humanities and Performing Arts, University of Wales Trinity St David, Lampeter, Ceredigion SA48 7ED, UK*

^f *Directorate, The British Museum, Great Russell Street, London WC1B 3DG, UK*

^g *Wessex Archaeology, Portway House, Old Sarum Park, Salisbury, Wiltshire SP4 6EB, UK*

* Corresponding author.

E-mail address: t.compton@nhm.ac.uk (T. Compton).

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1 The morphology of the Late Pleistocene hominin remains from the site of La Cotte de St
2 Brelade, Jersey (Channel Islands)

3

4 **ABSTRACT**

5 Thirteen permanent fully-erupted teeth were excavated at the Paleolithic site of La Cotte de
6 St Brelade in Jersey in 1910 and 1911. These were all found in the same location, on a ledge
7 behind a hearth in a Mousterian occupation level. They were originally identified as being
8 Neanderthal. A fragment of occipital bone was found in a separate locality in a later season.
9 Recent dating of adjacent sediments gives a probable age of <48 ka. The purpose of this
10 paper is to provide an updated description of the morphology of this material, and consider its
11 likely taxonomic assignment from comparison with Neanderthal and *Homo sapiens* samples.
12 One of the original teeth has been lost, and we identify one as non-hominin. At least two
13 adult individuals are represented. Cervix shape and the absence of common Neanderthal traits
14 in several teeth suggest affinities with *H. sapiens* in both individuals, while crown and root
15 dimensions and root morphology of all the teeth are entirely consistent with a Neanderthal
16 attribution, pointing towards a possible shared Neanderthal and *H. sapiens* ancestry (the
17 likely date of this material corresponds with the time in which both Neanderthals and *H.*
18 *sapiens* were present in Europe). The occipital fragment is stratigraphically more recent and
19 does not exhibit any diagnostic Neanderthal features.

20

21 **Keywords:** Hominin teeth; Late Pleistocene; Neanderthal; European Pleistocene *Homo*
22 *sapiens*; La Cotte de St. Brelade; Hominin morphology.

23

24 **1. Introduction**

25 The timing and duration of overlaps between *Homo sapiens* and Neanderthals in Europe,
26 and the nature of their interaction, have long been debated by archaeologists and
27 anthropologists (e.g., Stringer, 2006; Hoffercker, 2009). Recent evidence points towards
28 contemporaneity or alternation of occupation of the two populations (Benazzi et al., 2011;
29 Harvati et al., 2019). The application of improved radiocarbon dating methods has shown that
30 the Mousterian ended by ~41–39 ka cal BP across much of Europe (Higham et al., 2014).
31 Furthermore, new data from Bulgaria suggest that *H. sapiens* were already in Eastern Europe
32 by ~45 ka, several millennia before the physical disappearance of the Neanderthals from the
33 region. Hominin fossils from Bacho Kiro were identified as *H. sapiens* from morphology and
34 mtDNA analysis, and directly dated to ~46.8–42.8 ka cal BP (Fewlass et al., 2020; Hublin et
35 al., 2020). Radiocarbon dating shows a clear overlap of the initial Upper Paleolithic at Bacho
36 Kiro with the late Mousterian and Châtelperronian attributed to late Neanderthal populations
37 (Fewlass et al., 2020). In central and northwestern Europe, the Châtelperronian (~44–40 ka)
38 overlaps with both the Early Aurignacian, starting at ~43–42 ka, and the Proto-Aurignacian,
39 starting at ~42 ka (Hublin, 2015). In Western Europe, there is direct fossil evidence for the
40 presence of both *H. sapiens* and Neanderthals at ~41–40.4 ka. A tooth discovered in a Proto-
41 Aurignacian context at the site of Grotta di Fumane in northern Italy and dated to ~41–38.5
42 ka cal BP was found to have *H. sapiens* DNA (Benazzi et al., 2015), while a Neanderthal
43 tibia from Saint-Césaire in western France was directly dated to ~42–40.6 ka cal BP (Hublin
44 et al., 2012) and Neanderthal fossils from Spy in Belgium have been directly dated to
45 ~42.2–40.4 ka cal BP (Semal et al., 2013). The Oase 1 *H. sapiens* from Romania, dated to
46 ~42.5–40.5 ka cal BP (Zilhão et al., 2007), had a Neanderthal ancestor within the previous six
47 generations (Fu et al., 2015), which demonstrates that these populations probably did overlap
48 in Europe before 40 ka. In support of this, Peter (2019) has determined that, while the
49 majority of Neanderthal ancestry entered *H. sapiens* populations between ~55 and ~48 ka,

50 there was a lesser amount of gene flow within Europe, ending at ~40 ka. Interestingly,
51 Hajdinjak et al. (2018) found no evidence of recent gene flow from *H. sapiens* in four very
52 late Neanderthals, dated to <45 ka cal BP, from Goyet, Spy, Les Cottés and Mezmaiskaya.

53 The hominin remains from La Cotte de St Brelade on Jersey (Fig. 1) probably fall within
54 this key time period when both Neanderthals and *H. sapiens* were present in Western Europe.
55 Their taxonomic status is therefore of considerable interest. The hominin remains originate
56 from an area of complex sedimentation close to where the North and West Ravines meet (Fig.
57 2). Members of the Société Jersiaise undertook excavation in this area in 1910–1911 after the
58 cave entrance had been cleared of clay and granite rubble deposits. The investigators located
59 a series of fine-grained deposits, some of which were rich in ash and carbonized wood, which
60 they described as hearths (Nicolle and Sinel, 1910). The excavations of these deposits
61 continued until 1920 and produced at least 20,000 stone artifacts (Callow, 1986a), but it
62 appears that smaller debitage elements were largely discarded during the initial seasons.
63 These artifacts were described at the time as Mousterian in character (Marett, 1916), and
64 more recent analysis has confirmed that all the stone artifacts are consistent with Late Middle
65 Paleolithic technological practices (Callow, 1986a). The assemblage contains both Levallois
66 and discoidal production elements, as well as formal tools, including side scrapers and two
67 bifaces. No artifacts consistent with Upper Paleolithic technology have been identified among
68 the artifact collections of La Cotte de St Brelade.

69 It is not possible to determine what fauna were found within deposits directly associated
70 with the hominin remains from the surviving archive of the excavations carried out between
71 1910 and 1920. However, the faunal material recovered from ‘Weichselian’ units as a whole
72 includes *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp., *Rangifer tarandus*,
73 *Crocota crocuta*, and *Vulpes vulpes* (see Callow, 1986b), species which would be consistent
74 with a Marine Isotope Stage (MIS) 3 attribution in northern France (Auguste, 2009).

75 Mammoth, woolly rhinoceros and horse are specifically mentioned as coming from the same
76 general area as the hominin teeth (Nicolle and Sinel, 1910; Keith and Knowles, 1911).

77 The hominin teeth were discovered over two seasons. In 1910, nine teeth were found in a
78 mass of poorly preserved bone (for which no identifications are recorded) on a rock ledge
79 above the layer identified as a hearth (Fig. 3; Nicolle and Sinel, 1910). They were described
80 as lying side by side in original position, but with no trace of once supporting bone apparent.
81 A further four teeth were found in clay adhering to the rock at the same location in 1911
82 (Nicolle and Sinel, 1912). An occipital fragment, together with two other bone fragments,
83 were discovered in a ravine 6 ft (1.8 m) beyond the entrance of the cave and 18 ft (5.4 m)
84 above the Mousterian cave floor level by Ernest Daghorn in 1915 (Marett, 1916).

85 Analysis of the surviving archive and a modern survey of the site have allowed us to
86 broadly identify the location and position in the stratigraphic succession from which the
87 hominin teeth were recovered and, more generally, the position and context of the hominin
88 occipital fragment (Table 1). Although the deposits from this part of the site were removed
89 during the early 20th century, their stratigraphic equivalents appear to extend into areas of
90 remaining sediment within the main West Ravine (Bates et al., 2013). Optically stimulated
91 luminescence (OSL) dating undertaken in 2011 within the middle parts of this sequence,
92 approximately 4 m below the location where the teeth were discovered, suggests that the
93 deposits containing the teeth and the occipital fragment both postdate ~48 ka (Bates et al.,
94 2013). In view of the vertical extent of sediments between the lower dated horizon and the
95 location from which we understand the teeth to have been discovered, a date that is clearly
96 younger than 48 ka for the teeth is the only tenable proposition. It is plausible that these
97 deposits span a period in which both late Neanderthal populations and those of *H. sapiens*
98 were present in Western Europe, and during which sea levels were low enough for Jersey to
99 be part of a continuous landmass with France (Fig. 1B; Scott et al., 2014; Shaw et al., 2016).

100 Consequently, understanding the exact date and taxonomic affinity of these hominin fossils is
101 important for understanding Pleistocene population replacement at a regional scale.

102 The teeth were originally described by Keith and Knowles (1911, 1912). The 1912 paper
103 is a reprint of the 1911 paper, with additional details of the four teeth found in 1911. Keith
104 (1913) further addressed the considerable level of taurodontism in the molar teeth. The teeth
105 were briefly described in Marett (1911) and Oakley et al. (1975), and more recently were
106 studied by Stringer and Carrant (1986), who noted that by this date two of the teeth were only
107 represented by casts and one other tooth was missing. The missing tooth was a left I¹,
108 represented only by the root. The crown of this tooth had disintegrated before it was seen by
109 Arthur Keith, as the result of an accident during conservation (letter from J. Sinel to Keith
110 dated 1st September 1911, in the archives of the Royal College of Surgeons). In 1929 Tom
111 Watson, an amateur paleontologist/archaeologist on Jersey, sent a hominin lower canine that
112 he had found at La Cotte to Arthur Keith for identification (letter dated 17th January 1929, in
113 the archives of the Royal College of Surgeons). Although Tom Watson left all his finds to the
114 Jersey Museum, this tooth has not come to light. This letter also states that Tom Watson had
115 previously sent teeth and bones that he had discovered at La Cotte to Arthur Keith for
116 identification, but no record of these has been found. The three bone fragments recovered in
117 1915 were initially identified as parts of an occipital, malar and mandible from a single
118 juvenile skull (Marett, 1916). Angel and Coon (1954) reanalyzed the material and concluded
119 that only the occipital fragment was human, and that it belonged to a child about 5 years old.
120 This opinion was supported by Stringer and Carrant (1986), who agreed that the other two
121 fragments did not represent any part of the human skeleton.

122 The purpose of this paper is to provide an updated description of the morphology of the La
123 Cotte teeth and the occipital fragment, and present data relevant to their taxonomic
124 attribution.

125

126 **2. Materials and methods**

127 *2.1. Described material from La Cotte*

128 The material available for study consists of ten isolated permanent fully erupted teeth
129 (Table 2), and a fragment of occipital. These are held by the Jersey Museum, and were
130 temporarily loaned to the Natural History Museum, London, in 2015. Two other teeth,
131 SJMJ2462 (right I₁) and SJMJ2467 (left M³), are represented by casts. The casts made in
132 1911 and now held by the Natural History Museum, London, were used in this study because,
133 of several casts available, they are the most similar to the teeth described and illustrated by
134 Keith and Knowles (1912). The right I₁ (SJMJ2462) is thought to be non-hominin and is not
135 included in the analysis (see Supplementary Online Material [SOM] S1). With permission of
136 Jersey Heritage, the microtomographic scans of the La Cotte de St Brelade specimens
137 published in this paper are publically available (under a CC BY-NC 4.0 license) through the
138 Human Fossil Record online archive (<https://human-fossil-record.org/>).

139

140 *2.2. Comparative material*

141 Comparative samples for morphological traits scored at the outer enamel surface (OES)
142 principally come from Bailey (2006a) and, where the trait is not scored by Bailey (2006a),
143 from Martín-Torres et al. (2012)—see SOM Tables S1 and S2. These samples consist of
144 Neanderthals and fossil (primarily European Late Pleistocene) *H. sapiens*. Comparative CT-
145 scan samples employed for geometric morphometrics, and occurrence of Tomes' root
146 (Arizona State University dental anthropology system [ASUDAS] grades 4–5: Turner et al.,
147 1991) and taurodontism in P₃ and P₄, consist of Neanderthals, fossil (Pleistocene) *H. sapiens*
148 and recent (Holocene) *H. sapiens* (SOM Tables S1, S3, S4). Comparative metrics data for the
149 early Neanderthal site of Krapina, late Neanderthals and fossil (European Late Pleistocene)

150 *H. sapiens* were taken from the literature and the NESPOS database (2013), identified in
151 table legends and in SOM Tables S1–S3, S5, S6. For crown dimensions, the site of Krapina
152 was separated from late Neanderthals because of the distorting effect caused by the relatively
153 large size of the Krapina tooth crowns, and in some cases their different shape, together with
154 the fact that the Krapina teeth make up approximately one third of the total Neanderthal
155 sample.

156

157 *2.3. Methods*

158 Definitions We use the terms pre-Neanderthal (e.g., Atapuerca-SH, Pontnewydd), early
159 Neanderthal (e.g., Krapina, Bourgeois-Delaunay), and classic/late Neanderthal, as proposed
160 by Dean et al. (1998). Although this assumed a linear and almost certainly oversimplified
161 model of Neanderthal evolution (Hublin and Roebroeks, 2009), Compton and Stringer (2015)
162 found it useful in classifying morphological differences observed in Neanderthal dentitions.

163 Dental morphological traits Most of the morphological traits were assessed using the Arizona
164 State University Dental Anthropology System (ASUDAS), and associated reference plaques
165 (Turner et al., 1991; Scott and Turner, 1997; Scott et al., 2018). Additional traits described by
166 other authors and not included in the ASUDAS were also utilized (see SOM S2 for
167 descriptions of the traits studied). Wherever possible, traits were scored at the OES but, due
168 to wear, some traits could only be scored at the enamel dentine junction (EDJ). There are few
169 comparative data available for the frequency of traits at the EDJ, and they are only provided
170 here for P⁴. In other cases, traits scored at the EDJ were compared to frequencies of traits at
171 the OES. Several authors have found a strong positive correlation between the EDJ and the
172 OES in the expression of morphological traits in hominins (Krenn et al., 2019 for lower
173 premolars; Guy et al., 2015 for upper molars; Skinner et al., 2008, 2010 for lower molars) but
174 we recognize that wear obscures the OES and can lead to misidentification of trait

175 expression. For each trait, 95% confidence limits were calculated for trait frequency in each
176 taxon, and for the difference in frequencies between the two taxa (SOM S3). Traits that are of
177 potential use in making inferences about taxonomic affiliation are those where the confidence
178 intervals for the two comparative samples do not overlap, or where the confidence limits for
179 the difference in frequencies between the two comparative samples are both either above or
180 below zero (i.e., do not include zero; Altman et al., 2000).

181 Relative cusp areas and occlusal polygon Relative cusp areas, and the angles and relative size
182 of the occlusal polygon, on SJMJ2456 (right M¹) were measured from a high definition
183 photograph of the occlusal surface taken perpendicular to the plane of the cervix, using
184 ImageJ software (Rasband, 2008), according to the methodology described by Bailey (2004).
185 The original positions of the cusp tips were estimated by determining the point of intersection
186 of the principal ridges of each cusp visible at the EDJ,

187 Taurodontism The degree of taurodontism of the molars was determined using the method of
188 Shifman and Chananel (1978). Shifman and Chananel's (1978) method was employed (SOM
189 S2) because it provides an absolute measurement, rather than a relative measurement that
190 requires complete roots. The distance between the bicervical line and the highest point on the
191 floor of the pulp cavity of the molar teeth was measured from the CT scans (Table 2: pulp
192 chamber height). This is preferable to taking the measurement from the roof of the pulp
193 chamber, where secondary dentine may form as the tooth wears. The method presented by
194 Keene (1966; see SOM S2) was used to measure the degree of taurodontism in SJMJ2461
195 (right M₂), because the original root length could be estimated. The original length of the root
196 of this tooth, where the broken sides of the tooth's root are converging, was estimated by
197 extending these on a scaled photograph, and assuming a rounded tip.

198 Geometric morphometrics of cervix shape Microtomography was used to examine the
199 internal structures of the teeth. Specimens were scanned at the Natural History Museum using

200 an XTekCT scanner (180 kV, 205 μ A, 0.25mm copper filter, 3000 projections) with a
201 resultant isometric voxel size of \sim 30 μ m. To facilitate segmentation, each image stack was
202 filtered using a mean-of-least-variance filter (kernel size one) or a median and mean-of least
203 variance filter (each with kernel size three; Wollny et al., 2013). Each tooth was segmented
204 into its enamel and dentine components in Avizo 6.3 (ThermoFisher Scientific, Waltham).
205 Surface models of the EDJ were produced using the surface generation module
206 (unconstrained smoothing) and saved as PLY files.

207 Geometric morphometric analysis of cervix shape (in almost all cases the dentine horns,
208 and the ridges between, were too worn for landmark-based measurement) was conducted in
209 Mathematica 10 (Wolfram, Long Hanborough) following protocols outlined in previous
210 publications (Skinner and Gunz, 2010; Martin et al., 2017). Thirty semilandmarks were
211 placed around the cervix of each tooth. For the mandibular molars, the initial cervix landmark
212 was placed on the mesiobuccal corner of the crown (beneath the protoconid) and continued
213 mesially. In the maxillary molars, the initial landmark was placed on the middle part of the
214 buccal face of the crown (between the paracone and metacone) and continued mesially. For
215 mandibular and maxillary premolars the initial landmark was placed at the mid-point of the
216 buccal face and continued mesially. Estimations of missing portions of the cervix were made
217 for SJMJ 2457 (left P⁴), 2456 (right M¹) and 2461 (right M₂; SOM Fig. S1), and subjected to
218 Procrustes superimposition and then slid (Gunz and Mitteroecker, 2013) to create a
219 geometrically homologous set of shape variables. Principal components analysis (PCA) was
220 conducted to assess variation in cervix shape. Canonical variate analysis (CVA) was
221 conducted to assess taxonomic affinity using inclusive sets of principal component scores
222 (i.e., first set using 1–5 PCs, second set using 1–6 PCs, etc.) that represented \sim 95% of overall
223 shape variation. PCA was conducted in both shape space and form space; the latter including

224 the log of centroid size as a variable. CVA was only conducted in shape space and attempted
225 to assign La Cotte teeth to either Neanderthals or *H. sapiens*.

226 Crown and root measurements Measurements of the La Cotte teeth were taken with sliding
227 calipers to the nearest 0.1 mm. The crown dimensions and root lengths were measured using
228 the method of Moorrees (1957): crown = maximum dimensions parallel to and at right angles
229 to the buccal surface; root = maximum vertical dimension from the cervix of the mesiobuccal
230 root on the buccal aspect. In multirooted teeth, the term ‘trunk’ is used to describe the portion
231 of the root between the cervix and the point at which the individual roots furcate, and root
232 trunk length was measured as the distance between the cervix and the root furcation on the
233 aspect of the tooth on which this was at a minimum. The dimensions of the root at the cervix
234 were measured as the maximum dimensions at right angles to the mesial and buccal surfaces.
235 This definition was also used to measure cervical dimensions from CT scans of comparative
236 samples. Where the measurements for both left and right antimeres are available, the average
237 was used. Mesiodistal crown dimensions of the La Cotte teeth were adjusted for wear using
238 the method of Wood and Abbott (1983), in which the estimated original margins of the tooth
239 are drawn on a scaled photograph of the occlusal surface and the difference between these
240 and the actual margins measured. The adjusted measurements were used for comparisons
241 with other teeth. Where the length of the La Cotte teeth could not be estimated, only the
242 buccolingual dimension is used for comparison with other teeth. The level of occlusal wear
243 was quantified using Murphy's method, as summarized by Smith (1984; Table 2).

244 An adjusted z-score method, using Student's t inverse distribution (Maureille et al., 2001),
245 was employed to compare each of the La Cotte measurements with the means and standard
246 deviations of comparative groups. The formula applied was:

$$\frac{\text{La Cotte dimension} - X}{\text{Inv}t_{0.975; n-1} * SD}$$

249 where X , SD and n represent the mean, sample standard deviation and sample size
250 respectively of the comparative sample. The interval between -1 and $+1$ comprises 95% of
251 the variation in the comparative sample. A value of zero denotes that the La Cotte dimension
252 equals the mean of the comparative sample. A positive adjusted Z score indicates a La Cotte
253 dimension above the mean value and vice versa. All measurements and observations on the
254 La Cotte teeth were repeated by the same observer after an interval of one month.

255

256 **3. Results**

257 *3.1. Descriptions*

258 The tooth crown and roots appear to not have undergone any erosive taphonomic
259 processes. However, cracking and areas of taphonomic reworking of the dentine are evident
260 in the CT scans. Layers of cementum are apparent on the apical half of the root surfaces, with
261 the exception of SJMJ2459 (right M^3), but hypercementosis is not present. The pulp
262 chambers of the teeth exhibit what appears to be demineralisation and subsequent desiccation
263 of the circumpulpal primary dentine, leading to it having a 'feathered' appearance (C. Dean,
264 pers. comm.). There are deposits of secondary dentine in the molar pulp chambers. All the
265 teeth show some wear and this is generally flat and near horizontal. Most tooth crowns have
266 dentine exposed on individual cusps, and the surface morphology has largely been
267 obliterated.

268 Our identifications of tooth type are in agreement with those given by Keith and Knowles
269 (1912). Traits are described using the ASUDAS grades (Turner et al., 1991) unless otherwise
270 stated. X-ray photographs of the teeth are shown in SOM Figures S2 and S3. Discrete
271 morphological traits of the teeth, along with comparative data, are reported in Tables 3–7.

272 Lower left permanent canine (SJMJ2463) See Figure 4. The crown is complete, but the apex
273 of the root is missing. Severe cracking is evident on the buccal surface of the root below the

274 cervix and running down the distal surface from this point to the apex. This is also evident in
275 the buccolingual CT slice (Fig. 4h).

276 There is moderate (grade 2) shoveling (Fig. 4a), trace (grade 1) double shoveling (Fig. 4a),
277 a grade 4 distal accessory ridge (Fig. 4g), and a mesiobuccal bulge viewed occlusally.
278 Lingually, a tuberculum dentale is present as a mild medially placed bulge without a free
279 apex and there is a faint, wide but low, lingual medial ridge (Fig. 4g). The root is
280 labiolingually wide, with deep mesial and distal longitudinal grooves. The mesial groove is
281 particularly marked. The pulp canal is single and ovoid throughout the root, wide viewed
282 distally, and mesiodistally flattened (Fig. 4h, i). There is distinct vertical convex curvature of
283 the buccal aspect of the root, particularly towards the apex, and vertical convexity of the
284 lingual aspect.

285 Upper left fourth premolar (SJMJ2457) See Figure 5. The preserved morphology (narrow and
286 ovoid, rather than a more triangular crown shape) is consistent with a P⁴. The tooth has
287 matching occlusion (facets, wear shape and level of wear) with the left P₄ (SJMJ2465). The
288 crown has a postmortem chip on the distolingual corner of the occlusal rim, at the edge of a
289 large double fracture, and the root apices are missing. The distal aspect of the crown must
290 have broken off in life, since there is rounding and vertical striations on the occlusal edge of
291 the fracture.

292 The buccal surface of the crown is swollen, viewed mesially. The sagittal sulcus is visible
293 at the OES, curved lingually at the distal end (Fig. 5d) and, from the EDJ, it can be seen that
294 it terminates at the mesial margin (Fig. 5g). The EDJ reveals a small mesial accessory crest
295 (Fig. 5g), that likely delineated a small mesial fovea in the unworn tooth. A small pit is still
296 visible in this location on the worn occlusal surface (Fig. 5d). There are two robust roots,
297 with separate root canals, linked mesially by a radicular plate, creating a deep groove on the
298 distal root surface (cross-section in Fig. 5i). The buccal root is vertically convex. The pulp

299 chamber is taurodont, extending to the root furcation. It is mildly ovoid in distal and buccal
300 views (Fig. 5h; SOM Fig. S4).

301 Lower left third premolar (SJMJ2464) See Figure 6. The large size of the buccal cusp, and its
302 more lingual placement than in SJMJ2465 (left P₄), and our analysis of cervix shape (SOM
303 Fig. S5) indicate a P₃. Additionally, a buccal cingulum is present at the EDJ, which occurs
304 only on the P₃ in the comparative samples. The crown is complete, but the root apices are
305 missing.

306 The occlusal crown outline is buccolingually oblong, with slight mesiolingual truncation
307 (insufficient to score tooth as asymmetric) and the mesiodistal dimension greatest buccally.
308 Viewed mesially, the upper part of the buccal surface is curved sharply lingually and the
309 lingual surface is swollen. The bulbous metaconid is mesially placed, and there are two
310 smaller distolingual cusps observable at the OES (Fig. 6a). The Y-shaped mesiobuccally
311 slanted sagittal sulcus is not interrupted (Fig. 6a). It is narrow and the two foveae are
312 insignificant, the distal being the deepest. Traces of mesial and distal accessory ridges can be
313 seen on the buccal cusp at the OES, and are clearly visible at the EDJ (Fig. 6d, g). A faint
314 distolingual groove is present at the OES (Fig. 6a, d), but the lingual margin is uninterrupted
315 at the EDJ (Fig. 6g; Davies et al., 2019). The mesial and distal margins also both appear to
316 have been uninterrupted (there is no evidence of interruption at the EDJ). Examination of the
317 EDJ (Fig. 6g) indicates no evidence of a transverse crest. Small dentine horns underlie the
318 two accessory cusps distal to the metaconid (Fig 6g). Although not visible at the enamel
319 surface, there is a faint buccal cingulum at the EDJ, consisting of a mesially placed horizontal
320 ridge continuing from a slight mesial vertical groove/ridge (not shown).

321 There is a grade 4 Tomes' root (cross-section in Fig. 6i), with partial division into two
322 roots, each with a single root canal. In the mesiobuccal root there is a vertical mesial groove
323 and a prominent buccal groove. The buccal aspect of this root is vertically convex. The

324 taurodont pulp chamber extends to the root furcation and is mildly ovoid in lingual view
325 (SOM Fig. S6). In distal view it is convex lingually on the lingual side at the cervix, and is
326 hourglass shaped below this. The root canal in the buccal root is enlarged buccolingually
327 (Fig. 6h, i).

328 Lower left fourth premolar (SJM2465) See Figure 7. Morphological identification as a P₄ is
329 confirmed by analysis of cervix shape (SOM Fig. S5). The tooth cannot be a metamere of
330 SJMJ2464 (left P₃) because the interproximal facets do not match. The tooth is complete
331 apart from the apex of the root, which is chipped. Severe cracking can be seen on the lingual
332 side of the root in the buccolingual CT slice (Fig. 7h).

333 The occlusal outline is oblong, with very slight mesiolingual truncation. The worn down
334 buccal surface of the crown lacks the convexity and lingual inclination observed in
335 SJMJ2464 (left P₃), and the lingual face is less swollen. The narrow sagittal sulcus has a
336 small bridge of enamel centrally (Fig 7d). However, examination of the EDJ reveals no
337 evidence of a transverse crest (Fig. 7g). As with SJMJ2464 (left P₃), the mesial and distal
338 foveae (distal deepest) do not appear to have been large. The sagittal sulcus does not interrupt
339 either margin at the OES at this level of wear (Fig. 7d); and neither margin is interrupted at
340 the EDJ. The EDJ reveals a distolingual cusp, in addition to the metaconid, as well as a small
341 dentine horn on the mesial marginal ridge, and confirms the presence of a distal accessory
342 ridge on the buccal cusp (Fig. 7g).

343 There is a single straight-sided root, mesially convex viewed apically, with a longitudinal
344 groove in the apical half of the distal surface. The root is taurodont, with the pulp chamber
345 extending to the apex (SOM Fig. S6). In distal view it can be seen that there has been
346 considerable taphonomic alteration of the dentine towards the centre of the root, so that it is
347 difficult to determine the original shape of the pulp chamber but, as with the left P₃
348 (SJM2464), the lingual side appears to be convex at the cervix (Fig. 7h; SOM Fig. S6).

349 Molars The molar buccal and lingual faces are mildly convex viewed mesially. The buccal
350 surface grooves on upper molars are weak, and they are absent on lower molars. The loss of
351 occlusal surface morphology on the molars, despite a relatively low level of wear, suggests
352 that the unworn cusps were low. All the molar roots exhibit supraradicular taurodontism
353 (Kallay, 1970), where the pulp chamber is enlarged before the furcation of the roots.

354 Upper right permanent first molar (SJM2456) See Figure 8. The low crown index value
355 (equal mesiodistal and buccolingual measurements), particularly in relation to the other upper
356 molars in the comparative samples, and our analysis of cervix shape among Neanderthal and
357 *H. sapiens* M¹–M³, indicate an M¹ (SOM Fig. S7). Additionally, the oblique ridge at the EDJ
358 is type 1, running from the metacone dentine horn tip to the lingual marginal ridge distal to
359 the protocone. Type 1 is typical of M¹, but not of M² and M³ (Martin et al., 2017). The crown
360 is complete, but the roots are missing above the trunk. Part of the distal margin of the crown
361 broke off antemortem, as indicated by the presence of regular minor chipping along the
362 occlusal edge of the fracture.

363 The occlusal shape is a rounded and slightly skewed rhomboid, with a metacone that is
364 mesiolingually placed, resulting in distobuccal truncation, and a buccally protruding paracone
365 (Fig. 8a). Taking into account corrections for the missing fractured areas, the metacone and
366 hypocone are of similar size. Although worn, there appears to be a grade 2 metaconule (Fig.
367 8a; mesial and distal enamel protrusions from the uninterrupted oblique ridge: Reid and Van
368 Reenen, 1995). Examination of the EDJ (Fig. 8g) indicates no cusp 5 (hypoconule), two small
369 accessory dentine horns on the mesial marginal ridge, and a grade 3 post-paracone tubercle
370 (Ortiz et al., 2017) that cannot be detected at the enamel surface due to wear. The root is
371 hypertaurodont. The lingual aspect of the root trunk is flared lingually, and there is a vertical
372 groove reaching the cervix. At the broken root surface there is no evidence of separated roots

373 buccally or mesially, but the base of the trunk is visible distally. Due to taphonomic alteration
374 of the dentine it is difficult to determine the original shape of the pulp chamber.

375 Upper left permanent second molar (SJMJ2458) See Figure 9. The distal reduction in the
376 crown and presence of a distal interproximal facet indicate an M². This tooth occludes with
377 the left M₂ (SJMJ2455; Keith and Knowles, 1912). The tooth is complete apart from the root
378 apices.

379 The occlusal outline is near triangular, convex mesially and distally, and flattened
380 buccally. The tooth has a deep central fossa and no oblique ridge (Fig. 9a). No hypocone is
381 visible on the worn OES. There is a hypocone dentine horn at the EDJ (Fig. 9g), which is
382 likely to have been below grade 3 (reduced) on the original enamel surface due to its small
383 size. The presence of a cusp 5 is indicated by dentine exposure on the distal margin of the
384 OES (Fig. 9a). A grade 2 post-paracone tubercle (Ortiz et al., 2017) and a mesial marginal
385 ridge accessory tubercle are visible at the EDJ (Fig. 9g). The root is hypertaurodont. The
386 individual roots are furcated mesially at the level at which they are preserved, but with both
387 buccal and distal radicular plates (cross-section in Fig. 9i). Three individual root canals are
388 evident. The roots curve inwards in the apical half viewed distally (Fig. 9b), and both root
389 trunk and individual roots have a pronounced distal inclination. Though taphonomically
390 altered buccally, the pulp chamber appears to have been hour glass shaped in distal view (Fig.
391 9h).

392 Upper right third molar (SJMJ2459) See Figure 10. The diminutive distal portion of the
393 crown, and the lack of a distal interproximal facet despite the presence of substantial occlusal
394 wear, indicate an M³. The crown is complete, but the lingual root has been broken off at the
395 trunk, and the buccal roots are missing above the trunk.

396 Viewed occlusally, the mesial aspect of the tooth, including the root trunk, is markedly
397 concave, and the remainder of the tooth is near circular (Fig. 10a). Most surface morphology

398 has been obliterated due to wear. It is unclear which cusps were present in the large distal
399 area of dentine exposure, even at the EDJ (Fig. 10g). There are two dentine horns evident at
400 the EDJ between this area and the protocone (Fig 10g). If one of these is the hypocone, it is
401 most likely to be the more distally placed of the two, both from its position and its larger size.
402 If this is the case, it implies the presence of multiple lingual cusps along the distal rim of the
403 unworn tooth in addition to metacone, hypocone and cusp 5. No oblique ridge is evident at
404 the EDJ. There is a faint horizontal ridge on the buccal OES of the paracone (Fig. 10a), not
405 seen at the EDJ. The root is mesotaurodont. The lingual root is separated from the buccal root
406 mesially and distally just below the fragmented root surface. The buccal root is not bifurcated
407 at this level, though separate root canals are apparent.

408 Upper left third molar (SJM2467, cast) See Figure 11. The description is based on the 1911
409 Natural History Museum cast, and published details (Keith and Knowles, 1912; see SOM Fig.
410 S8B). The crown appears to have been complete. Only part of the root trunk is present in the
411 cast, but the root appears to have been complete in the original tooth according to the
412 photograph in Keith and Knowles (1912; Fig. 11e).

413 Viewed occlusally, the crown is strongly tapered distally, and flattened mesially. Details
414 of morphology are not clear due to the poor quality of the cast. There is a deep central fossa
415 and no oblique ridge (Fig. 11a). Keith and Knowles (1912) described the tooth as three-
416 cusped, lacking the hypocone. There is no evidence of a cusp 5 (Fig. 11e). The roots were
417 described as more compressed together than in the left M², but otherwise similar in form to
418 those of the molars found previously (Keith and Knowles, 1911, 1912). The roots appear to
419 have been hypertaurodont, with a greater degree of taurodontism than the other La Cotte
420 molars (Fig. 11e).

421 Lower right permanent second molar (SJM2461) See Figure 12. This tooth is identified as
422 an antimere of SJM2455 (left M₂). It has a distal interproximal facet, which is located

423 lingually, implying lingual displacement of the adjacent tooth. Displacement of this nature is
424 more likely to occur in an M₃ than in an M₂. The tooth is complete apart from the root apices.

425 The occlusal shape is rectangular, wider distally than mesially. It has rounded buccal and
426 distal aspects (mesial worn), and partial flattening lingually. There is a 'Y' groove pattern,
427 and a large (grade 5) distally oriented hypoconulid (cusp 5) visible at the OES (Fig. 12a). A
428 small dentine horn at the EDJ indicates that a cusp 6 (entoconulid) was present (Fig. 12g).
429 The sagittal sulcus is uninterrupted at the OES and no mid-trigonid crest is evident. It is
430 absent also at the EDJ, with only a weak crest on the protoconid (grade 0: Bailey et al., 2011).
431 Traces of a wide mesial fovea (trait referred to as an anterior fovea in the ASUDAS: Turner
432 et al., 1991; Scott and Turner, 1997; Scott and Irish, 2017; Scott et al., 2018) can be identified
433 at the OES and it is present as a linear depression at the EDJ. The entoconid dentine horn tip
434 is positioned on the margin of the tooth (Martin et al., 2017; Fig. 12g). There is a pit (grade 1)
435 protostylid at the OES (Fig. 12a), with a corresponding horizontal cingular crest at the EDJ
436 (Fig. 12g).

437 The mesial root is rectangular in shape and bifurcated at the apex, but fused to the distal
438 root buccally. The lingual furcation of the mesial root is convex mesially. The buccal sides of
439 both roots curve lingually. Marginal ridges are present mesially and distally on the mesial
440 root, and mesially on the distal root. The root is classed as hypertaurodont using Shifman and
441 Chananel's (1978) method but, with an estimated root length of 14.9 mm, Keene's (1966)
442 method gives a figure of 37%, which is classed as hypotaurodont (25–49.9%). The pulp
443 chamber is barrel shaped, viewed lingually, and widening of the mesial root canals is evident
444 in the mesiodistal CT slices (Fig. 12h; SOM Fig. S9).

445 Lower left permanent second molar (SJMJ2455) See Figure 13. This tooth occludes with the
446 left M² (SJMJ2458; Fig. 13i). It has mesial and distal interproximal wear facets, and, as with
447 SJMJ2461 (right M₂), the distal interproximal facet is located lingually. Based on a similar

448 degree of wear, similar dimensions and crown morphology, and the description of the
449 original root morphology (Keith and Knowles, 1912), this is likely to be the antimere to
450 SJMJ2461 (right M₂). The crown is complete, but Keith and Knowles (1912) sectioned the
451 root just below, and parallel to, the cervix (line visible in Fig. 13b). Part of the root has been
452 restored with filler. Only 9 mm of the trunk remains and the apical part of the root has been
453 lost. The tooth was described by Keith and Knowles (1912) as having roots of the same form
454 as the right M₂, fused buccally but not lingually, inclined distally and lingually, and having a
455 trunk length of 7 mm.

456 The occlusal shape is rectangular, with rounded margins (mesial worn), and partially
457 flattened lingually. As with the right M₂, there is a ‘Y’ groove pattern, and a large (grade 5)
458 distally placed hypoconulid is present (Fig. 13a, d). Unlike the right M₂ there is no cusp 6
459 dentine horn and no protostylid crest at the EDJ, though a trace protostylid is present on the
460 hypoconid (Fig. 13g). However, as with the right M₂, there is no mid-trigonid crest at the EDJ
461 (site worn at the OES; grade 0: Bailey et al., 2011) and only a weak crest evident on the
462 protoconid. The entoconid dentine horn tip is positioned on the margin of the tooth (Martin et
463 al., 2017).

464 Lower right third molar (SJMJ2460) See Figure 14. This tooth lacks a distal interproximal
465 facet despite the presence of dentine exposure. This, together with its shape and the presence
466 of a large number of accessory crests, indicates an M₃. The interproximal wear facet matches
467 with that of the right M₂ (SJMJ2461) (Fig. 14i) and it is likely the teeth are metameres. Only
468 the crown and less than one-quarter of the root are present. A portion of the mesial margin of
469 the crown has broken off postmortem. A lingual crack can be seen in the CT slice (Fig. 14h).

470 The overall occlusal shape of the crown is near circular. The unworn lingual half of the
471 tooth is very wrinkled, with multiple cusps present at the OES (Fig. 14a, d). There is an ‘X’
472 groove pattern (Fig. 14a). There are three crests running from the mesial margin into, and

473 filling, the mesial (anterior) fovea at the OES, but the presence of any associated mesial
474 marginal ridge tubercles cannot be assessed because the mesial face of the tooth is missing
475 (Fig. 14a). There is no mid-trigonid crest (grade 0 at the EDJ: Bailey et al., 2011). There is a
476 single mesiodistal groove at the OES on the buccal slope of the hypoconid, and lingual to the
477 dentine exposure, that delineates the large protostylid cingular crest seen at the EDJ (Fig.
478 14d, g). Examination of the EDJ (Fig. 14g) reveals the presence of numerous primary and
479 accessory dentine horns. Some of these can be reasonably identified as cusps, while others
480 reflect repeated enamel knot initiation (Martin et al., 2017). Moving distally from the
481 metaconid dentine horn, there is a small (grade 3) cusp 7, the entoconid, an undulating ridge
482 that potentially exhibits incipient dentine horns, a cusp 6, and then one additional dentine
483 horn lingual to the grade 4 hypoconulid. Additionally, there is a small dentine horn on the
484 protostylid ridge on the buccal aspect of the hypoconulid. The degree of internal placement of
485 the hypoconid relative to the protostylid cingulum is uncommon (not seen in any of the CT-
486 scan comparative samples), and may further reflect a general perturbation of the development
487 of this tooth. The metaconid and entoconid dentine horn tips are positioned on the margin of
488 the tooth (Martin et al., 2017).

489 Occipital fragment (SJM2452) See Figure 15. The occipital fragment comprises a small part
490 of a left squamous, measuring 53 mm between the broken anterior and posterior edges, and
491 37 mm from the asterion to the broken medial edge. The endocranial and exocranial surfaces
492 are weathered and marked by superficial cracks and abraded areas. One edge of the piece is
493 defined by the lambdoid suture, which extends 45 mm from the asterion. All the other edges
494 are defined by natural breaks. The thickness of the bone, and weak markings on the external
495 surface, are consistent with an immature age at death. The lambdoid suture has several
496 abraded patches but appears to be mostly open. An area of interdigitated bone, visible on the
497 external surface located 35 mm from the asterion, may represent an early stage of fusion at

498 the lambdoid suture. A finger of bone projecting inwards from the lambdoid suture, situated 6
499 mm from the asterion, and measuring 6.2 by 2.6 mm, appears to be a small wormian bone.
500 The endocranial surface has a well demarcated transverse sulcus that extends 35 mm from
501 just below the asterion to the broken medial edge along the lower border, and 32 mm from
502 the lambdoid suture to the broken medial edge along the upper border. The transverse sulcus
503 passes directly across the asterion and would have crossed the posteroinferior (mastoid)
504 corner of the parietal bone before reaching the temporal bone, instead of crossing directly
505 onto the temporal bone (Fig. 15B, indicated by dotted lines). Taken together, the size and
506 morphology of the occipital fragment are consistent with an immature individual who died in
507 late childhood or adolescence.

508

509 3.2. *Qualitative morphological comparisons*

510 Trait frequencies for the tooth types found in the La Cotte material, and in comparative
511 samples of Late Pleistocene hominins, are reported in Tables 3–7. Traits that show a
512 significant difference between Neanderthal and fossil *H. sapiens* are identified: (1) where the
513 95% confidence interval for the difference between the proportions for the two samples is
514 entirely above or below zero, i.e., does not include 0% difference; (2) where the 95%
515 confidence intervals for the two sample proportions do not overlap (SOM S3). These are the
516 traits principally discussed.

517 Lower canine (SJM2463) The characteristics of this tooth support a Neanderthal affinity.
518 Shoveling is present in the entire Neanderthal comparative sample and most (88%) of the
519 fossil *H. sapiens* sample (Table 3). The distal accessory ridge is more common in
520 Neanderthals (78%) than fossil *H. sapiens* (42%; Table 3). It tends to be more strongly
521 expressed in Neanderthals, as it is at La Cotte, than in fossil *H. sapiens* (50% compared to 8%
522 at their grade 2 in Martín-Torres et al.'s [2012: Table 17] samples). The mild expressions

523 of the tuberculum dentale and lingual medial ridge in SJMJ2463 (C₁) are the forms frequently
524 found in both comparative samples (Martín-Torres et al., 2012).

525 The buccal curvature of the root is typical of Neanderthals, but not of *H. sapiens*
526 (Bilsborough and Thompson, 2005; Le Cabec et al., 2013), as is the convex buccal contour of
527 crown and root together, known as 'cyrtodonty' (Patte, 1962; Brabant and Sahly, 1964). The
528 wide root canal, as viewed distally, is unlike the narrow straight sided canals found in recent
529 human teeth (van Beek, 1983).

530 Upper fourth premolar (SJMJ2457) The morphological traits of this tooth support a
531 Neanderthal affinity. The swollen buccal surface, viewed mesially, and sharp lingual
532 inclination from the point of maximum curvature, is typical of Neanderthals, and more
533 pronounced than is generally found in *H. sapiens* (TC, personal observation). The absence of
534 a buccal mesial accessory ridge is also typical of Neanderthals (83%) and less common in
535 fossil *H. sapiens* (40%; Table 4).

536 The roots are robust compared to *H. sapiens*. The two-rooted form present is the most
537 common type in Neanderthals (Maureille et al., 2008). The taurodontism, and a relatively
538 longer root trunk before furcation of the roots than in recent humans, are also seen in some
539 Neanderthal P⁴ (Kallay, 1963).

540 Lower third (SJMJ2464) and fourth (SJMJ2465) premolars The characteristics of both
541 premolars give an ambiguous picture. For the P₃ (SJMJ2464) the Neanderthal features are the
542 large lingually placed buccal cusp (Gómez-Robles et al., 2008), and the presence of a buccal
543 cingulum at the EDJ, which occurs frequently in the Neanderthal sample but is not seen in the
544 recent human sample. For the P₄ (SJMJ2465) the Neanderthal features are the presence of
545 multiple lingual cusps (94%), a mesially placed metaconid (97%), and a buccal distal
546 accessory ridge (88%; Table 4). The corresponding figures for fossil *H. sapiens* are
547 significantly lower (Table 4). The cusp on the mesial margin, represented by a dentine horn at

548 the EDJ, found on SJMJ2465 (left P₄), also occurs on three Krapina P₄ (Compton and
549 Stringer, 2012). Three or more lingual cusps on P₄ (three at La Cotte) are present in 89% of
550 Neanderthals but only 20% of fossil *H. sapiens* (Martinón-Torres et al 2012: Table 19).

551 In contrast, the absence of a transverse crest, and a symmetrical shape, found on both
552 premolars, are rare in Neanderthal P₃ (3% and 6% respectively) and P₄ (both at 6%; Table 4).
553 Additionally, Davies et al. (2019) recorded the presence of a transverse crest in their entire
554 Neanderthal P₃ sample. Martinón-Torres et al. (2012: Tables 18 and 19), however, reported
555 absence of a transverse crest in 15% of P₃ and 19% of P₄ in their Neanderthal sample. The
556 absence of a transverse crest, and a symmetrical shape, are more frequently observed for P₃
557 and P₄ in fossil *H. sapiens* (Table 4). Bailey (2002) looked at the combination of three
558 characteristics (well-developed metaconid, transverse crest and asymmetry) in P₄ and found
559 that 98% of modern humans had only one of these traits, as at La Cotte, compared to only 6%
560 of Neanderthals.

561 The robust roots of SJMJ2464 (left P₃) are more typical of Neanderthals than of *H.*
562 *sapiens*. Interestingly, grade 4–5 Tomes' root, present on the P₃, occurs less frequently in the
563 P₃ (12%) than in the P₄ (25%) in Neanderthals, the reverse of that found in fossil *H. sapiens*
564 (38% and 23% respectively; Table 4) and recent humans. Tomes' root occurs less frequently
565 in recent humans than in fossil *H. sapiens* (12.5% and 2.5% respectively for P₃ and P₄ in a
566 large mixed sample; Shields, 2005). The wide root canal observed in SJMJ2465 (left P₄) is
567 typical of Neanderthal P₄ but uncommon in recent humans (Prado-Simón et al., 2012). The
568 extended taurodont pulp chambers in SJMJ2464 (left P₃) and SJMJ2465 (left P₄) are apparent
569 as widening in both buccolingual and mesiodistal directions (SOM Fig. S6). In some teeth, in
570 both comparative samples (Table 4), extension of the pulp chamber into the root is only
571 apparent as widening in a buccolingual direction. Considering the small samples involved
572 (Table 4), the frequency of taurodontism is similar between P₃ and P₄ and between

573 Neanderthals and fossil *H. sapiens*. Taken overall, widening in a buccolingual direction, with
574 or without mesiodistal widening, occurs at approximately twice the frequency as widening in
575 both directions together (51% against 23%; Table 4).

576 Molars The upper molar cusps are internally placed, as is often observed in Neanderthals.
577 Carabelli's trait is absent in the upper molars. This was previously thought to be unusual in
578 Neanderthals (McCown and Keith, 1939; Smith, 1989). More recently Martínón-Torres et al.
579 (2012) reported 20% absence for M¹, 42% for M² and 80% for M³, in their Neanderthal
580 sample. The post-paracone dentine horn, which is present at the EDJ in SJMJ2456 (right M¹)
581 and SJMJ2458 (left M²) and could not be scored in SJMJ2459 (right M³), was ubiquitous in a
582 sample of Neanderthal maxillary molars and present in 86% of a recent human sample
583 (Martin et al., 2017: Table 10). In contrast, Ortiz et al. (2017: Table 4) reported the presence
584 of post-paracone dentine horns in 98% of a Neanderthal sample but only 25% of a recent
585 human sample. Taurodontism is particularly associated with Neanderthals, but it is also found
586 in fossil *H. sapiens* from Skhül and Qafzeh (McCown and Keith, 1939; Vandermeersch,
587 1981) and in Aterians (Kupczik and Hublin, 2010). Kupczik et al. (2019: Table S1) found
588 taurodontism (grades III and IV of their bifurcation index) in 88% (14 of 16) of their sample
589 of Neanderthal M₂. Studies of recent Europeans have shown taurodontism is present in less
590 than 10% of molars (Jafarzadeh et al., 2008: Table 3). The absence of enamel extensions
591 above trace level on any of the molars is also typical of Neanderthals, and most *H. sapiens*
592 outside Asia (Bailey, 2006b).

593 Upper first molar (SJMJ2456) The Neanderthal M¹ crown has a distinct shape (Bailey, 2004;
594 Gómez-Robles et al., 2007; Martínón-Torres et al., 2013): The main cusp tips are more
595 internally placed, leading to a relatively smaller occlusal polygon (formed by linking the tips
596 of the four principal cusps) compared to the total occlusal area (Table 5). There is a
597 statistically significant difference at $p \leq 0.01$ between Neanderthal and *H. sapiens* for this

598 percentage figure (Martín-Torres et al., 2013). The occlusal shape is skewed and there is a
599 large distally projected and swollen hypocone, leading to a narrow hypocone angle (Table 5;
600 Fig. 16). The metacone is relatively smaller than the hypocone and mesiolingually oriented,
601 leading to distobuccal truncation of the occlusal outline and a wide metacone angle (Table 5;
602 Fig. 16). The hypocone is larger than the metacone in 14/16 molars in Bailey's (2004)
603 Neanderthal sample. The occlusal polygon is narrower distally than mesially (Fig. 16).

604 The M¹ (SJM2456) shows clear Neanderthal affinities (see Table 5; Fig. 16). It has a
605 relatively small occlusal polygon (24%), a mesiolingually placed metacone, along with a
606 large metacone angle (116°), and an occlusal polygon that is narrower distally than mesially.

607 However, in contrast, the crown has only a mildly skewed appearance, with a small
608 protocone angle (100°) compared to the means of both the comparative samples (106°). The
609 relative size of the hypocone compared to total occlusal area (19%) is small in comparison to
610 the Neanderthal sample mean (23.7%) and smaller than the metacone (21%), and the
611 hypocone angle (76°) is large. While being within the Neanderthal range of variation, both of
612 these features are more similar to the fossil *H. sapiens* sample. Additionally, the protocone is
613 relatively large (33%) compared to Neanderthal (29.9%).

614 Upper second molar (SJM2458) The presence of a cusp 5 is common in Neanderthals
615 (68%), and the presence of a mesial accessory cusp is ubiquitous. Both are less frequent in
616 fossil *H. sapiens* (39% and 13% respectively; Table 6). The reduced hypocone is unusual,
617 though, in both Neanderthals and fossil *H. sapiens*, occurring at frequencies of only 6% and
618 15% respectively (Table 6). It is, however, common in the pre-Neanderthal Atapuerca-SH
619 sample (Martín-Torres et al., 2012).

620 Upper third molars (SJM2459 and SJM2467) The concave mesial aspect, viewed
621 occlusally, of SJM2459 (right M³) is distinctly unusual. The presence of multiple cusps
622 along the distal rim (i.e., in excess of metacone, hypocone and a single cusp 5), as inferred for

623 SJMJ2459 (right M³), has been reported in Krapina M³ (Compton and Stringer, 2012); and
624 Martin et al. (2017) found considerable variation in distal cusp pattern in Neanderthal M³.
625 Multiple distal cusps and split hypocones occur in Aterian teeth (Bailey et al., 2017), and split
626 hypocones have been reported in recent humans (Greene et al., 1967; Bermúdez de Castro
627 and Martínez, 1986), but mention of multiple distal cusps in recent humans is rare in the
628 literature. Ortiz et al. (2017: Table S3) found multiple cusp 5 at the EDJ in ~20% of
629 Neanderthals but only in ~1% of recent humans.

630 Lower molars (SJMJ2455 and SJMJ2461 M₂; SJMJ2460 M₃) We did not observe the
631 protostylid forms seen at the EDJ on SJMJ2461 (right M₂) and SJMJ2460 (right M₃) in our
632 comparative samples. The hypoconulid expression in the M₂ (SJMJ2455 and SJMJ2461) is
633 particularly large. Martínón-Torres et al. (2012: Table 21) found only 16.6% of Neanderthal
634 and 4% of fossil *H. sapiens* M₂ with grade 5 hypoconulids. The characteristics of the La
635 Cotte lower molars give an ambiguous picture. Neanderthal characteristics include the
636 presence of a hypoconulid (found in the entire Neanderthal sample), a wide mesial (anterior)
637 fovea (89% of M₂ and 93% of M₃), and a ‘Y’ groove pattern in M₂ (75%; Table 7). The
638 corresponding figures for fossil *H. sapiens* are significantly lower (Table 7). Additionally, the
639 multiple cusps and accessory crests found on SJMJ2460 (right M₃) have been observed in
640 Neanderthals (McCown and Keith, 1939; Radovčić et al., 1988; Bailey and Hublin, 2006), as
641 has the repeated enamel knot initiation seen at the EDJ (Martin et al., 2017).

642 In contrast, the absence of a mid-trigonid crest at the OES, observed in SJMJ2461 (right
643 M₂) and SJMJ2460 (right M₃), is rare in Neanderthal M₂ and M₃ (4% and 7% respectively),
644 but almost ubiquitous in the fossil *H. sapiens* sample, at 96% and 100% respectively (Table
645 7). At the EDJ, Bailey et al. (2011: Table 3) recorded the presence of a continuous mid-
646 trigonid crest in their entire Neanderthal M₂ and M₃ sample (absent at La Cotte), but only
647 35.5% and 14.3% respectively of a recent European sample. Furthermore, the position of the

648 metaconid dentine horn tip on the occlusal margin of SJMJ2460 (right M₃) is rare in
649 Neanderthals. The metaconid dentine horn was centrally placed in 95% of a late Neanderthal
650 sample but only 36% of a recent human sample (Martin et al., 2017: Table 9).

651 The non-tapering shape and bifurcation of the mesial root, and the presence of longitudinal
652 marginal ridges on mesial and distal roots, observed in SJMJ2461 (right M₂), are typical of
653 Neanderthal M₂ (Compton and Stringer, 2015).

654 Occipital fragment (SJMJ2452) The occipital lacks any diagnostic Neanderthal anatomical
655 features. The transverse sulcus pathway is typical of recent humans, and differs from the
656 pathway observed in some Neanderthals, in which the transverse sulcus passes directly from
657 the occipital to the temporal without crossing the parietal bone (Arsuaga et al., 2002).

658

659 3.3. Geometric morphometric analysis of cervix shape

660 Figures 17–23 illustrate PCAs of cervix morphology in shape and form (form including
661 the log of centroid size as a variable) space for upper and lower molars and premolars.

662 The P⁴ (SJMJ2457) falls closer to the *H. sapiens* samples (fossil and recent humans) in
663 shape space but with the Neanderthals in form space, reflecting its large size (Fig. 17a, b). It
664 differs from the mean Neanderthal cervix shape in being somewhat compressed
665 mesiolingually and distobuccally (Fig. 17c, d). Using 11 shape PCs, attribution accuracy of
666 the comparative P⁴ sample is ~65% (i.e., the proportion of specimens of known taxonomic
667 affiliation that are attributed correctly using cross-validated canonical variate analysis) and
668 posterior probabilities of discriminant analysis consistently assign SJMJ2457 (P⁴) to *H.*
669 *sapiens* rather than Neanderthal.

670 The identification of SJMJ2464 as a P₃ and SJMJ2465 as a P₄ is supported by their cervix
671 shape that groups them with the *H. sapiens* (fossil and recent humans) P₃ and P₄ samples
672 (SOM Fig. S5). The P₃ falls with the *H. sapiens* samples in shape space but closer to the

673 Neanderthal sample in form space due to its large size (Fig 18a, b). Wireframe models
674 indicate Neanderthals have a distally expanded cervix compared to the *H. sapiens* samples
675 and SJMJ2464 (P₃; Fig. 18c, d). Using 11 shape PCs, attribution accuracy of the comparative
676 P₃ sample is ~70% (with cross-validation), and posterior probabilities consistently assign
677 SJMJ2464 (P₃) to *H. sapiens*. The P₄ falls with the *H. sapiens* samples in both shape and
678 form space (Fig. 19a, b), sharing a buccolingually expanded cervix with both *H. sapiens*
679 samples (Fig. 19c, d) but being more similar in size to the earlier sample. Using 9 shape PCs,
680 attribution accuracy of the P₄ sample is ~90% (with cross-validation) and posterior
681 probabilities consistently assign SJMJ2465 (P₄) to *H. sapiens*.

682 The SJMJ2456 M¹ plots with Neanderthals in both shape space and form space (Fig. 20a,
683 b). It shares a distolingual expansion of the cervix with Neanderthals although it is not as
684 marked as the average Neanderthal M¹ wireframe (Fig. 20c, d). Using 11 shape PCs,
685 attribution accuracy of the comparative M¹ sample is ~90% (with cross-validation) and
686 posterior probabilities consistently assign SJMJ2456 (M¹) to Neanderthals.

687 The SJMJ2458 M² falls on the margin of the overlapping distributions of the *H. sapiens*
688 and Neanderthal samples in shape space, and the form analysis demonstrates it is larger than
689 most of the *H. sapiens* comparative sample and of average size for a Neanderthal (Fig. 21a,
690 b). The wireframe model highlights the unusually small hypocone of SJMJ2458 (M²)
691 compared to the mean *H. sapiens* and Neanderthal cervix shapes (Fig. 21c, d). Using 13
692 shape PCs, attribution accuracy of the comparative M² sample is ~70% (with cross-
693 validation) and SJMJ2458 (M²) assigns with near equal frequency as either a Neanderthal or
694 *H. sapiens* (i.e., its taxonomic attribution cannot be determined based on cervix shape).

695 The SJMJ2459 M³ falls well outside of both Neanderthal and *H. sapiens* ranges and it is
696 considerably larger than the largest Neanderthals in this analysis (Fig 22a, b). As with the
697 SJMJ2458 M², the wireframe comparisons of mean shape illustrate the particularly strange

698 contour of the SJMJ2459 M³ (Fig. 22c, d). Using 9 shape PCs, attribution accuracy of the
699 comparative M³ sample is ~70% (with cross-validation) and SJMJ2459 (M³) is consistently
700 assigned to Neanderthals.

701 The two M₂ (SJMJ2455 and SJMJ2461) fall in an intermediate position between the
702 Neanderthals and *H. sapiens* in shape space but fall closer to the fossil *H. sapiens* and
703 Neanderthal samples when size is included (Fig. 23a, b). The M₂s are similar to the
704 Neanderthal sample in having a buccally expanded cervix without the buccal pinching distal
705 to the protoconid present in the *H. sapiens* samples (Fig. 23c, d). Using 14 shape PCs,
706 attribution accuracy of the comparative sample is ~85% (with cross-validation) and posterior
707 probabilities consistently assign both SJMJ2455 and SJMJ2461 (M₂) to Neanderthals.

708 Cervix shape alone tends to perform less well at taxonomic discrimination than analyzes
709 that also incorporate the EDJ marginal ridge (Martin et al., 2017) and, at a number of tooth
710 positions, attribution accuracy of the comparative sample (in which taxonomic affiliation is
711 known) ranges between 60–90%. In summary, the P₃, P₄ and P⁴ are consistently assigned as
712 *H. sapiens*, while the two M₂, the M¹ and the M³ are consistently assigned as Neanderthals.
713 Attribution of the M² is less consistent and cervix shape cannot contribute strongly to its
714 taxonomic assessment.

715

716 3.4. Metrical comparisons

717 Comparative data for crown dimensions are presented in SOM Tables S7 and S8, and
718 adjusted Z scores for crown dimensions are illustrated in Figures 24 and 25.

719 Crown area See Figure 24. The crown areas of the La Cotte teeth are all close to or above the
720 late Neanderthal comparative sample means, with associated adjusted Z scores under ±0.5,
721 except for SJMJ2463 (left C₁) and SJMJ2464 (left P₃), which are particularly large. The C₁
722 crown area is above the range of the late Neanderthal comparative sample, and its

723 buccolingual dimension is only exceeded by Kebara 2 (10.2 mm). The buccolingual
724 dimension of the P₃ is only exceeded by La Quina 9 (11.0 mm), and this is the only tooth in
725 the late Neanderthal comparative sample with a larger crown area (99 sq mm). With the
726 exception of these two teeth, the crown areas of the La Cotte teeth are all within the ranges of
727 the other comparative samples, with associated adjusted Z scores up to ±0.7 (-0.8 for the
728 Krapina P₄). In contrast, the adjusted Z scores for SJMJ2463 (left C₁) and SJMJ2464 (left P₃)
729 are 0.8 and 0.7 respectively in relation to late Neanderthals, and 1.0 and 1.4 in relation to
730 fossil *H. sapiens*.

731 Crown index See Figure 25. The crown indices of the La Cotte teeth all have adjusted Z
732 scores under ±0.5 in relation to the late Neanderthal comparative sample except for the left
733 M³ SJMJ2467 (-0.7). The La Cotte M¹, M² and M³ have crown indices below the means of all
734 the comparative samples (SOM Table S7; with the lone exception of the right M³ SJMJ2459
735 in relation to Krapina), indicating that they are squarer; and C₁, P₃ and P₄ have crown indices
736 above the means of the comparative samples (SOM Table S8), indicating that they are
737 relatively buccolingually expanded. Two large differences in the comparative samples stand
738 out. The fossil *H. sapiens* M¹ has an adjusted Z score of -1.3, reflecting the more rectangular
739 shape of these teeth compared to Neanderthals. The Krapina P₃ has an adjusted Z score of 2.2
740 due to the lower crown indices of these teeth and this is also apparent in the Krapina lower
741 molars.

742 Cervical dimensions See Table 8. In all but one case (SJMJ2461, right M₂) the La Cotte
743 dimensions are above the Neanderthal comparative sample means. The mesiodistal
744 dimensions of SJMJ2463 (left C₁) and SJMJ2464 (left P₃), and the buccolingual dimension of
745 SJMJ2457 (left P⁴), at the cervix are either above or at the upper end of the Neanderthal
746 ranges. SJMJ2464 (left P₃) has adjusted Z scores for Neanderthal of 1.5 for the mesiodistal
747 dimension and 1.0 for the buccolingual dimension. Keith and Knowles (1912) noted the large

748 cervical dimensions; and the particularly high cervical dimensions of the La Cotte canine and
749 premolars, other than SJMJ2465 (left P₄), is very distinctive. Fossil *H. sapiens* have smaller
750 cervical dimensions than Neanderthals, and this difference is most pronounced in the P₄, M²
751 and M₂. The fossil *H. sapiens* adjusted Z scores for SJMJ2463 (left C₁) and SJMJ2464 (left
752 P₃) in both mesiodistal and buccolingual dimensions, and for SJMJ2458 (left M²) in the
753 mesiodistal dimension, are all at 1.0 or above.

754 Root length The only La Cotte tooth with a complete root is SJMJ2467 (LM³), for which only
755 a cast is now available (Keith and Knowles, 1912: preface). It has a length of 16.0 mm, which
756 is within the Neanderthal range (13.5–16.7 mm, mean 15.2 mm; Bailey, 2005), and above the
757 ranges for Předmostí (11.0–14.0 mm; Matiegka, 1934) and contemporary humans (8.0–15.0
758 mm; Black, 1902).

759

760 3.5. Number of individuals

761 Since all the teeth from La Cotte were found in one place, and are broadly similar in their
762 degree of development and wear, the ‘null hypothesis’ would be that they all come from the
763 same individual (Keith and Knowles, 1912). Our observations demonstrate that the eleven
764 teeth from La Cotte represent a maximum of six individuals, made up of three groups of teeth
765 that can be confidently associated with one another and three isolated teeth:

766 i) The largest group of unambiguously associated teeth comprises four molars, SJMJ
767 2455, 2458, 2460 and 2461 (referred to hereafter as individual A-1). SJMJ2455 (left
768 M₂) and SJMJ2458 (left M²) occlude (Fig. 13i). SJMJ2455 (left M₂) and SJMJ2461
769 (right M₂) are likely to be antimeres, due to the similarities of morphology and size,
770 and the shared presence of lingually placed distal interproximal facets, a highly
771 unusual pattern of distal wear (Fig. 12a, marked ‘a’) and unusually lingually inclined
772 roots. SJMJ2461 (right M₂) and SJMJ2460 (right M₃) are likely metamerer. The

773 lingual placement of the interproximal facet on SJMJ2461 suggests lingual
774 displacement of the adjacent M₃, and the form of wear on SJMJ2460 is consistent
775 with this (Fig. 14i). SJMJ2460 (right M₃) also has a prominent form of the protostylid,
776 similar to, although larger than, that seen on SJMJ2461.

777 ii) The matching interproximal wear between SJMJ2463 (left C₁) and SJMJ2464 (left
778 P₃), and their unusually large size, demonstrates that they are metamerer (A-2)

779 iii) SJMJ2456, right M¹ (A-3)

780 iv) SJMJ2467, left M³ (A-4)

781 v) SJMJ2457 (left P⁴) and SJMJ2465 (left P₄) occlude (B-1)

782 vi) SJMJ2459, right M³ (B-2).

783 The minimum number of individuals (MNI) represented by these eleven teeth is two,
784 referred to as Individuals A and B. This can be confidently inferred from the fact that some of
785 the groupings identified above cannot belong to the same dentition. Firstly, SJMJ2459 (right
786 M³; B-2) does not occlude with either the right M₂ or the right M₃ from A-1. Secondly,
787 premolars SJMJ2464 (left P₃; A-2) and SJMJ2465 (left P₄; B-1) are not metamerer, since the
788 interproximal facets do not match, and their large difference in size is inconsistent with a
789 single dentition.

790 Teeth from individual B (SJMJ2457 [left P⁴; B-1] and SJMJ2465 [left P₄; B-1] and
791 SJMJ2459 [right M³; B-2]) exhibit a similar degree of wear that is proportionally greater than
792 that of the other teeth and consistent with a single individual. The remaining four teeth, SJMJ
793 2456, 2467, 2463 and 2464, cannot with complete confidence be associated with either
794 Individual A or B, but are tentatively included with Individual A on the basis of dental
795 metrics. SJMJ2456 (right M¹; A-3), SJMJ2467 (left M³; A-4) and SJMJ2458 (left M²; A-1)
796 have similar crown area and crown index values in relation to the Neanderthal means.

797 Likewise, the relationship of crown area to the Neanderthal mean in SJMJ2463 (left C₁) and
798 SJMJ2464 (left P₃; A-2) is similar to that in M₂ SJMJ2461 and SJMJ2455 (A-1).

799 In summary, Individual A is represented by four teeth that are unambiguously associated
800 and another four teeth that could belong to this individual, and Individual B is represented by
801 three teeth. Based on the level of wear and the fact that there is dentine exposure on third
802 molars in both individuals, it is likely that Individuals A and B were (young) adults. Trinkaus
803 (1995) found a uniform pattern of wear in a sample of Neanderthals and noted that there was
804 slight dentine exposure on first molars, as at La Cotte, in the third decade of life. However,
805 the accumulation of cementum on the apical two thirds of the roots and the amount of
806 secondary dentine in the pulp chambers of the molars, from both individuals, could indicate a
807 greater age at death, as these are age related processes (Hillson, 1996; Guatelli-Steinberg and
808 Huffman, 2012). The teeth found in the first season (1910) clearly did not all come from a
809 right mandible as stated by Nicolle and Sinel (1910), but the fact that the teeth were in a row
810 suggests that those from Individual A, at least, might have been originally deposited in
811 anatomical association.

812 The occipital fragment came from an individual who died in late childhood or
813 adolescence. It can therefore be concluded, from the degree of root development and wear on
814 the teeth, that this fragment is not associated with the dental remains and therefore comes
815 from a third individual.

816

817 **4. Discussion**

818 Individually, all of the La Cotte teeth have diagnostically Neanderthal characteristics and
819 seven teeth also have *H. sapiens* characteristics. The teeth that lack *H. sapiens* characteristics
820 are SJMJ2463 (left C₁), SJMJ2458 (left M²), and the upper third molars, SJMJ2459 (right
821 M³) and SJMJ2467 (left M³). Table 9 summarizes the mix of Neanderthal and *H. sapiens*

822 characteristics within the individual teeth, grouped according to the maximum number of six
823 individuals (A-1, A-2, A-3, A-4, B-1 and B-2) and minimum number of two individuals (A
824 and B).

825 Within A-1 (SJMJ2458, left M²; SJMJ2461, right M₂; SJMJ2455, left M₂; SJMJ2460,
826 right M₃), the M² has no *H. sapiens* characteristics and the other three molars have a mixture
827 of characteristics. Within A-2 (SJMJ2463, left C₁; SJMJ2464, left P₃), the canine has entirely
828 Neanderthal diagnostic characteristics but those of the premolar are mixed. A-3 (SJMJ2456,
829 right M¹) has mixed characteristics. A-4 (SJMJ2467, left M³) only has Neanderthal
830 characteristics. Within B1, both premolars (SJMJ2457, left P⁴; SJMJ2465, left P₄) have a
831 mixture of characteristics. B-2 (SJMJ2459, right M³) only has Neanderthal characteristics.

832 Traits that are specific to one of these six groups include absence of mid-trigonid crest in
833 lower molars (A-1), and particularly large teeth compared to Neanderthal and *H. sapiens* (A-
834 2). Traits that occur in more than one group include absence of transverse crest and
835 mesiolingual truncation in lower premolars, and cervix shape of *H. sapiens* form (A-2 and B-
836 1). It is notable that for teeth with multiple crown traits that show a significant difference in
837 prevalence between Neanderthals and fossil *H. sapiens* (P₄, M₂, M₃) there is an ambiguous
838 picture.

839 Four of the maximum of six individuals have a mixture of diagnostic Neanderthal, and *H.*
840 *sapiens*, characteristics. Three of these sets of teeth could belong to the same dentition
841 (Individual A) but the fourth belongs to a second dentition (Individual B). This suggests that
842 the occurrence of mixed characteristics relates to a group of individuals, rather than being
843 specific to one individual. The *H. sapiens* characteristics occur principally in the lower
844 premolars, are less common in the P⁴, M¹ and lower molars, and are reflected in cervix shape
845 and crown morphological traits. The analysis of cervix shape gives a varied picture. The
846 molars (other than M²) are assigned to Neanderthals, while the premolars are assigned to *H.*

847 *sapiens*. The root forms and the tooth dimensions are entirely compatible with Neanderthals.
848 Several traits that are considered to be particularly typical of Neanderthals (Bailey, 2002,
849 2004, 2006a; Martin et al., 2017) are absent in the La Cotte teeth. These are the presence of a
850 transverse crest, and mesiolingual truncation in lower premolars; the presence of a mid-
851 trigonid crest, and metaconid central dentine horn tip placement in lower molars; and
852 peculiarities of the occlusal shape of M¹. The first four of these traits are not diagnostic of
853 either Neanderthals or *H. sapiens*, but they are consistently present in Neanderthals and less
854 common in *H. sapiens*. The small occlusal polygon of the M¹ from La Cotte is diagnostically
855 Neanderthal, but other aspects of the M¹ morphology are more ambiguous.

856 Three aspects of the morphology of the La Cotte teeth are unusual in both Neanderthals
857 and fossil *H. sapiens*. These are the reduced hypocone on SJMJ2458 (left M²); the concave
858 mesial surface and unusual cervical shape of SJMJ2459 (right M³); and the protostylid form
859 on SJMJ2461 (right M₂) and SJMJ2460 (right M₃). The protostylid form of SJMJ2461 (right
860 M₂) is superficially similar to that observed in *Paranthropus robustus* (Skinner et al., 2009),
861 although not identical. We consider the SJMJ2460 (right M₃) protostylid form to reflect
862 abnormal development of the distal part of the crown and thus not useful for its taxonomic
863 assessment.

864 With the exception of the possibly early form of the protostylid, there are no traits relating
865 to earlier hominins in the La Cotte teeth. Traits that are only seen in *Homo heidelbergensis*,
866 pre-Neanderthals or early Neanderthals (Compton and Stringer, 2015) are absent. These
867 include a buccal cingulum at the enamel surface on P₃ (*H. heidelbergensis*); a distal
868 occlusolingual cleft on P₃ (*H. heidelbergensis* and pre-Neanderthal); mesiobuccal swelling
869 (viewed occlusally) of P₄ (*H. heidelbergensis*, pre-Neanderthal and early Neanderthal); and
870 grade 2 buccal vertical grooves/cingula on lower molars (*H. heidelbergensis*, pre-Neanderthal
871 and early Neanderthal). Multiple lingual cusps on the P₃ (present at La Cotte) are not found in

872 *H. heidelbergensis* (Compton and Stringer, 2015; M. Bermúdez de Castro, pers. comm.
873 regarding Arago),

874 The dental morphology of at least two dental individuals from La Cotte therefore displays
875 a mixture of Neanderthal and *H. sapiens* characteristics, with Neanderthal features more
876 strongly represented, and is clearly distinct from earlier hominins. Since there is more than
877 one individual involved, abnormality of development can be dismissed as a likely cause. This
878 mix of features could suggest shared ancestry or, alternatively, a need to extend the
879 phenotype of one or other species to accommodate this variation. If this combination of
880 features is not the result of introgression, it could be due to genetic drift as a consequence of
881 isolation, but this does not seem probable since, at the likely date of these fossils (<48 ka),
882 sea levels were lower and Jersey was connected to mainland Europe. Another possibility is
883 short term evolutionary pressures, although it is difficult to see what advantage would be
884 conveyed by these minor morphological differences. The small sample of teeth from La Cotte
885 does not enable us to determine which of these scenarios is more likely. Attempts to extract
886 DNA and resolve the issue through genetic analysis have thus far proved unsuccessful.

887 The site of Palomas in southern Spain has hominin dental material from secure
888 stratigraphic contexts dated to ~45–38 ka cal BP (Walker et al., 2017), which shows a
889 comparable mix of dental features to those found at La Cotte. The traits of the Palomas teeth
890 are primarily Neanderthal, but not all the P₄ exhibit asymmetry and a transverse crest (present
891 in 50% and 75% respectively); only one of the eight lower molars has a mid-trigonid crest at
892 the OES, and fewer than half (43%) have a mesial (anterior) fovea of grade >1 (Zapata et al.,
893 2017). However, unlike La Cotte, the crown breadths of some of the anterior teeth, and crown
894 areas of some of the lower molars, are more than two standard deviations below the
895 Neanderthal mean (Pinilla and Trinkaus, 2017). Trinkaus (2017) concluded that the Palomas
896 remains were Neanderthals, but acknowledged that the Neanderthal range of variation would

897 need to be extended to accommodate this group within Neanderthals because of differences
898 in dental traits, their small size, and other aspects of their skeletal morphology. DNA analysis
899 might help resolve the taxonomic ambiguity, but to date none has been reported.

900 Trinkaus (2007) identified distinct Neanderthal dental characteristics that appear in
901 European Late Pleistocene *H. sapiens* dated earlier than 33 ka, and considered these to be due
902 to the assimilation of Neanderthals into these populations. The characteristics listed involve:
903 (1) morphological traits in I¹, C¹ and P₄ (multiple lingual cusps, mesially placed metaconid,
904 and asymmetry for P₄) that are present in the earlier material and generally absent in later,
905 post 33 ka, material; (2) relatively large anterior teeth; and (3) megadont distal molars. The
906 only *H. sapiens* specimen known to have a high level of Neanderthal ancestry is the Oase 1
907 mandible and, by association, the Oase 2 cranium (Fu et al., 2015). Between 6 and 9% of its
908 genome was derived from Neanderthals and it was concluded that there had been a
909 Neanderthal ancestor 4–6 generations back (Fu et al., 2015). However, the Oase teeth
910 (molars) do not exhibit any Neanderthal features. The lower molar mesial (anterior) foveae
911 are small and there are no mid-trigonid crests; the M¹ is of *H. sapiens* form; and the teeth are
912 non-taurodont. The complex crown morphology of the M³ was considered unique (Trinkaus
913 et al., 2012). The teeth, however, are very large, particularly the second and third molars. A
914 discriminant function analysis of the lower molar crown dimensions plotted them with
915 Neanderthals (Trinkaus et al., 2003).

916 There is no evidence of transitional or Upper Paleolithic characteristics in the stone
917 artifacts retained from the excavations at La Cotte. However, the degree of association
918 between the teeth and the Mousterian artifacts in the occupation level is uncertain because the
919 teeth were found on a ledge above the occupation level (though clearly accessible). The stone
920 artifacts recovered at Palomas are similarly described as Mousterian (Walker et al., 2017).

921 The supraradicular taurodontism found in the La Cotte molars is the type generally found
922 in Neanderthals. The more extreme radicular or total taurodontism, where the pulp chamber
923 extends to the tip of a single root, is only found at a few sites, e.g., Krapina (Smith, 1976);
924 Fondo Cattíe (Tarli, 1983); Palomas (Walker et al., 2008). Pyramidal roots, defined by
925 Kupczik and Hublin (2010) as fused roots that can have apical root canal branches in addition
926 to radicular or total taurodontism, are found at Regourdou, Kebara and La Quina (Kupczik
927 and Hublin, 2010) and Aubesier (Lebel et al., 2001). The description of SJMJ2461 (M₂),
928 where both Shifman and Chananel's (1978) and Keene's (1966) methods are used to measure
929 the degree of taurodontism, demonstrates that different methods can give very different
930 results. The degree of taurodontism in the La Cotte premolars is particularly notable. The
931 extent of taurodontism in molars can be identified by the type, the height of the pulp
932 chamber, and its shape—hourglass or barrel. In the comparative samples of Neanderthal P₃
933 and P₄ there is considerably greater variation of form than is found in molars. There is
934 variation in the degrees of buccolingual and mesiodistal widening, and in the overall shape
935 and the degree of tapering, in addition to the extent to which the pulp chamber expands
936 towards the root apex. Consideration is needed as to how this should be measured. A point of
937 interest is that P₃ and P₄ show a similar degree and shape of the taurodontism when both teeth
938 are present in a specimen in the comparative samples in six of nine cases, and the P₄ has a
939 slightly greater level of taurodontism in the remainder. This contrasts with the situation in
940 molars, where the degree of taurodontism frequently increases from first to third (Dumančić
941 et al., 2001).

942

943 **5. Conclusions**

944 The crown and root dimensions for the La Cotte teeth fit well with the Neanderthal
945 comparative samples, and the morphology of the crowns and roots are, in most aspects,

946 typical of Neanderthals. However, there are also *H. sapiens* characteristics, specifically the
947 lack of asymmetry and absence of transverse crests in the lower premolars; the mixture of
948 characteristics in the M¹; and the absence of mid-trigonid crests, and the marginal position of
949 the metaconid dentine horn tip, in the lower molars. Furthermore, the cervix shape of molars
950 and premolars gives a mixed picture, Neanderthal for molars and *H. sapiens* for premolars.
951 The taxonomic attribution of the teeth is therefore ambiguous. Neanderthal characteristics are
952 present in all eleven teeth, but seven of the teeth also have *H. sapiens* characteristics. *Homo*
953 *sapiens* characteristics occur in teeth from both the minimum of two adult individuals
954 identified, suggesting a group or kin with these characteristics. Also of note is the unusual
955 form of the protostylids found at the EDJ on lower molars, which has not previously been
956 observed in Neanderthal or *H. sapiens* teeth.

957 The occipital fragment, which was found in a stratigraphically higher archaeological
958 horizon, is likely to be from an immature individual who died in late childhood or
959 adolescence. Its taxonomic status cannot be determined with certainty, but there are no
960 anatomical features preserved in the bone that clearly indicate a Neanderthal affinity.

961 Of the various scenarios that can be considered to explain the mix of features in the La
962 Cotte teeth, we favor shared Neanderthal and *H. sapiens* ancestry. The likely dating of the
963 fossils during a period of temporal overlap between these groups is consistent with this
964 interpretation.

965

966 **References**

- 967 Altman, D.G., Machin, D., Bryant, T.N., Gardner, M.J., 2000. *Statistics with Confidence:*
968 *Confidence Intervals and Statistical Guidelines*, 2nd ed. BMJ Books, London.
- 969 Angel, J.L., Coon, C.S., 1954. La Cotte de St. Brelade II: Present status. *Man* 54, 53–55.

970 Arsuaga, J.L., Villaverde, V., Quam, R., Gracia, A., Lorenzo, C., Martínez, I., Carretero,
971 J.M., 2002. The Gravettian occipital bone from the site of Malladetes (Barx, Valencia,
972 Spain). *Journal of Human Evolution* 43, 381–393.

973 Auguste, P., 2009. Évolution des peuplements mammaliens en Europe du Nord-Ouest durant
974 le Pléistocène moyen et supérieur. Le cas de la France septentrionale. *Quaternaire. Revue*
975 *de l'Association Française pour l'étude du Quaternaire* 20, 527–550.

976 Bailey, S.E., 2002. A closer look at Neanderthal postcanine dental morphology. I. The
977 mandibular dentition. *Anatomical Record* 269, 148–156.

978 Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle–Late
979 Pleistocene hominins. *Journal of Human Evolution* 47, 183–198.

980 Bailey, S.E., 2005. Diagnostic dental differences between Neandertals and Upper Paleolithic
981 modern humans: Getting to the root of the matter. In: Zadinska, E. (Ed.), *Current Trends*
982 *in Dental Morphology Research*. University of Lodz Press, Lodz, pp. 201–210.

983 Bailey, S.E., 2006a. Beyond shovel-shaped incisors: Neanderthal dental morphology in a
984 comparative context. *Periodicum Biologorum* 108, 253–267.

985 Bailey, S.E., 2006b. The evolution of non-metric dental variation in Europe. *Mitteilungen der*
986 *Gesellschaft für Urgeschichte* 15, 9–30.

987 Bailey, S.E., Hublin, J.J., 2006. Dental remains from the Grotte du Renne at Arcy-sur-Cure
988 (Yonne). *Journal of Human Evolution* 50, 485–508.

989 Bailey, S.E., Glantz, M., Weaver, T.D., Viola, B., 2008. The affinity of the dental remains
990 from Obi-Rakhmat Grotto, Uzbekistan. *Journal of Human Evolution* 55, 238–248.

991 Bailey, S.E., Skinner, M.M., Hublin, J.J., 2011. What lies beneath? An evaluation of lower
992 molar trigonid crest patterns based on both dentine and enamel expression. *American*
993 *Journal of Physical Anthropology* 145, 505–518.

- 994 Bailey, S.E., Weaver, T.D., Hublin, J.J., 2017. The dentition of the earliest modern humans:
995 How ‘modern’ are they? In: Marom, A., Hovers, E. (Eds), *Human Paleontology and*
996 *Prehistory*. Springer, Cham, pp. 215–232.
- 997 Bates, M., Pope, M., Shaw, A., Scott, B., Schwenninger, J.L., 2013. Late Neanderthal
998 occupation in North-West Europe: rediscovery, investigation and dating of a last glacial
999 sediment sequence at the site of La Cotte de Saint Brelade, Jersey. *Journal of Quaternary*
1000 *Science* 28, 647–652.
- 1001 Becam, G., Verna, C., Gómez-Robles, A., Gómez-Olivencia, A., Albessard, L., Arnaud, J.,
1002 Frelat, M.A., Madelaine, S., Schwab, C., Souday, C., Turq, A., 2019. Isolated teeth from
1003 La Ferrassie: Reassessment of the old collections, new remains, and their implications.
1004 *American Journal of Physical Anthropology* 169, 132–142.
- 1005 Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni,
1006 F., Bayle, P., Coquerelle, M., Condemi, S., 2011. Early dispersal of modern humans in
1007 Europe and implications for Neanderthal behaviour. *Nature* 479, 525–528.
- 1008 Benazzi, S., Slon, V., Talamo, S., Negrino, F., Peresani, M., Bailey, S.E., Sawyer, S., Panetta,
1009 D., Vicino, G., Starnini, E., Mannino, M.A., 2015. The makers of the Protoaurignacian
1010 and implications for Neandertal extinction. *Science* 348, 793–796.
- 1011 Bermúdez de Castro, J.M., Martínez, I., 1986. Hypocone and metaconule: identification and
1012 variability on human molars. *International Journal of Anthropology* 1, 165–168.
- 1013 Biltsborough, A., Thompson, J.L., 2005. The dentition of the Le Moustier 1 Neandertal. In:
1014 Ullrich, H. (Ed.), *The Neandertal Adolescent Le Moustier 1 – New Aspects, New Results*.
1015 *Staatliche Museum, Berlin*, pp. 157–186.
- 1016 Black, G.V., 1902. *Descriptive Anatomy of the Human Teeth*, 4th ed. S White Dental
1017 *Manufacturing Co., Philadelphia*.

1018 Brabant, H., Sahly, A., 1964. Étude des dents Néandertaliennes découvertes dans la Grotte du
1019 Portel, en Ariège (France). Bulletin du Groupement International pour la Recherche
1020 Scientifique en Stomatologie & Odontologie 7, 237–254.

1021 Burdo, C., 1960. La Cotte-de-Saint-Brelade, Jersey, British Channel Islands: Excavation of a
1022 Pre-Mousterian Horizon, 1950-1958. Société Jersiaise, St. Helier.

1023 Callow, P., 1986a. Appendix B: Artefacts from the Weichselian deposits. In: Callow, P.,
1024 Cornford, J.M. (Eds.), La Cotte de St. Brelade 1961–1978. Excavations by C.B.M.
1025 McBurney. Geobooks, Norwich, pp. 397–408.

1026 Callow, P., 1986b. Appendix F: Fauna from deposits of the last cold stage at La Cotte de St
1027 Brelade. In: Callow, P., Cornford, J.M. (Eds.), La Cotte de St. Brelade 1961–1978.
1028 Excavations by C.B.M. McBurney. Geobooks, Norwich, microfiche bound with book.

1029 Callow, P., 1986c. Interpreting the La Cotte sequence. In: Callow, P., Cornford, J.M. (Eds.),
1030 La Cotte de St. Brelade 1961–1978. Excavations by C.B.M. McBurney. Geobooks,
1031 Norwich, pp. 73–82.

1032 Compton, T., Stringer, C.B., 2012. The human remains. In: Aldhouse-Green, S., Peterson, R.,
1033 Walker, E.A. (Eds.), Neanderthals in Wales: Pontnewydd and the Elwy Valley Caves.
1034 Oxbow Books, Oxford, pp. 118–230.

1035 Compton, T., Stringer, C., 2015. The morphological affinities of the Middle Pleistocene
1036 hominin teeth from Pontnewydd Cave, Wales. Journal of Quaternary Science 30, 713–730.

1037 Davies, T.W., Delezene, L.K., Gunz, P., Hublin, J.J., Skinner, M.M., 2019. Endostructural
1038 morphology in hominoid mandibular third premolars: Discrete traits at the enamel-dentine
1039 junction. Journal of Human Evolution 136, 102670.

1040 Dean, D., Hublin, J.-J., Holloway, R., Ziegler, R., 1998. On the phylogenetic position of the
1041 pre-Neandertal specimen from Reilingen, Germany. Journal of Human Evolution 34, 485–
1042 508.

- 1043 Dumančić, J., Kaić, Z., Petrovečki, M., 2001. Evaluation of taurodontism in Krapina
1044 Neanderthals. In: Brook, A. (Ed.), *Dental Morphology 2001*. Sheffield Academic Press,
1045 Sheffield, pp. 111–121.
- 1046 Fewlass, H., Talamo, S., Wacker, L., Kromer, B., Tuna, T., Fagault, Y., Bard, E., McPherron,
1047 S.P., Aldeias, V., Maria, R., Martisius, N.L., 2020. A ¹⁴C chronology for the Middle to
1048 Upper Palaeolithic transition at Bacho Kiro Cave, Bulgaria. *Nature Ecology & Evolution*
1049 4, 794–801.
- 1050 Fu, Q., Hajdinjak, M., Moldovan, O.T., Constantin, S., Mallick, S., Skoglund, P., Patterson,
1051 N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J.,
1052 Reich, D., Pääbo, S., 2015. An early modern human from Romania with a recent
1053 Neanderthal ancestor. *Nature* 524, 216–219.
- 1054 Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A.,
1055 Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., Martínez, L.M., 2007. A
1056 geometric morphometric analysis of hominin upper first molar shape. *Journal of Human*
1057 *Evolution* 53, 272–285.
- 1058 Gómez-Robles, A., Martínón-Torres, M., de Castro, J.M.B., Prado, L., Sarmiento, S.,
1059 Arsuaga, J.L., 2008. Geometric morphometric analysis of the crown morphology of the
1060 lower first premolar of hominins, with special attention to Pleistocene *Homo*. *Journal of*
1061 *Human Evolution* 55, 627–638.
- 1062 Greene, D.L., Ewing, G.H., Armelagos, G.J., 1967. Dentition of a Mesolithic population from
1063 Wadi Halfa, Sudan. *American Journal of Physical Anthropology* 27, 41–55.
- 1064 Guatelli-Steinberg, D., Huffman, M., 2012. Histological features of dental hard tissues and
1065 their utility in forensic anthropology. In: Crowder, C., Stout, S.D. (Eds.), *Bone Histology.*
1066 *An Anthropological Perspective*. CRC Press, Boca Raton, pp. 91–107.

1067 Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and
1068 surfaces. *Hystrix* 24, 103–109.

1069 Guy, F., Lazzari, V., Gilissen, E., Thiery, G., 2015. To what extent is primate second molar
1070 enamel occlusal morphology shaped by the enamel-dentine junction? *PLoS One* 10,
1071 e0138802.

1072 Hajdinjak, M., Fu, Q., Hübner, A., Petr, M., Mafessoni, F., Grote, S., Skoglund, P.,
1073 Narasimham, V., Rougier, H., Crevecoeur, I., Semal, P., 2018. Reconstructing the genetic
1074 history of late Neanderthals. *Nature* 555, 652–656.

1075 Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C., Karkanas,
1076 P., Thompson, N.C., Koutoulidis, V., Mouloupoulos, L.A., Gorgoulis, V.G., 2019. Apidima
1077 Cave fossils provide earliest evidence of *Homo sapiens* in Eurasia. *Nature* 571, 500–504.

1078 Higham, T., Douka, K., Wood, R., Ramsey, C.B., Brock, F., Basell, L., Camps, M.,
1079 Arrizabalaga, A., Baena, J., Barroso-Ruíz, C., Bergman, C., 2014. The timing and
1080 spatiotemporal patterning of Neanderthal disappearance. *Nature* 512, 306–309.

1081 Hillson, S., 1996. *Dental Anthropology*. Cambridge University Press, Cambridge.

1082 Hoffecker, J.F., 2009. The spread of modern humans in Europe. *Proceedings of the National*
1083 *Academy of Sciences USA* 106, 16040–16045.

1084 Hublin, J.J., 2015. The modern human colonization of western Eurasia: when and where?
1085 *Quaternary Science Reviews* 118, 194–210.

1086 Hublin, J.-J., Roebroeks, W., 2009. Ebb and flow or regional extinctions? On the character of
1087 Neandertal occupation of northern environments. *Comptes Rendus Palevol* 8, 503–509.

1088 Hublin, J.J., Talamo, S., Julien, M., David, F., Connet, N., Bodu, P., Vandermeersch, B.,
1089 Richards, M.P., 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire
1090 support a Neandertal origin for the Châtelperronian. *Proceedings of the National Academy*
1091 *of Sciences USA* 109, 18743–18748.

- 1092 Hublin, J.J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E.,
1093 Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., 2020. Initial Upper Palaeolithic
1094 *Homo sapiens* from Bacho Kiro Cave, Bulgaria. *Nature* 581, 299–302.
- 1095 Jafarzadeh, H., Azarpazhooh, A., Mayhall, J.T., 2008. Taurodontism: a review of the
1096 condition and endodontic treatment challenges. *International Endodontic Journal* 41,
1097 375–388.
- 1098 Kallay, J., 1963. A radiographic study of the Neanderthal teeth from Krapina, Croatia. In:
1099 Brothwell, D.R. (Ed.), *Dental Anthropology*. Pergamon Press, Oxford, pp. 75–86.
- 1100 Kallay, J., 1970. A new classification of the taurodont teeth of the Krapina Neanderthal man.
1101 *Bulletin Scientifique (Yugoslavie)* 15, 2–3.
- 1102 Keene, H., 1966. A morphologic and biometric study of taurodontism in a contemporary
1103 population. *American Journal of Physical Anthropology* 25, 208–209.
- 1104 Keith, A., 1913. Problems relating to the teeth of the earlier forms of prehistoric man.
1105 *Proceedings of the Royal Society of Medicine* 6, 103–124.
- 1106 Keith, A., Knowles, F.H., 1911. A description of teeth of Palaeolithic man from Jersey.
1107 *Journal of Anatomy and Physiology* 46, 12–27.
- 1108 Keith, A., Knowles, F.H., 1912. A description of teeth of Palaeolithic man from Jersey.
1109 *Bulletin Société Jersiaise* 37, 222–240.
- 1110 Krenn, V.A., Fornai, C., Wurm, L., Bookstein, F.L., Haeusler, M., Weber, G.W., 2019.
1111 Variation of 3D outer and inner crown morphology in modern human mandibular
1112 premolars. *American Journal of Physical Anthropology* 169, 646–663.
- 1113 Kupczik, K., Hublin, J.J., 2010. Mandibular molar root morphology in Neanderthals and Late
1114 Pleistocene and recent *Homo sapiens*. *Journal of Human Evolution* 59, 525–541.

- 1115 Kupczik, K., Delezene, L.K., Skinner, M.M., 2019. Mandibular molar root and pulp cavity
1116 morphology in *Homo naledi* and other Plio-Pleistocene hominins. *Journal of Human*
1117 *Evolution* 130, 83–95.
- 1118 Lebel, S., Trinkaus, E., Faure, M., Fernandez, P., Guérin, C., Richter, D., Mercier, N.,
1119 Valladas, H., Wagner, G.A., 2001. Comparative morphology and paleobiology of Middle
1120 Pleistocene human remains from the Bau de l'Aubesier, Vaucluse, France. *Proceedings of*
1121 *the National Academy of Sciences USA* 98, 11097–11102.
- 1122 Le Cabec, A., 2013. Anterior dental loading and root morphology in Neanderthals. Ph.D.
1123 Dissertation, Université Toulouse III-Paul Sabatier.
- 1124 Le Cabec, A., Gunz, P., Kupczik, K., Braga, J., Hublin, J.-J., 2013. Anterior tooth root
1125 morphology and size in Neanderthals: Taxonomic and functional implications. *Journal of*
1126 *Human Evolution* 64, 169–193.
- 1127 McCown, T.D., Keith, A., 1939. *The Stone Age of Mount Carmel II*. Clarendon Press,
1128 Oxford.
- 1129 Marett, R.R., 1911. XX.—Pleistocene man in Jersey. *Archaeologia* 62, 449–480.
- 1130 Marett, R.R., 1916. IV.—The site, fauna, and industry of La Cotte de St. Brelade, Jersey.
1131 *Archaeologia* 67, 75–118.
- 1132 Martin, R.M., Hublin, J.-J., Gunz, P., Skinner, M.M., 2017. The morphology of the enamel–
1133 dentine junction in Neanderthal molars: gross morphology, non-metric traits, and temporal
1134 trends. *Journal of Human Evolution* 103, 20–44.
- 1135 Martínón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L.,
1136 Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains
1137 from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution* 62, 7–58.
- 1138 Martínón-Torres, M., Spěváčková, P., Gracia-Téllez, A., Martínez, I., Bruner, E., Arsuaga,
1139 J.L., Bermúdez de Castro, J.M., 2013. Morphometric analysis of molars in a Middle

- 1140 Pleistocene population shows a mosaic of ‘modern’ and Neanderthal features. *Journal of*
1141 *Anatomy* 223, 353–363.
- 1142 Matiegka, J., 1934. *Homo předmostensis* – Fossilní Člověk z Předmostí Na Morarě I Lebký.
1143 Česká Akademie Věd a Umění, Prague.
- 1144 Maureille, B., Rougier, H., Houët, F., Vandermeersch, B., 2001. Les dents inférieures du
1145 Néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne):
1146 analyses métriques et comparatives. *Paléo* 13, 183–200.
- 1147 Maureille, B., Djindjian, F., Garralda, M.D., Mann, A., Vandermeersch, B., 2008. Les dents
1148 moustériennes de la grotte Bocard, lieu-dit Bas-de-Morant (commune de Créancey, Côte-
1149 d’Or, Bourgogne). *Bulletins et Mémoires de la Société d’Anthropologie de Paris* 20,
1150 59–78.
- 1151 Moorrees, C.F.A., 1957. *The Aleut Dentition*. Harvard University Press, Cambridge.
- 1152 NESPOS, 2013. NESPOS – Pleistocene People and Places.
1153 <https://www.nespos.org/display/openspace/Home> (last accessed on 20/12/2013).
- 1154 Nicolle, E.T., Sinel, J., 1910. 102. Report on the exploration of the Palaeolithic cave-dwelling
1155 known as La Cotte, St. Brelade, Jersey. *Man* 10, 185–188.
- 1156 Nicolle, E.T., Sinel, J., 1912. 88. Report on the resumed exploration of "La Cotte", St.
1157 Brelade, by the Societe Jersiaise. *Man* 12, 158–162.
- 1158 Oakley, K.P., Campbell, B.G., Molleson, T.I., 1975. *Catalogue of Fossil Hominids (Vol. 2)*.
1159 British Museum (Natural History), London.
- 1160 Ortiz, A., Bailey, S.E., Hublin, J.J., Skinner, M.M., 2017. Homology, homoplasy and cusp
1161 variability at the enamel–dentine junction of hominoid molars. *Journal of Anatomy* 231,
1162 585–599.
- 1163 Patte, É., 1962. *La Dentition des Néandertaliens*. Masson et Cie, Paris.

- 1164 Peter, B., 2019. Gene flow between hominins was common. *Proceedings of the European*
1165 *Society for the Study of Human Evolution* 8, 147.
- 1166 Pinilla, B., Trinkaus, E., 2017. The Palomas dental remains: Size and proportions. In:
1167 Trinkaus, E., Walker, M.J. (Eds.), *The People of Palomas: Neandertals from the Sima de*
1168 *las Palomas del Cabezo Gordo, Southeastern Spain*. Texas A&M University Press,
1169 College Station, pp. 89–104.
- 1170 Prado-Simón, L., Martín-Torres, M., Baca, P., Olejniczak, A.J., Gómez-Robles, A.,
1171 Lapresa, M., Arsuaga, J.L., Bermúdez de Castro, J.M., 2012. Three-dimensional
1172 evaluation of root canal morphology in lower second premolars of Early and Middle
1173 Pleistocene human populations from Atapuerca (Burgos, Spain). *American Journal of*
1174 *Physical Anthropology* 147, 452–461.
- 1175 Quam, R., Bailey, S., Wood, B., 2009. Evolution of M¹ crown size and cusp proportions in
1176 the genus *Homo*. *Journal of Anatomy* 214, 655–670.
- 1177 Radovčić, J., Smith, F.H., Trinkaus, E., Wolpoff, M.H., 1988. *The Krapina Hominids an*
1178 *Illustrated Catalog of Skeletal Collection*. Mladost, Zagreb.
- 1179 Rasband, W.S., 2008. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland,
1180 <http://rsb.info.nih.gov/ij/>.
- 1181 Reid, C., Reenen, J.F. Van, 1995. Remnants of the metaconule in recent man. In: Radlanski,
1182 R.J., Renz, H. (Eds.), *Proceedings of the 10th International Symposium on Dental*
1183 *Morphology*. C. and M. Brunne, Berlin, pp. 172–176.
- 1184 Scott, B., Bates, M., Bates, R., Conneller, C., Pope, M., Shaw, A., Smith, G., 2014. A new
1185 view from la Cotte de St Brelade, Jersey. *Antiquity* 88, 13–29.
- 1186 Scott, G.R., Turner II, C.G., 1997. *The Anthropology of Modern Human Teeth*. Cambridge
1187 *Studies in Biological Anthropology*, Cambridge University Press, Cambridge.

- 1188 Scott, G.R., Irish, J.D., 2017. Human Tooth Crown and Root Morphology. Cambridge
1189 University Press, Cambridge.
- 1190 Scott, G.R., Turner, C.G. II, Townsend, G.C., Martínón-Torres, M., 2018. The Anthropology
1191 of Modern Human Teeth: Dental Morphology and its Variation in Recent and Fossil *Homo*
1192 *sapiens*. 2nd ed. Cambridge University Press, Cambridge.
- 1193 Semal, P., Hauzeur, A., Rougier, H., Crevecoeur, I., Germonpré, M., Pirson, S., Haesaerts, P.,
1194 Jungels, C., Flas, D., Toussaint, M., Maureille, B., 2013. Radiocarbon dating of human
1195 remains and associated archaeological material. In: Rougier, H., Semal, P. (Eds), Spy
1196 Cave: 125 Years of Multidisciplinary Research at the Betche Aux Rotches (Jemeppe-sur-
1197 Sambre, Province of Namur, Belgium). Société Royale Belge d'Anthropologie et de
1198 Préhistoire, Brussels, pp. 331–356.
- 1199 Shaw, A., Bates, M., Conneller, C., Gamble, C., Julien, M.A., McNabb, J., Pope, M., Scott,
1200 B., 2016. The archaeology of persistent places: the Palaeolithic case of La Cotte de St
1201 Brelade, Jersey. *Antiquity* 90, 1437–1453.
- 1202 Shields, E.D., 2005. Mandibular premolar and second molar root morphological variation in
1203 modern humans: What root number can tell us about tooth morphogenesis. *American*
1204 *Journal of Physical Anthropology* 128, 299–311.
- 1205 Shifman, A., Chananel, I., 1978. Prevalence of taurodontism found in radiographic dental
1206 examination of 1,200 young adult Israeli patients. *Community Dental Oral Epidemiology*
1207 6, 200–203.
- 1208 Skinner, M.M., Gunz, P., 2010. The presence of accessory cusps in chimpanzee lower molars
1209 is consistent with a patterning cascade model of development. *Journal of Anatomy* 217,
1210 245–253.

- 1211 Skinner, M.M., Wood, B.A., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M., Hublin,
1212 J.J., 2008. Dental trait expression at the enamel-dentine junction of lower molars in extant
1213 and fossil hominoids. *Journal of Human Evolution* 54, 173–186.
- 1214 Skinner, M.M., Wood, B.A., Hublin, J.-J., 2009. Protostylid expression at the enamel-dentine
1215 junction and enamel surface of mandibular molars of *Paranthropus robustus* and
1216 *Australopithecus africanus*. *Journal of Human Evolution* 56, 76–85.
- 1217 Skinner, M.M., Evans, A., Smith, T., Jernvall, J., Tafforeau, P., Kupczik, K., Olejniczak,
1218 A.J., Rosas, A., Radovčić, J., Thackeray, J.F., Toussaint, M., 2010. Brief communication:
1219 Contributions of enamel-dentine junction shape and enamel deposition to primate molar
1220 crown complexity. *American Journal of Physical Anthropology* 142, 157–163.
- 1221 Smith, B.H., 1984. Patterns of molar wear in hunter–gatherers and agriculturalists. *American*
1222 *Journal of Physical Anthropology* 63, 39–56.
- 1223 Smith, F.H., 1976. The Neandertal remains from Krapina: a descriptive and comparative
1224 study. Ph.D. Dissertation, University of Tennessee.
- 1225 Smith, P., 1989. Dental evidence for phylogenetic relationships of Middle Palaeolithic
1226 hominids. In: Vandermeersch, B. (Ed.), *L’Homme de Neandertal Vol 7. L’Extinction*.
1227 Université de Liège, pp. 111–120.
- 1228 Stringer, C.B., 2006. The Neanderthal-*H. sapiens* interface in Eurasia. In: Harvati, K.,
1229 Harrison, T. (Eds.), *Neanderthals Revisited: New Approaches and Perspectives*. Springer,
1230 Dordrecht, pp. 315–323.
- 1231 Stringer, C.B., Carrant, A.P., 1986. Hominid specimens from La Cotte de St. Brelade. In:
1232 Callow, P., Cornford, J.M. (Eds.), *La Cotte de St. Brelade 1961–1978. Excavations by*
1233 *C.B.M. McBurney*. Geo Books, Norwich, pp. 155–158.
- 1234 Tarli, S.M.B., 1983. A Neanderthal lower molar from Fondo Cattíe (Maglie, Lecce). *Journal*
1235 *of Human Evolution* 12, 383–401.

- 1236 Trinkaus, E., 1995. Neanderthal mortality patterns. *Journal of Archaeological Science* 22,
1237 121–142.
- 1238 Trinkaus, E., 2007. European early modern humans and the fate of the Neandertals.
1239 *Proceedings of the National Academy of Sciences USA* 104, 7367–7372.
- 1240 Trinkaus, E., 2017. The people of Palomas. In: Trinkaus, E., Walker, M.J. (Eds.), *The People*
1241 *of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern*
1242 *Spain*. Texas A&M University Press, College Station, pp. 245–247.
- 1243 Trinkaus, E., Moldovan, O., Bilgăr, A., Sarcina, L., Athreya, S., Bailey, S.E., Rodrigo, R.,
1244 Mircea, G., Higham, T., Ramsey, C.B., van der Plicht, J., 2003. An early modern human
1245 from the Peștera cu Oase, Romania. *Proceedings of the National Academy of Sciences*
1246 *USA* 100, 11231–11236.
- 1247 Trinkaus, E., Bailey, S., Rougier, H., 2012. The dental and alveolar remains of Oase 1 and 2.
1248 In: Trinkaus, E., Constantin, S., Zilhão, J. (Eds.), *Life and Death at the Pesterera cu Oase: A*
1249 *Setting for Modern Human Emergence in Europe*. Oxford University Press, New York,
1250 pp. 781–851.
- 1251 Turner, C.G., Nichol, C.R., Scott, G.R., 1991. Scoring procedures for key morphological
1252 traits of the permanent dentition. In: Kelley, M.A., Larsen, C.S. (Eds.), *Advances in*
1253 *Dental Anthropology*. Wiley-Liss, New York, pp. 13–31.
- 1254 Van Beek, G.C., 1983. *Dental Morphology: an Illustrated Guide*. Wright, Oxford.
- 1255 Vandermeersch, B., 1981. *Les Hommes Fossiles de Qafzeh (Israel)*. CNRS, Paris.
- 1256 Walker, M.J., Gibert, J., López, M.V., Lombardi, A.V., Pérez-Pérez, A., Zapata, J., Ortega,
1257 J., Higham, T., Pike, A., Schwenninger, J.L., Zilhão, J., 2008. Late Neandertals in
1258 southeastern Iberia: Sima de las Palomas del Cabezo Gordo, Murcia, Spain. *Proceedings*
1259 *of the National Academy of Sciences USA* 105, 20631–20636.

- 1260 Walker, M.J., López, M.V., Haber, M., Trinkaus, E., 2017. The context of the Sima de las
1261 Palomas Neandertals. In: Trinkaus, E., Walker, M.J. (Eds.), *The People of Palomas:
1262 Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain*. Texas
1263 A&M University Press, College Station, pp. 4–18.
- 1264 Wollny, G., Kellman, P., Ledesma-Carbayo, M.J., Skinner, M.M., Hublin, J.-J., Hierl, T.,
1265 2013. MIA-A free and open source software for gray scale medical image analysis. *Source
1266 Code for Biology and Medicine* 8, 20.
- 1267 Wood, B.A., Abbott, S.A., 1983. Analysis of the dental morphology of Plio–Pleistocene
1268 hominids. I. Mandibular molars: crown area measurements and morphological traits.
1269 *Journal of Anatomy* 136, 197–219.
- 1270 Zapata, J., Bayle, P., Lombardi, A.V., Pérez-Pérez, A., Trinkaus, E., 2017. The Palomas
1271 dental remains: preservation, wear, and morphology. In: Trinkaus, E., Walker, M.J. (Eds.),
1272 *The People of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo,
1273 Southeastern Spain*. Texas A&M University Press, College Station, pp. 52–88.
- 1274 Zeuner, F.E., 1940. *The age of Neanderthal man, with notes on the Cotte de St Brelade,
1275 Jersey*, C.I. London University Institute of Archaeology, London.
- 1276 Zilhão, J., Trinkaus, E., Constantin, S., Milota, S., Gherase, M., Sacrina, L., Danciu, A.,
1277 Rougier, H., Quilès, J., Rodrigo, R., 2007. The Peștera cu Oase people, Europe’s earliest
1278 modern humans. In: Mellars, P.M., Bar-Yosef, O., Stringer, C., Boyle, K.V. (Eds.),
1279 *Rethinking the Human Revolution: New Behavioural and Biological Perspectives on the
1280 Origin and Dispersal of Modern Humans*. McDonald Institute for Archaeological
1281 Research, Cambridge, pp. 249–262.

1282

1283 **Figure legends**

1284

1285 **Figure 1.** Location of La Cotte de St Brelade (from Shaw et al., 2016). A) Channel Islands
1286 within north-western Europe. B) Jersey in relation to other Channel Islands and the French
1287 coast, showing the ~7 m drop in sea level necessary to reconnect to the continent. C)
1288 simplified geological map of Jersey showing main sites. Based on an image supplied by John
1289 Renouf, with permission.

1290 **Figure 2.** Site plan (A) and cross-section (B) of La Cotte de St. Brelade.

1291 **Figure 3.** E.T. Nicolle shown standing on the level of the hearth, with what might be the
1292 ledge on which the teeth were found on the left-hand side. Photograph by R. Mollet.
1293 Reproduced with the kind permission of the Société Jersiaise.

1294 **Figure 4.** SJMJ2463, left C₁. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1295 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in lingual
1296 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1297 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1298 **Figure 5.** SJMJ2457, left P⁴. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1299 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1300 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1301 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1302 **Figure 6.** SJMJ2464, left P₃. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1303 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1304 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1305 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1306 **Figure 7.** SJMJ2465, left P₄. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1307 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1308 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1309 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1310 **Figure 8.** SJMJ2456, right M¹. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1311 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1312 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1313 shown in f). Occlusal polygon shape shown on occlusal photograph. Abbreviations: B =
1314 buccal; D = distal; L = lingual; M = mesial.

1315 **Figure 9.** SJMJ2458, left M². a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1316 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1317 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1318 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1319 **Figure 10.** SJMJ2459, right M³. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1320 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1321 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1322 shown in f). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1323 **Figure 11.** Cast of SJMJ2467, left M³. a–f) Photographs in occlusal (a), mesial (b), buccal
1324 (c), apical (d), distal (e), lingual (f) views. Note that a black and white photo of the original
1325 tooth taken after casting is provided in distal view. Abbreviations: B = buccal; D = distal; L =
1326 lingual; M = mesial.

1327 **Figure 12.** SJMJ2461, right M₂. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1328 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1329 view. h) CT cross-section (plane of section shown in d); i) CT cross-section (plane of section
1330 shown in f). Letters (a and b) on occlusal image denote mesiodistally concave/convex facets.
1331 Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1332 **Figure 13.** SJMJ2455, left M₂. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1333 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal

1334 view. h) CT cross-section (plane of section shown in d). i) occlusion of SJMJ2455 and
1335 SJMJ2458 (not to scale). Abbreviations: B = buccal; D = distal; L = lingual; M = mesial.

1336 **Figure 14.** SJMJ2460, right M₃. a–c) Photographs in occlusal (a), distal (b), and mesial (c)
1337 views. d–f) Surface models in occlusal (d), distal (e), and mesial (f) views. g) EDJ in occlusal
1338 view showing numerous accessory dentine horns (*). h) CT cross-section (plane of section
1339 shown in d). i) articulation of SJMJ2460 and SJMJ2461 (not to scale). Abbreviations: B =
1340 buccal; D = distal; L = lingual; M = mesial.

1341 **Figure 15.** La Cotte SJMJ2452 occipital fragment (right) compared to a modern child aged
1342 about 6 years. A) ectocranial surface; B) endocranial surface, dotted lines indicating the
1343 pathway of the transverse sulcus, which passes directly across the asterion in both bones.

1344 **Figure 16.** Comparison of M¹ occlusal polygon shapes. Neanderthal: Krapina D161; La
1345 Cotte: SJMJ2456; fossil *H. sapiens*: La Madeleine. Abbreviations: B = buccal; D = distal; L =
1346 lingual; M = mesial.

1347 **Figure 17.** Results of the principal components analysis of cervix shape landmarks in P⁴ in
1348 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1349 form (d) space. The percentage of variance depicted by each principal component (PC) is
1350 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1351 **Figure 18.** Results of the principal components analysis of cervix shape landmarks in P₃ in
1352 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1353 form (d) space. The percentage of variance depicted by each principal component (PC) is
1354 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1355 **Figure 19.** Results of the principal components analysis of cervix shape landmarks in P₄ in
1356 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1357 form (d) space. The percentage of variance depicted by each principal component (PC) is
1358 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1359 **Figure 20.** Results of the principal components analysis of cervix shape landmarks in M^1 in
1360 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1361 form (d) space. The percentage of variance depicted by each principal component (PC) is
1362 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

1363 **Figure 21.** Results of the principal components analysis of cervix shape landmarks in M^2 in
1364 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1365 form (d) space. The percentage of variance depicted by each principal component (PC) is
1366 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

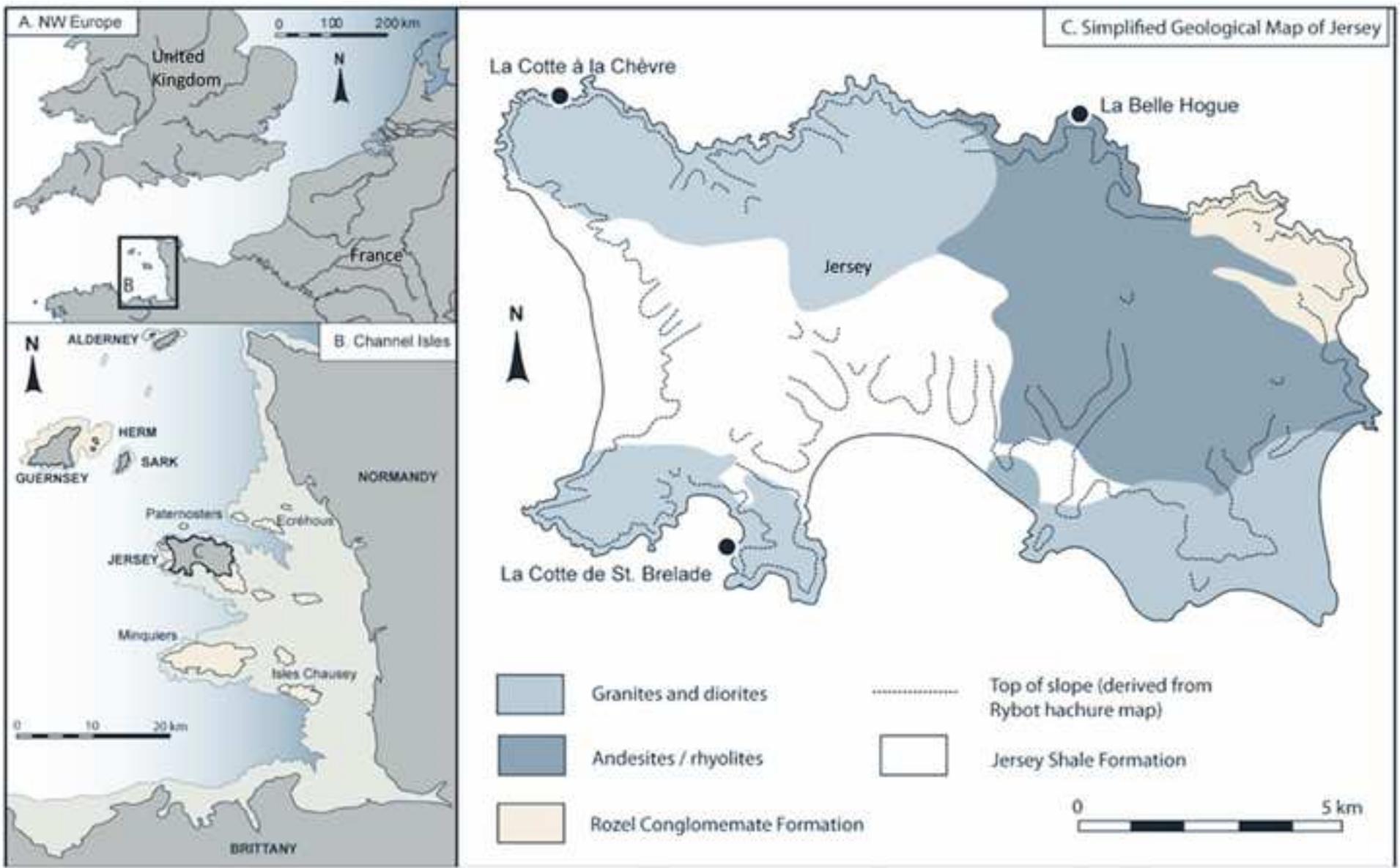
1367 **Figure 22.** Results of the principal components analysis of cervix shape landmarks in M^3 in
1368 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1369 form (d) space. The percentage of variance depicted by each principal component (PC) is
1370 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

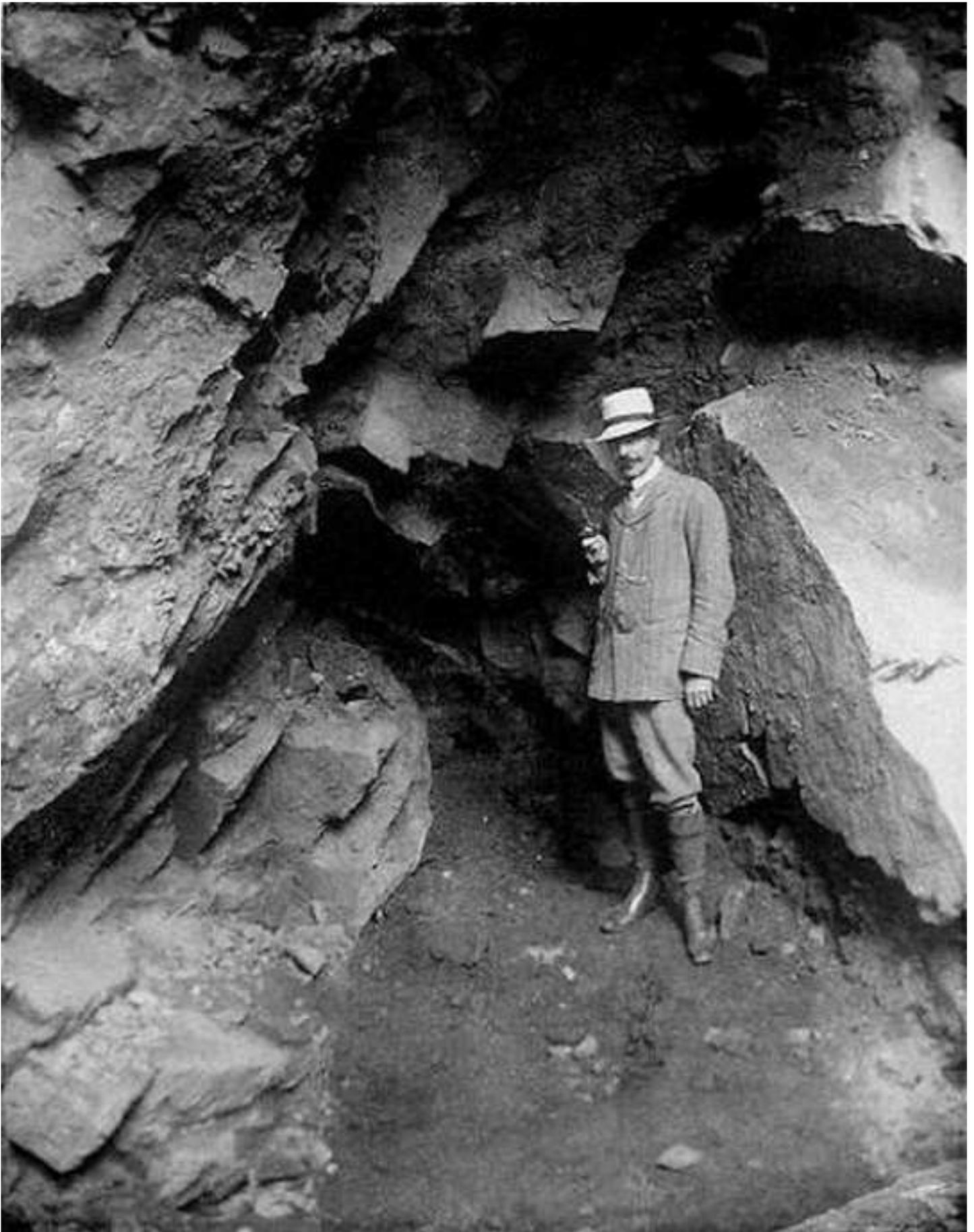
1371 **Figure 23.** Results of the principal components analysis of cervix shape landmarks in M_2 in
1372 shape (a) and form (b) space, and wireframe models of mean cervix shape in shape (c) and
1373 form (d) space. The percentage of variance depicted by each principal component (PC) is
1374 indicated. Abbreviations: Hn = *Homo neanderthalensis*; Hs = *Homo sapiens*.

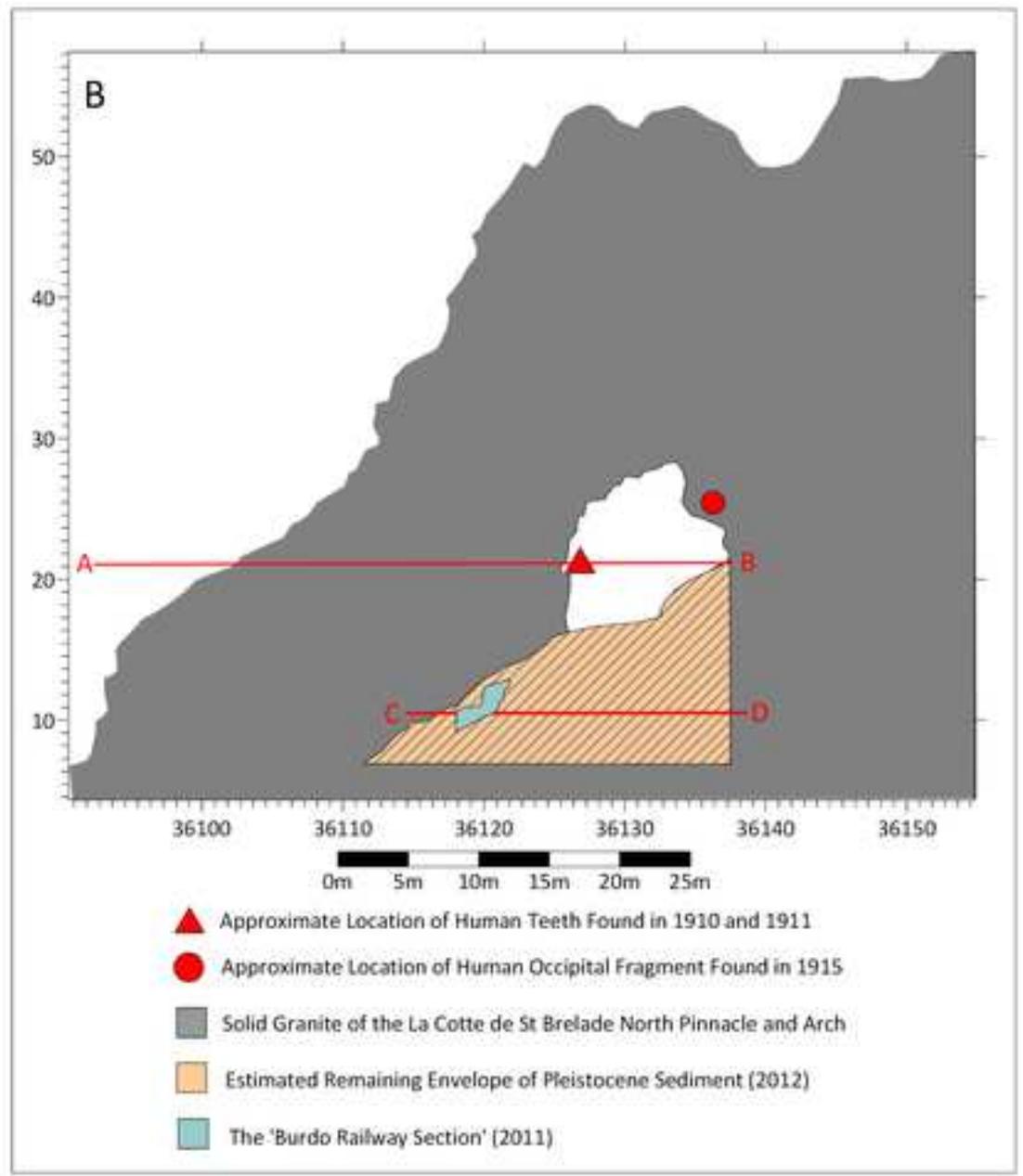
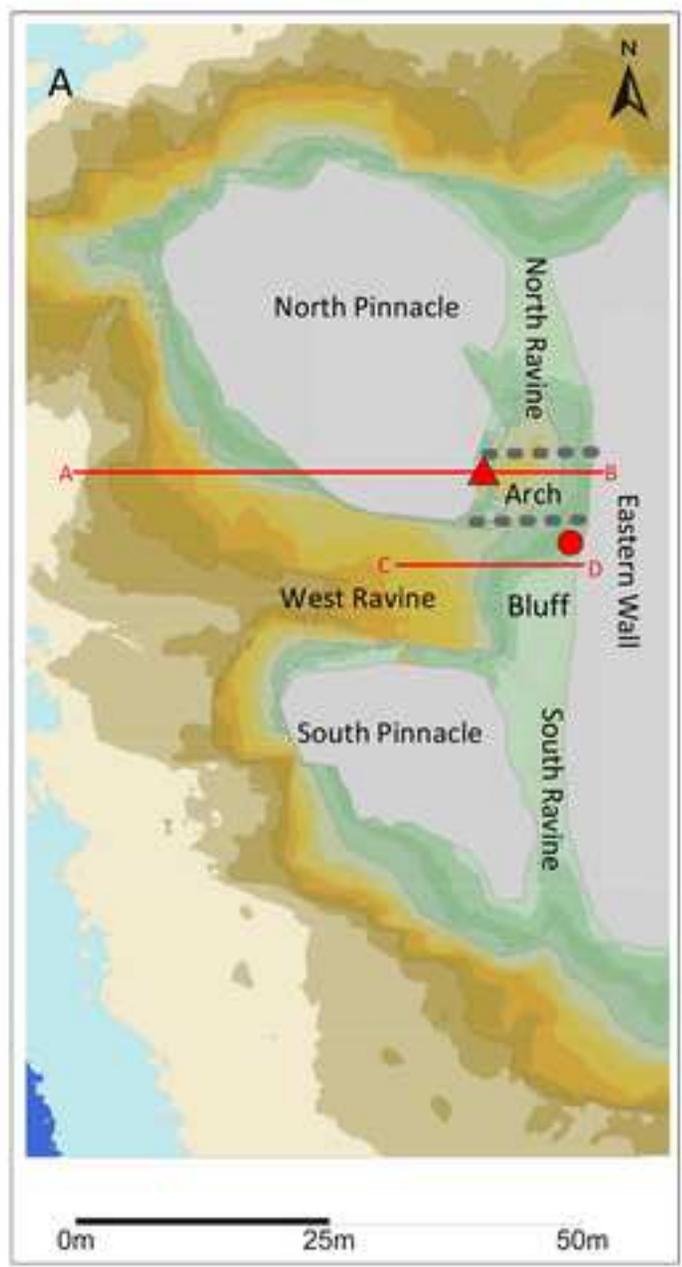
1375 **Figure 24.** Crown area adjusted Z scores; distances of La Cotte dimensions from comparative
1376 sample means of late Neanderthal, fossil *Homo sapiens* and Krapina. Abbreviations: Hs = *H.*
1377 *sapiens*; U = upper; L = lower; C = canine; P = premolar; M = molar; UM3a = SJMJ2467;
1378 UM3b = SJMJ2459. P⁴: buccolingual dimension only.

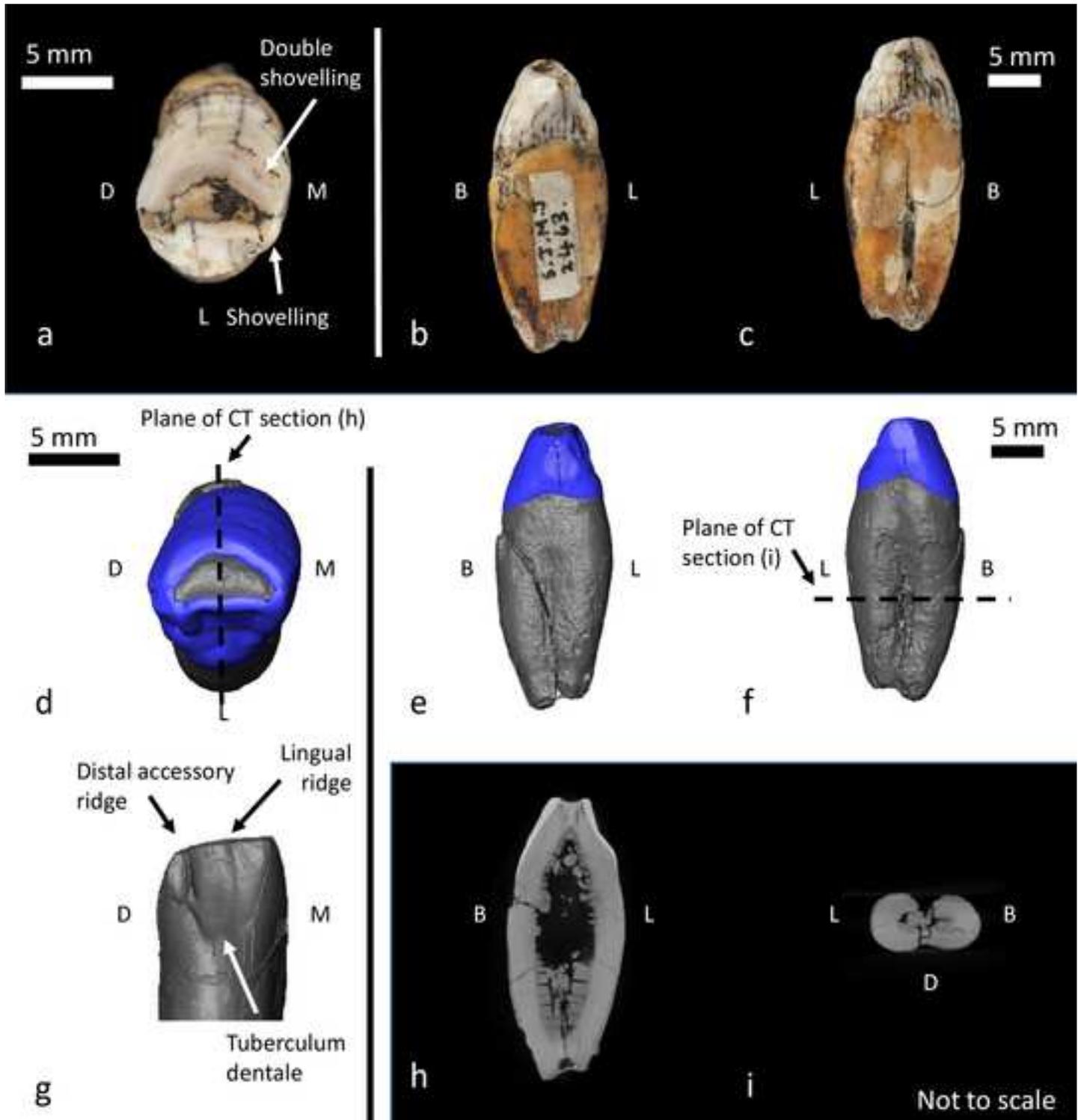
1379 **Figure 25.** Crown index adjusted Z scores; distances of La Cotte dimensions from
1380 comparative sample means of late Neanderthal, fossil *Homo sapiens* and Krapina.
1381 Abbreviations: Hs = *H. sapiens*; U = upper; L = lower; C = canine; P = premolar; M = molar;
1382 UM3a = SJMJ2467; UM3b = SJMJ2459.

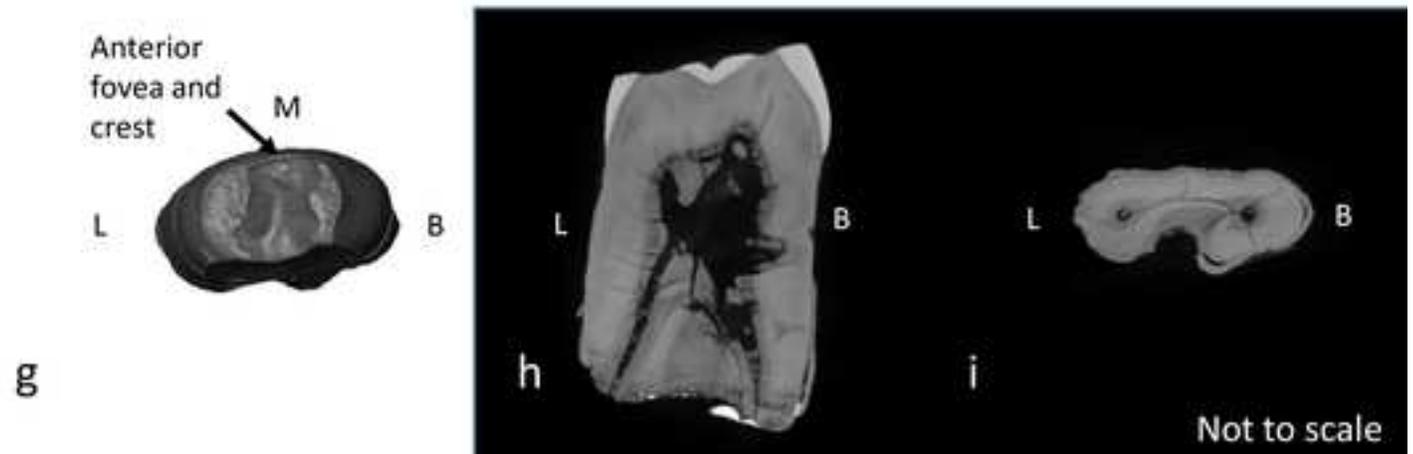
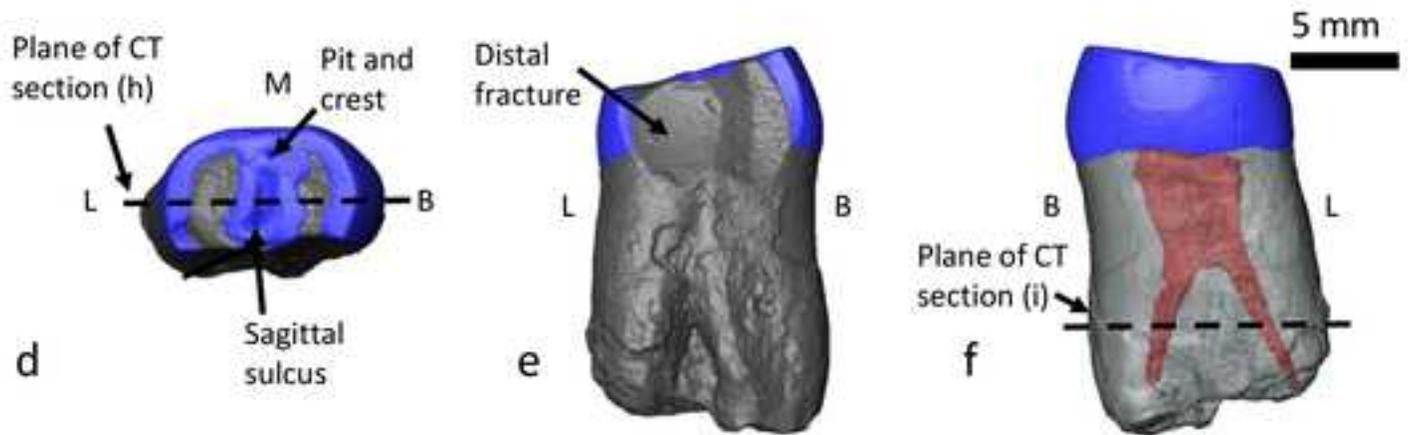
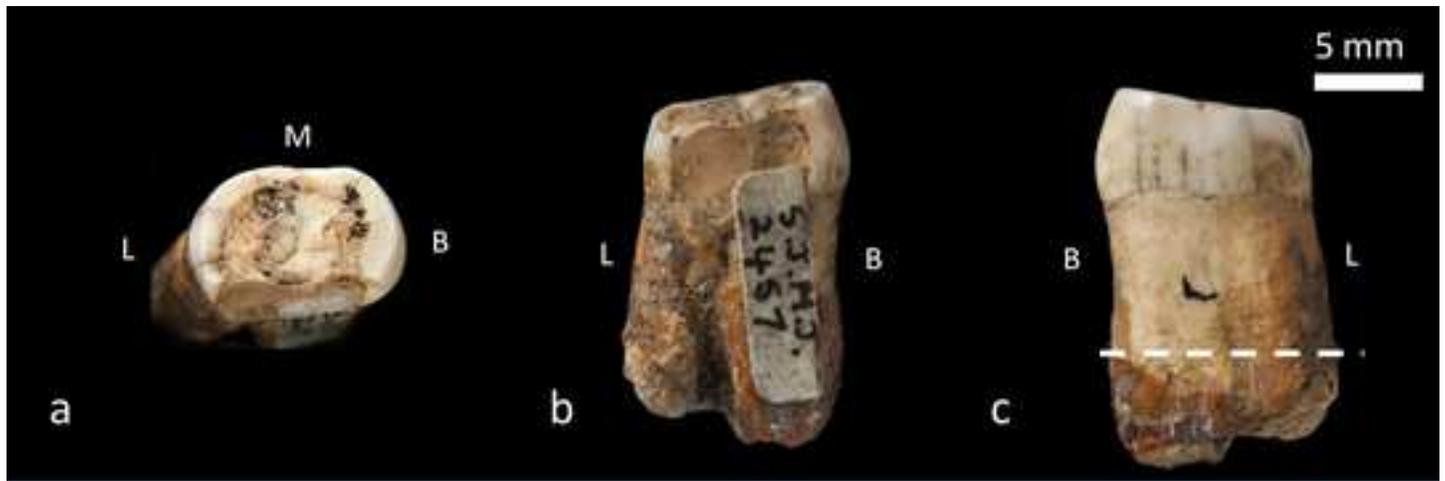
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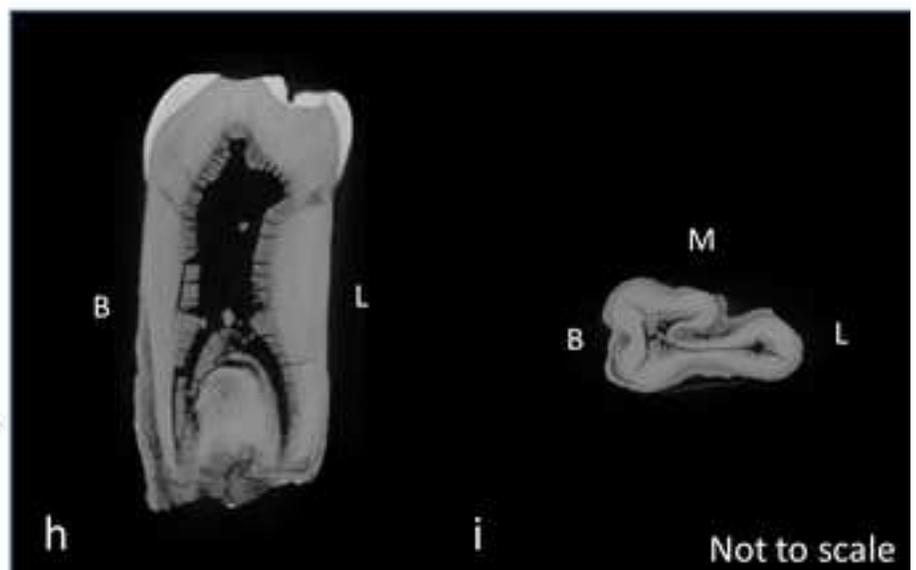
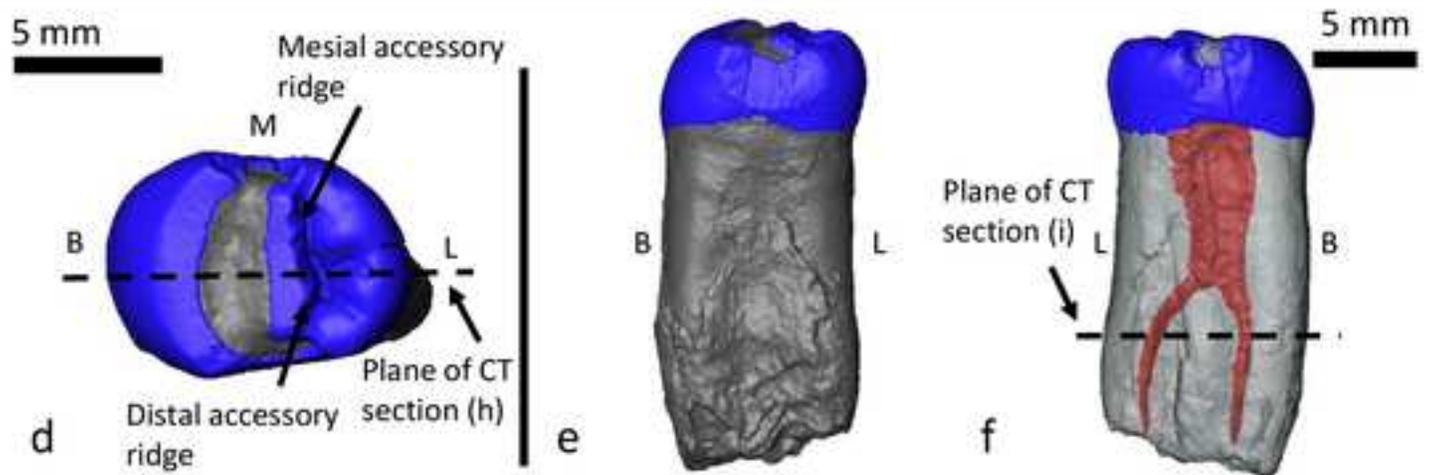
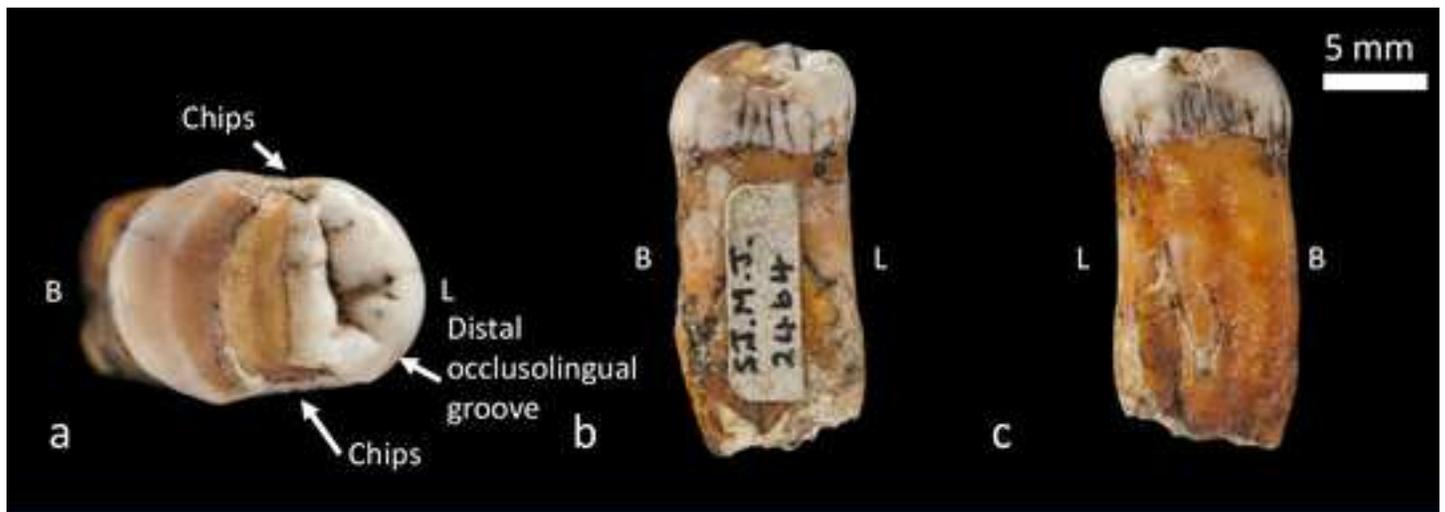


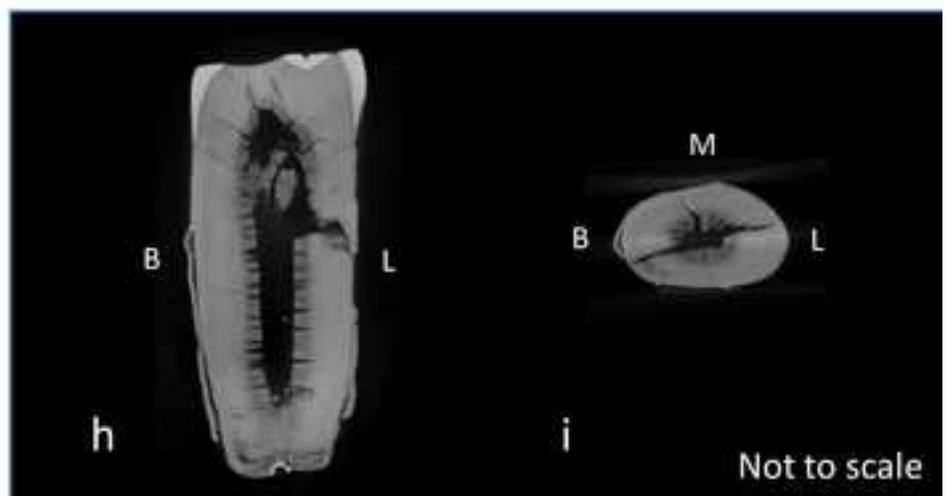
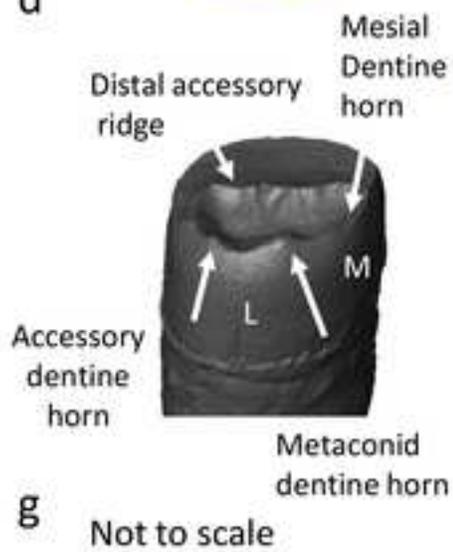
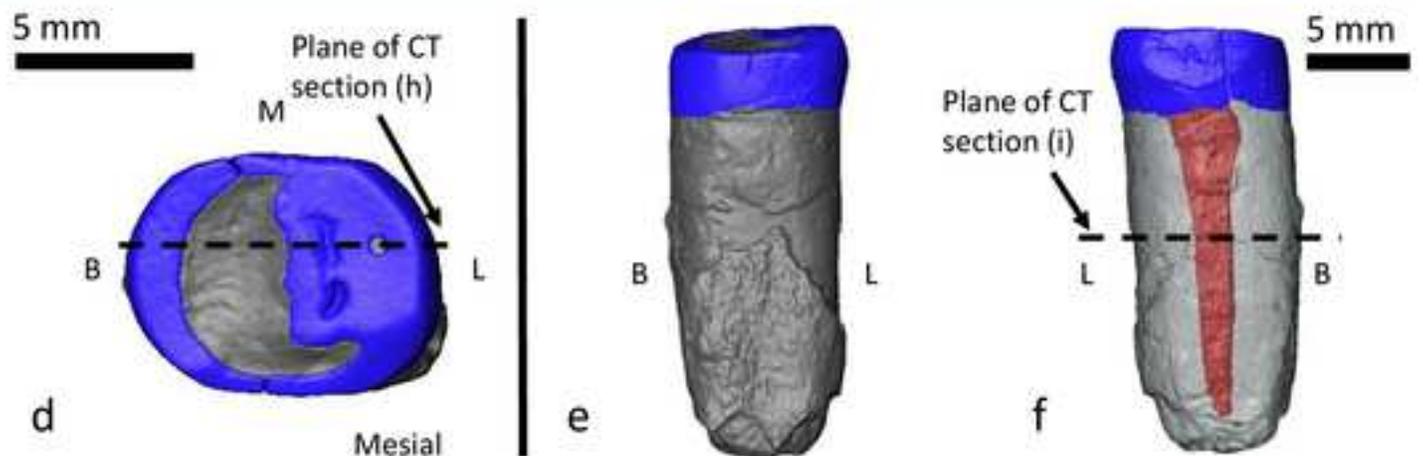
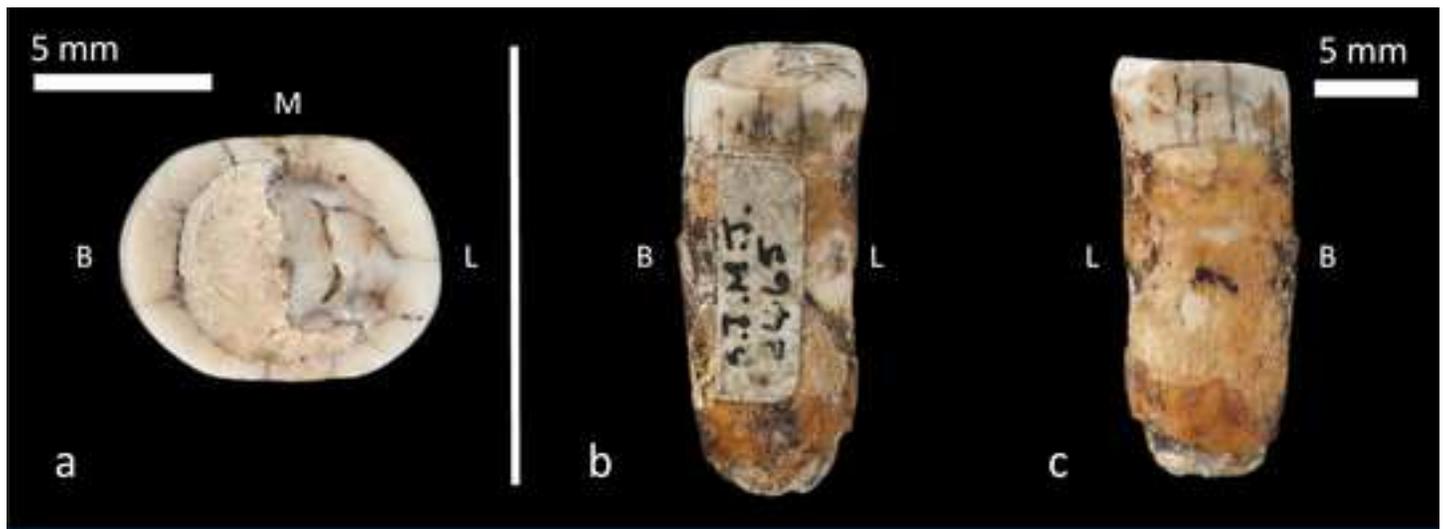


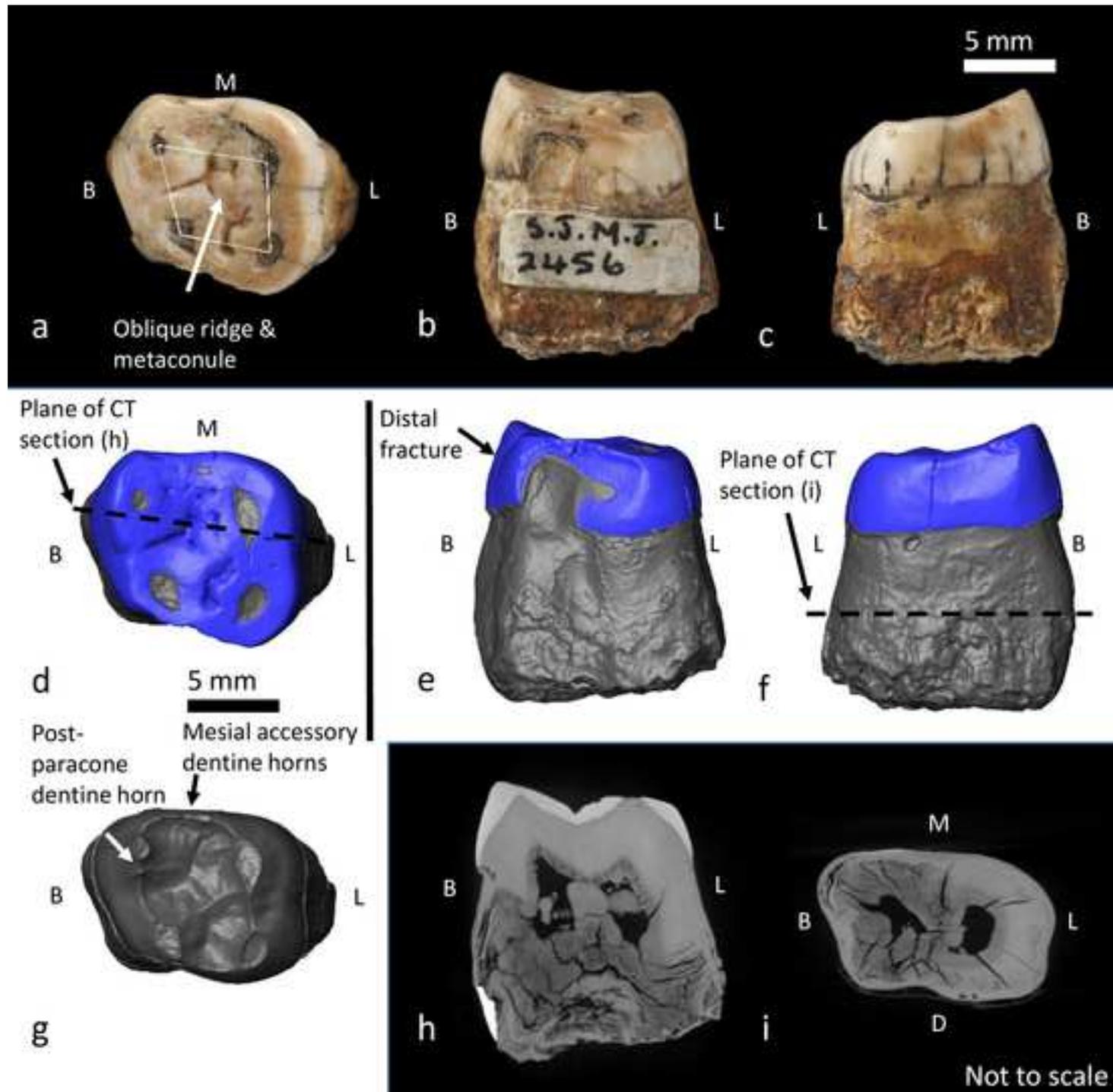


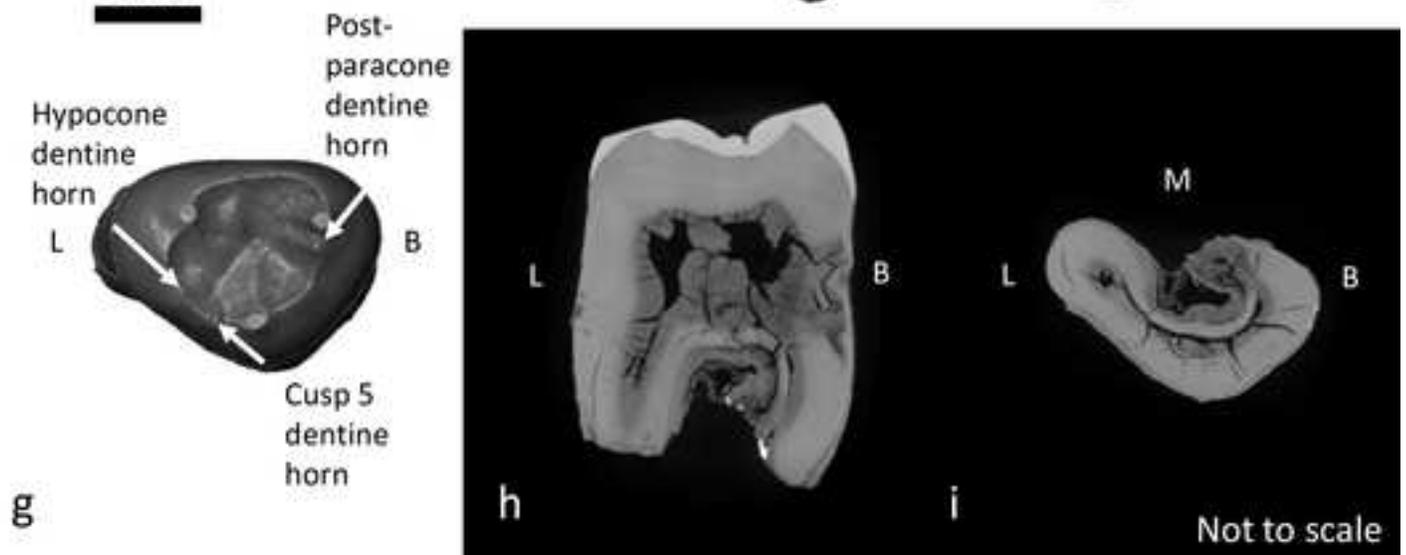
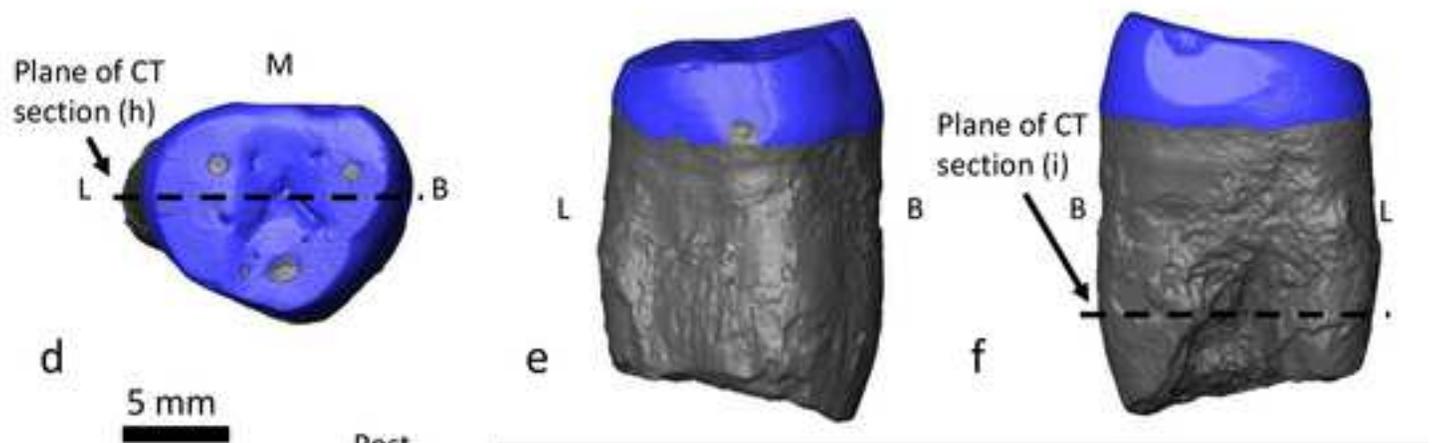


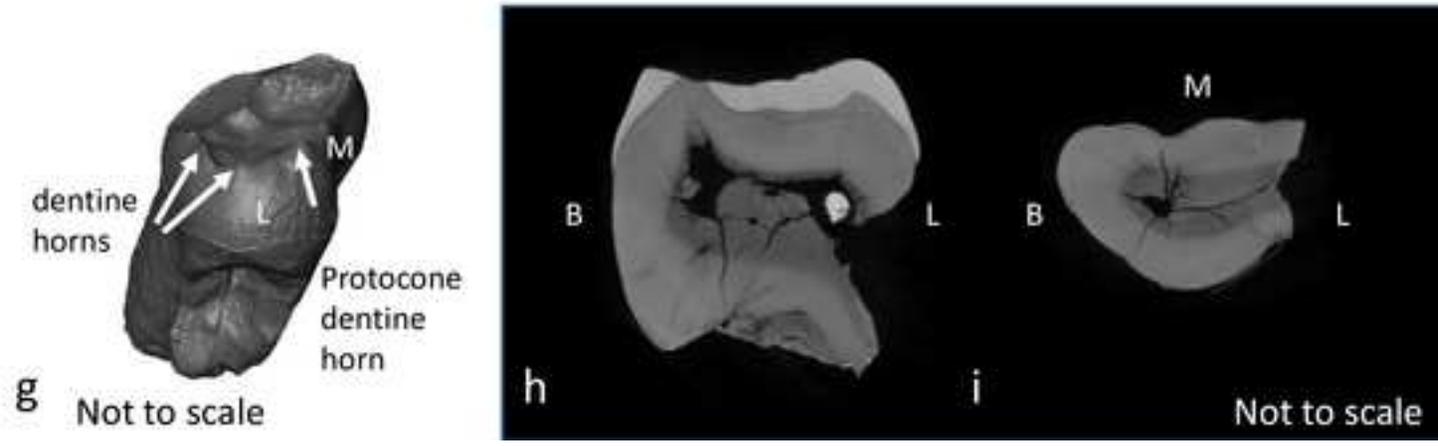
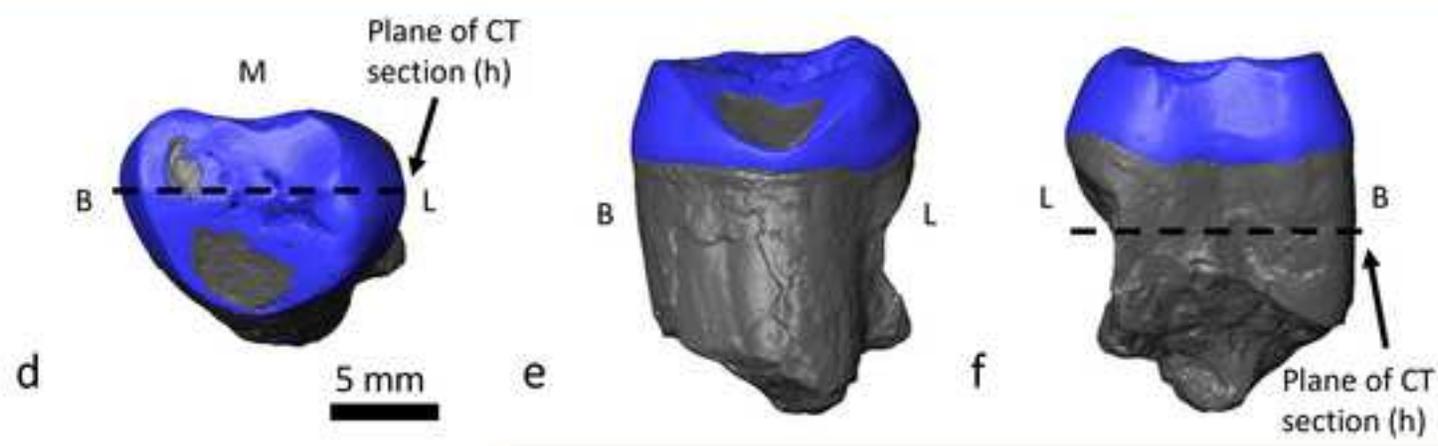
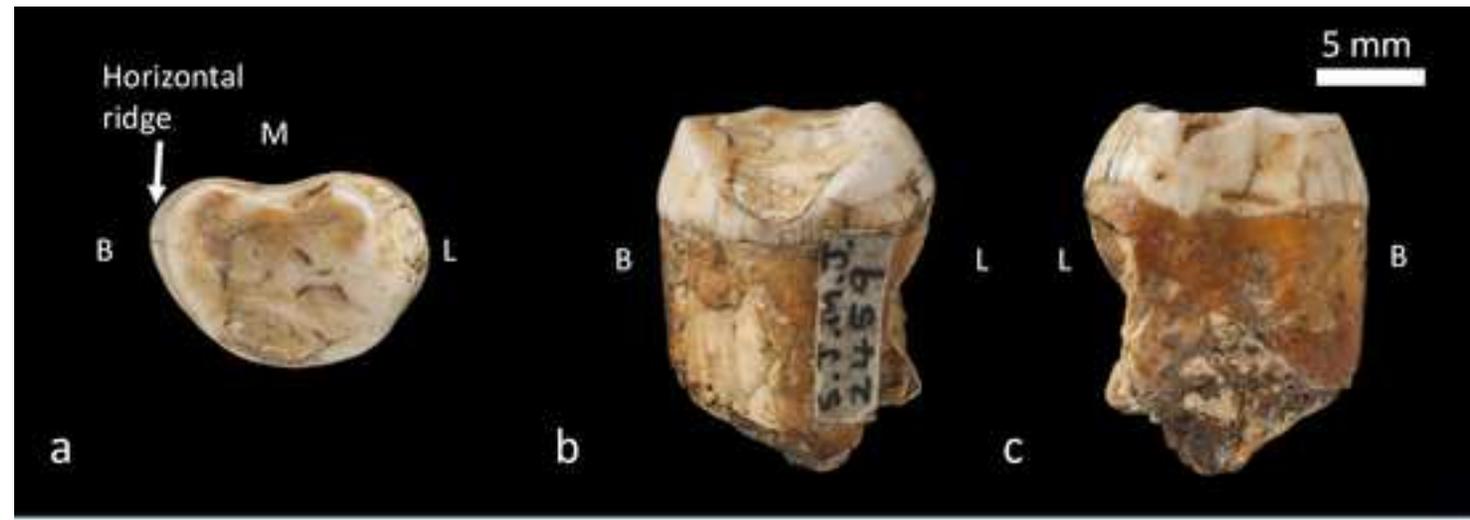


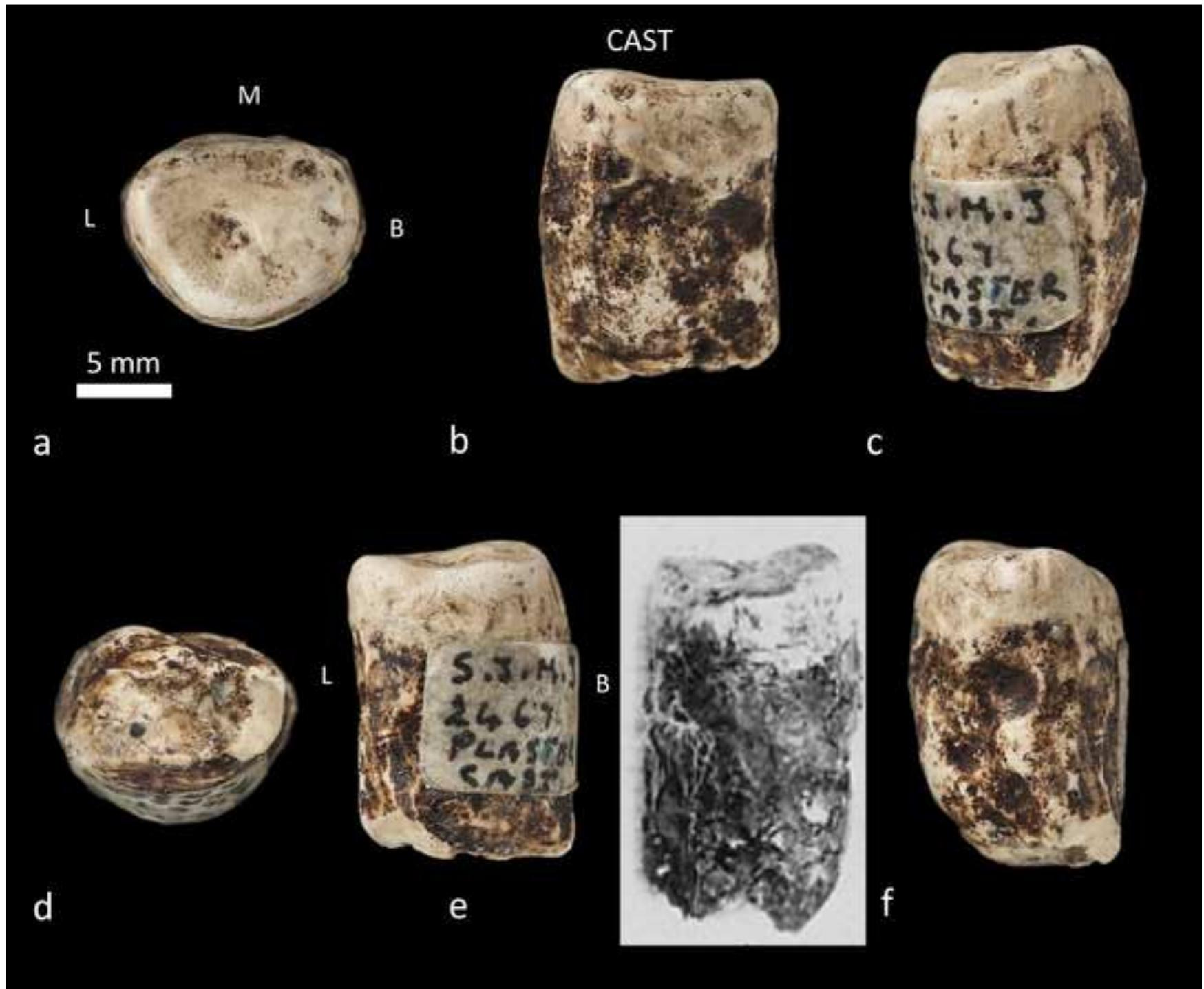


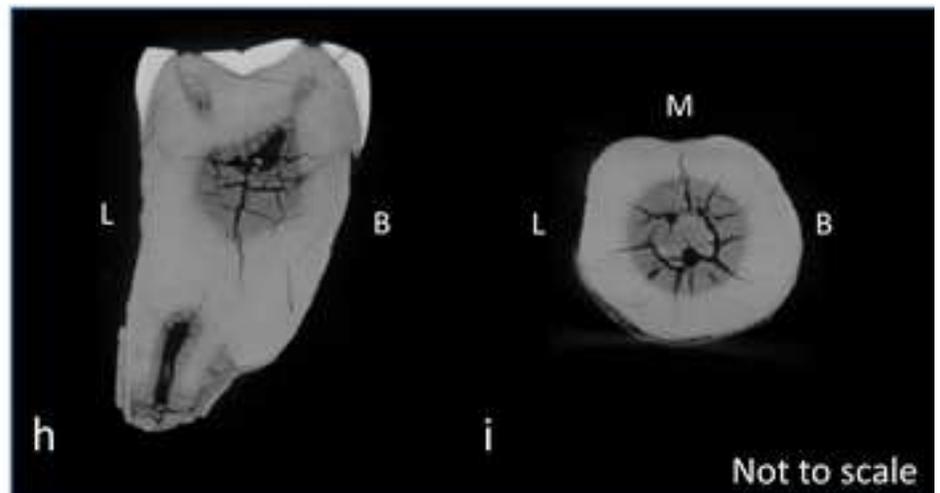
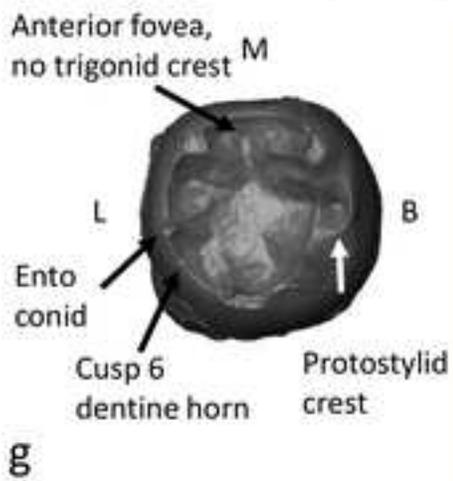
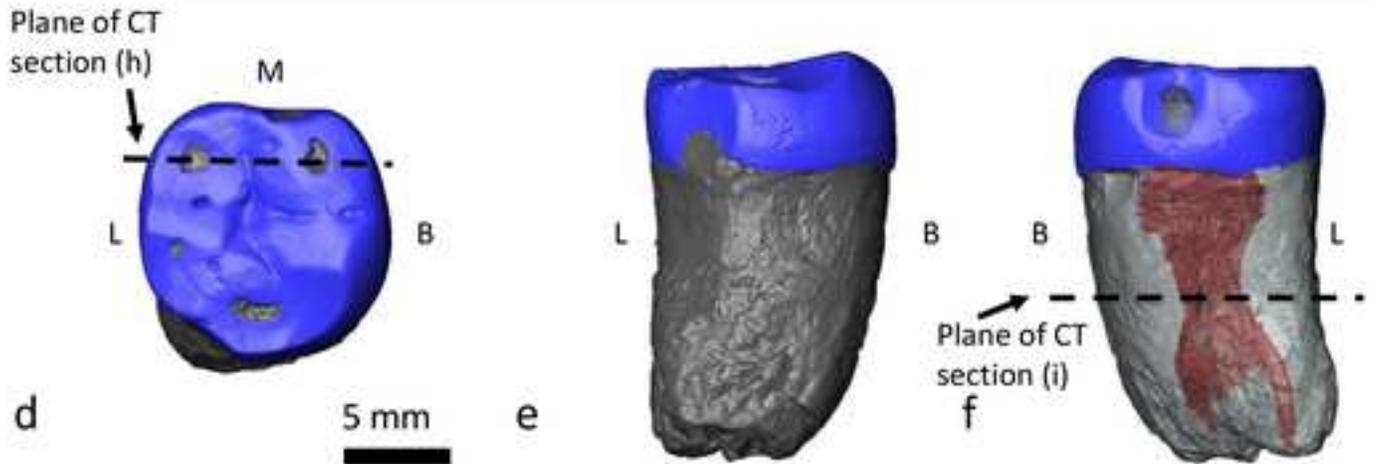
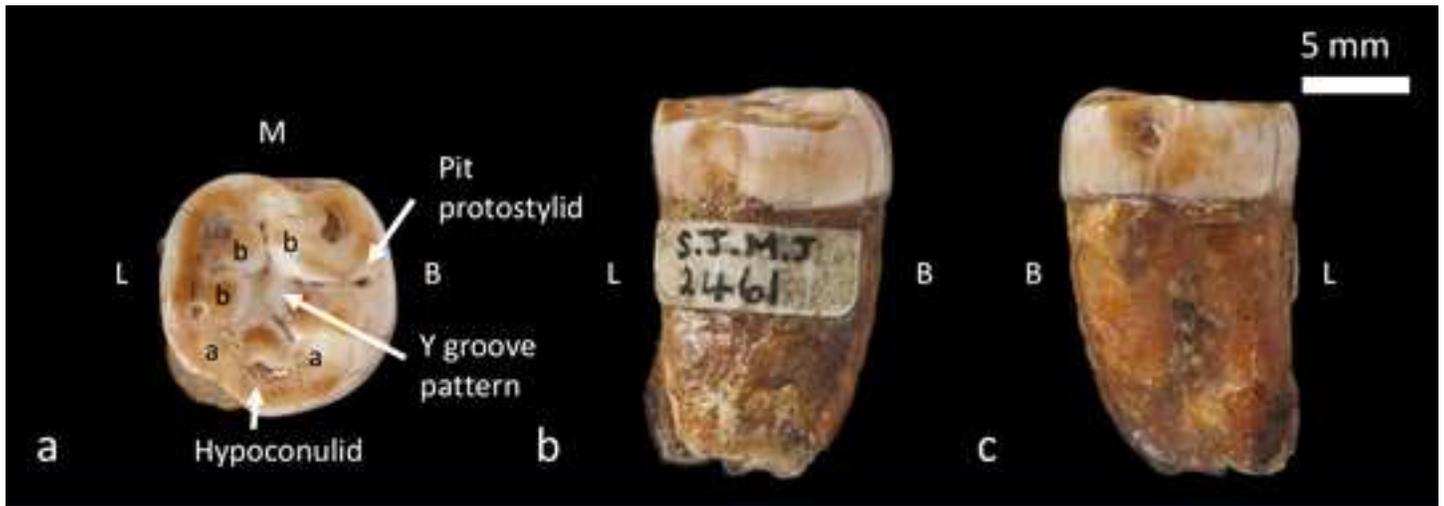


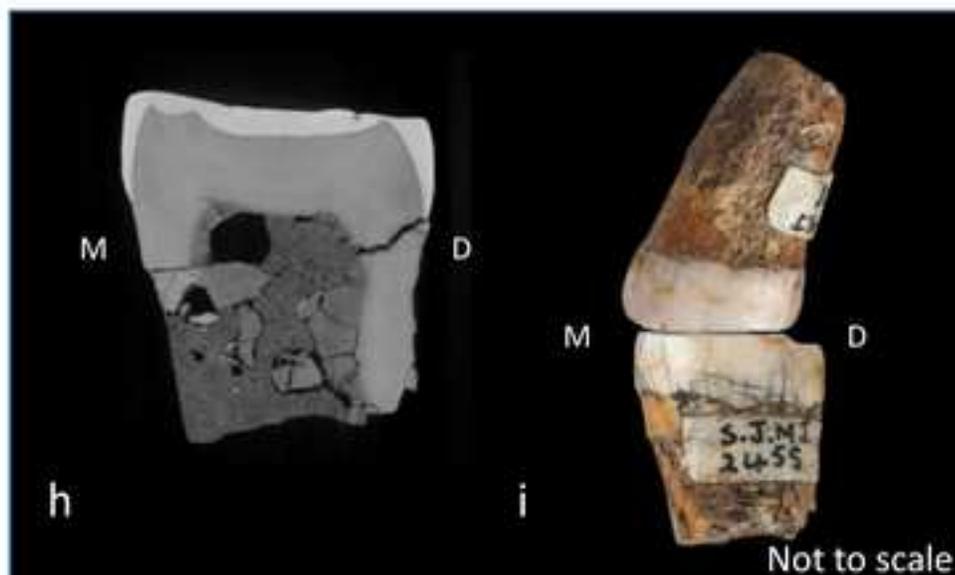
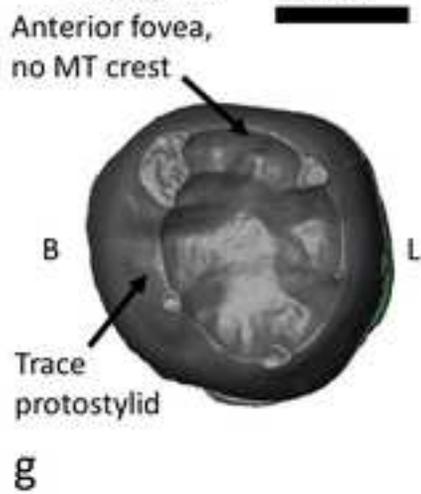
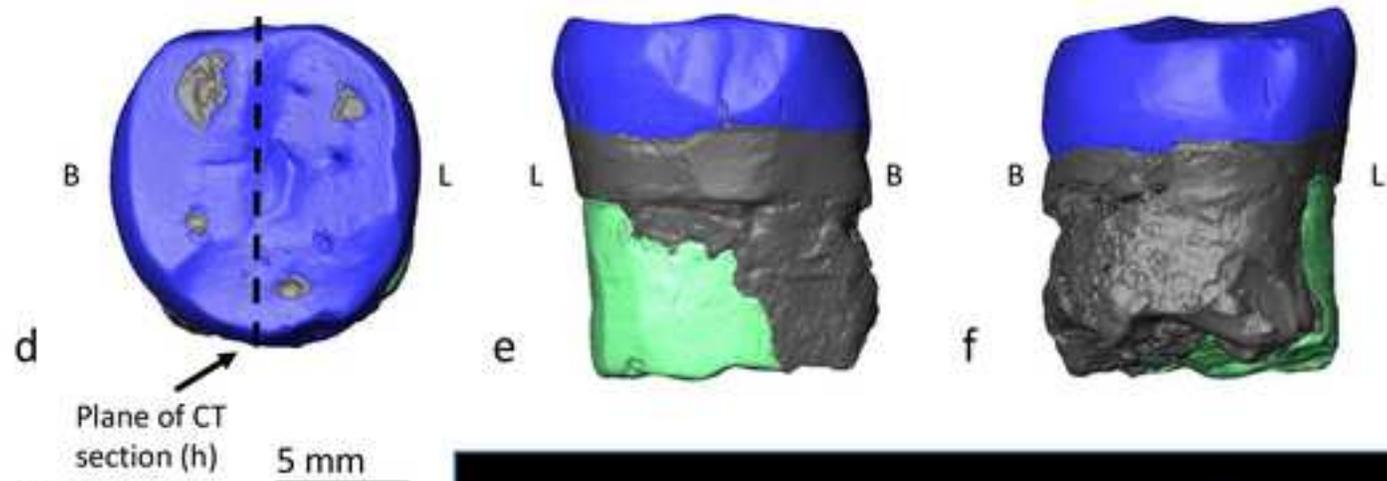
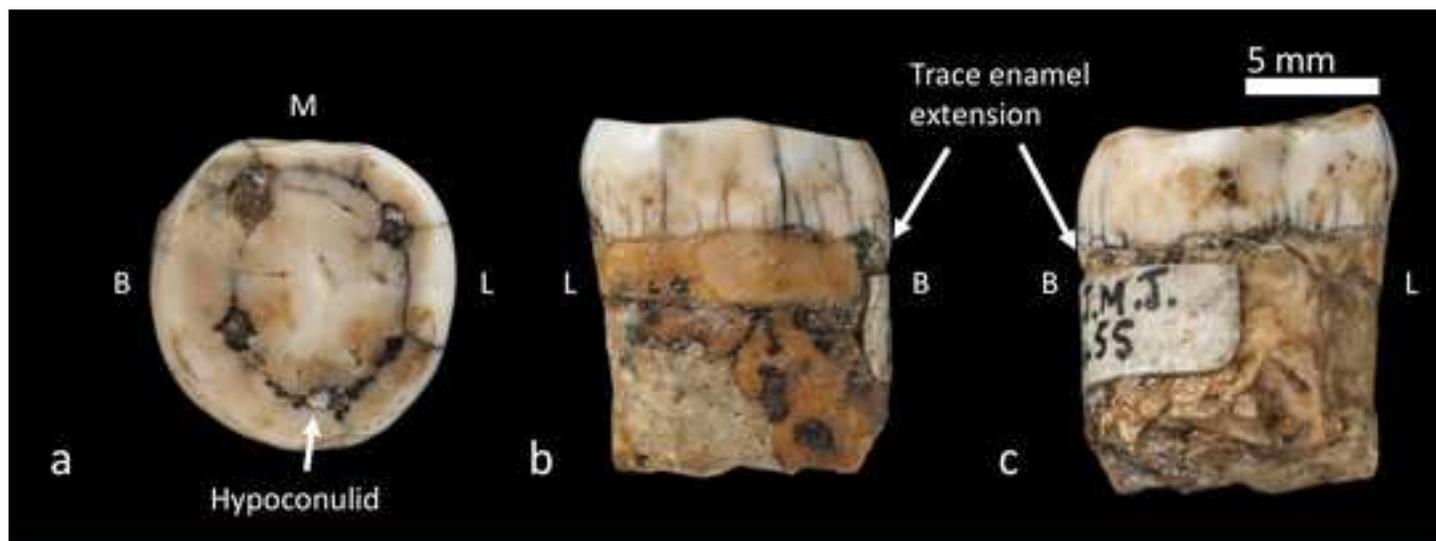




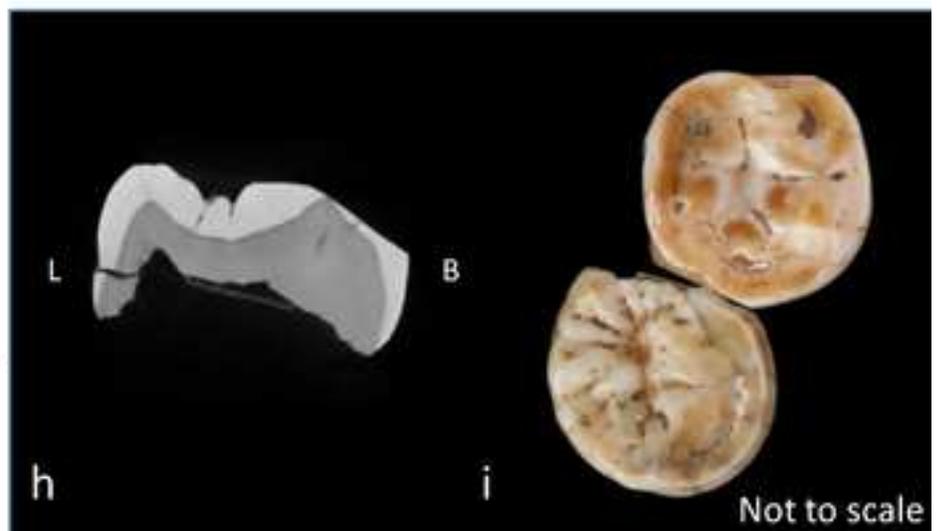
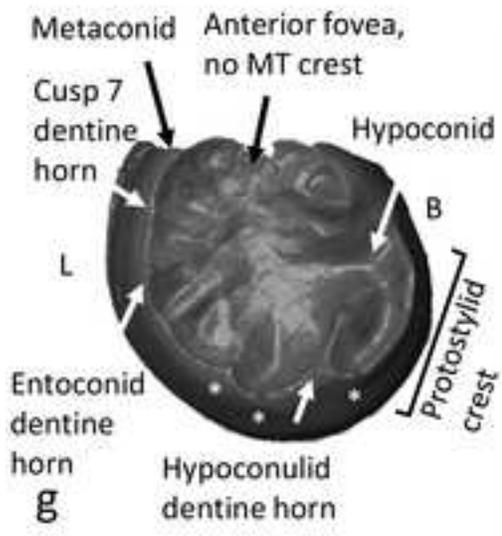
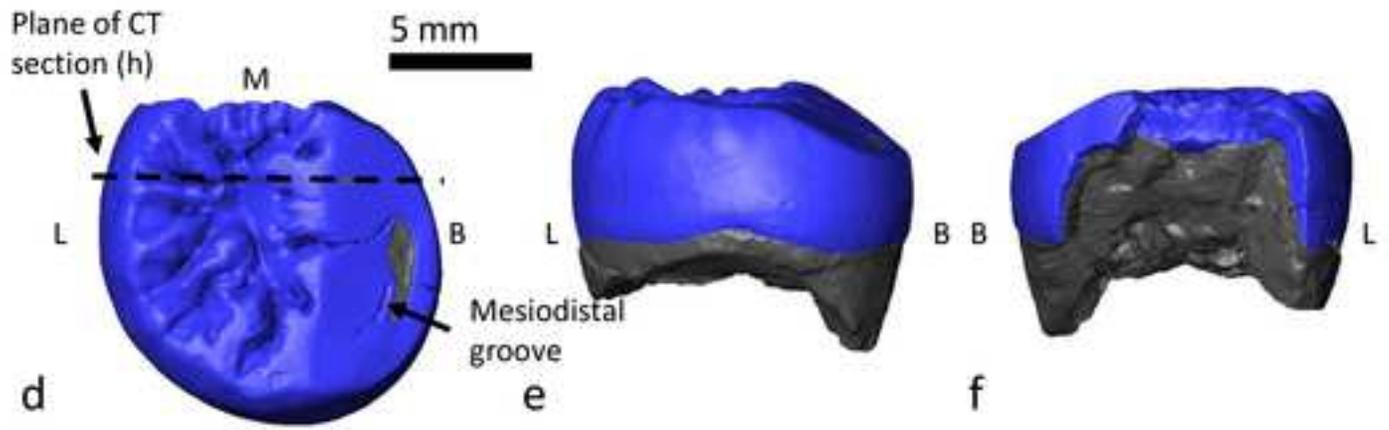
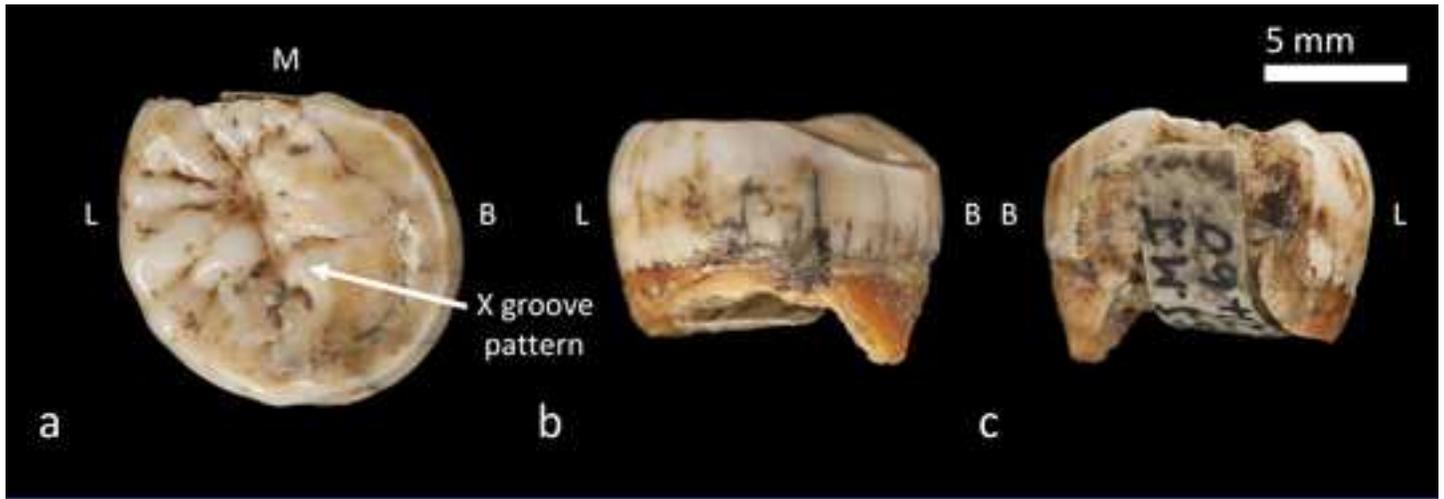


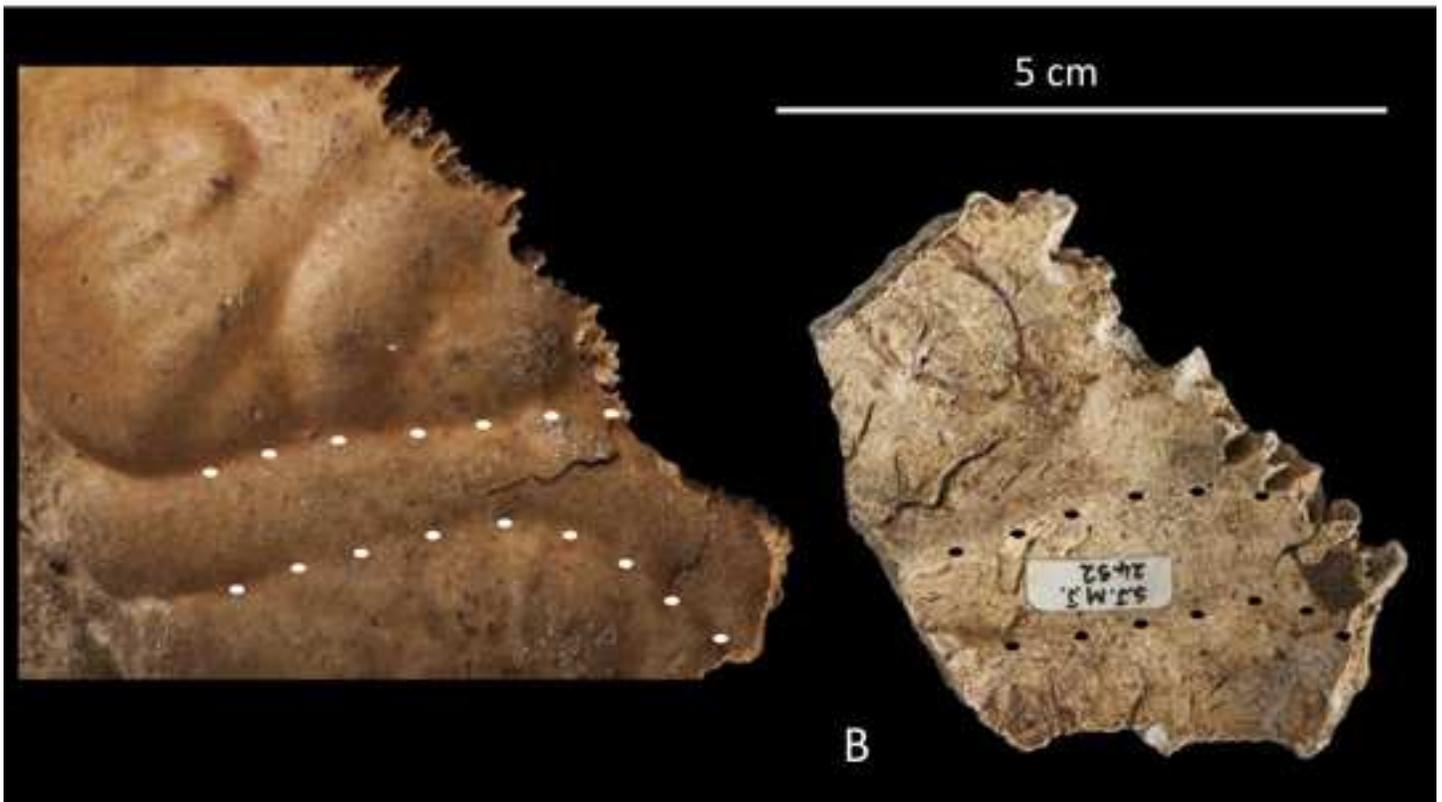
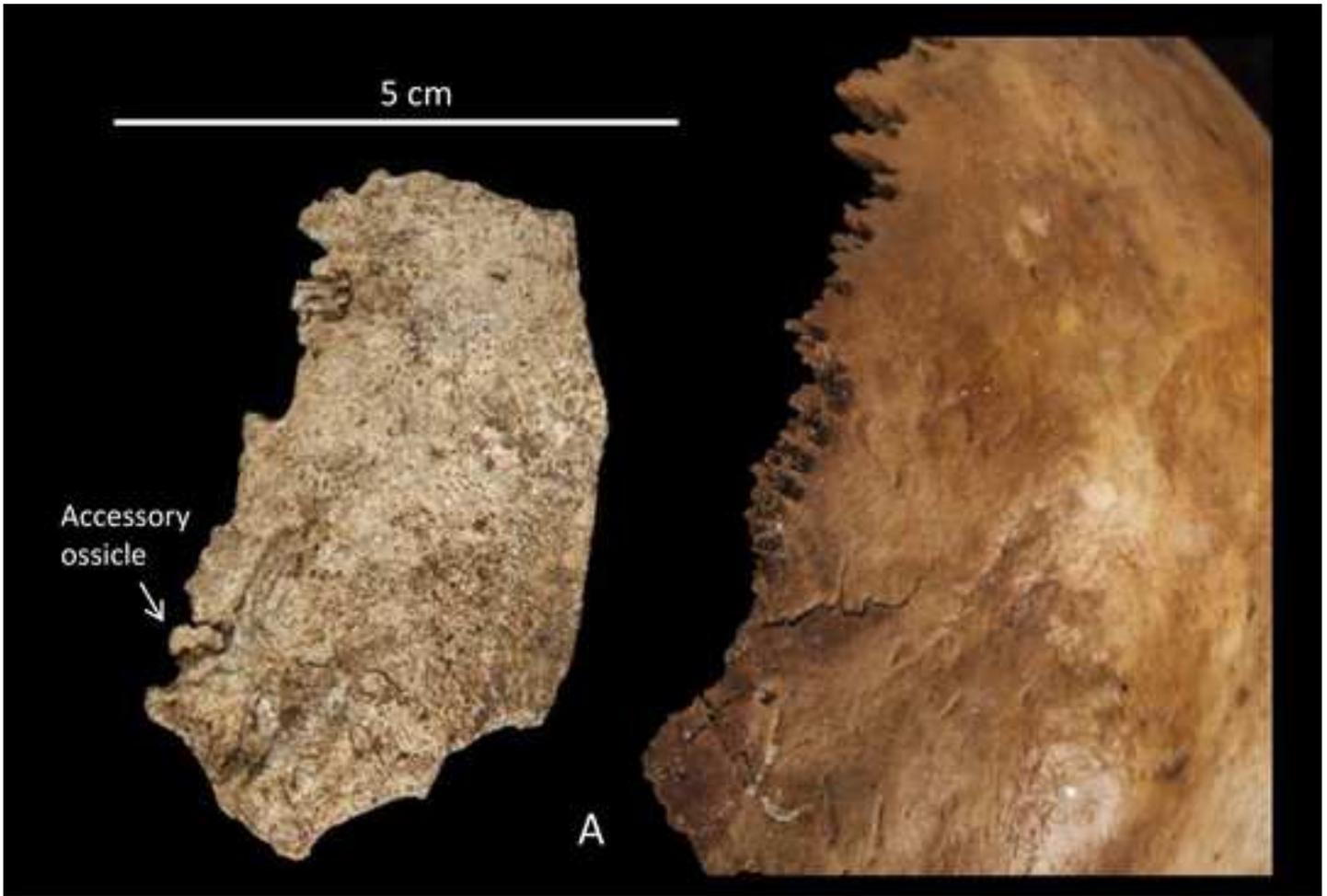


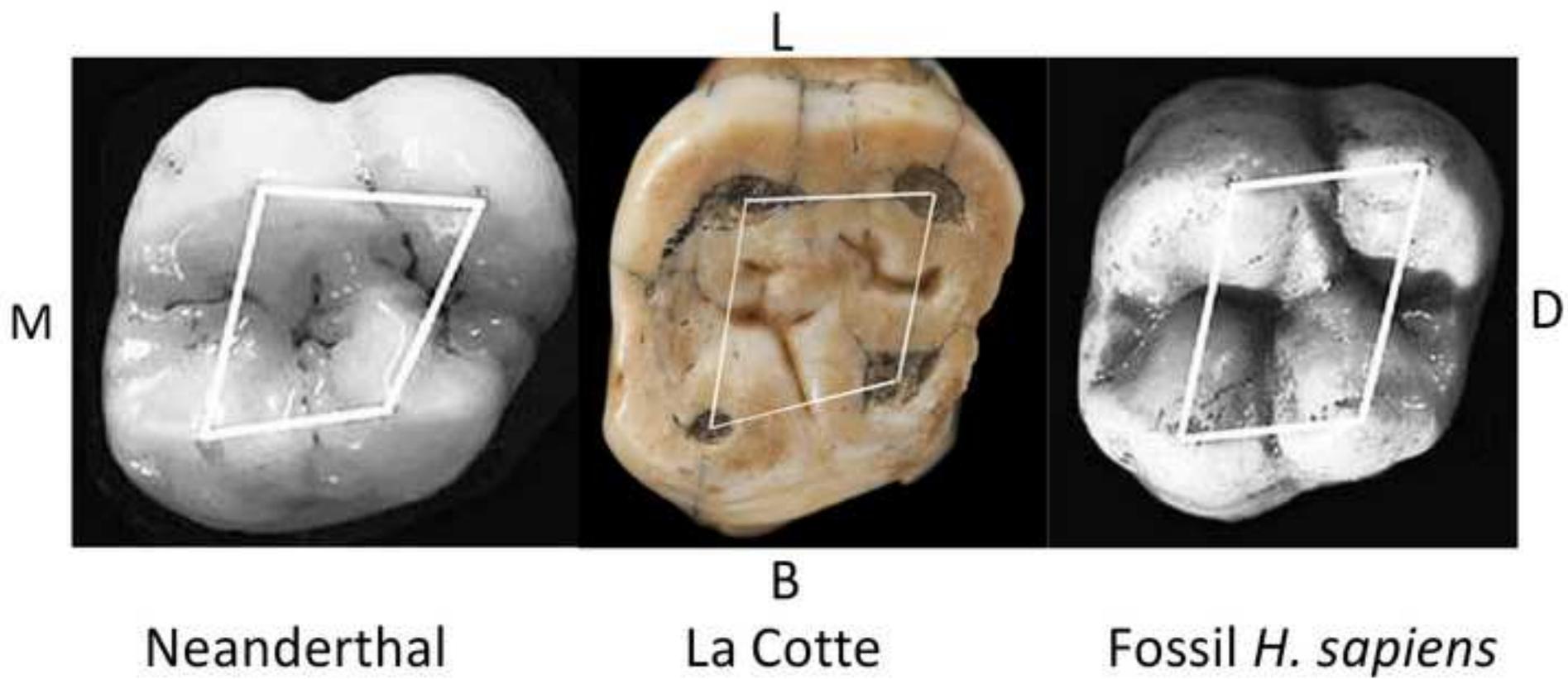


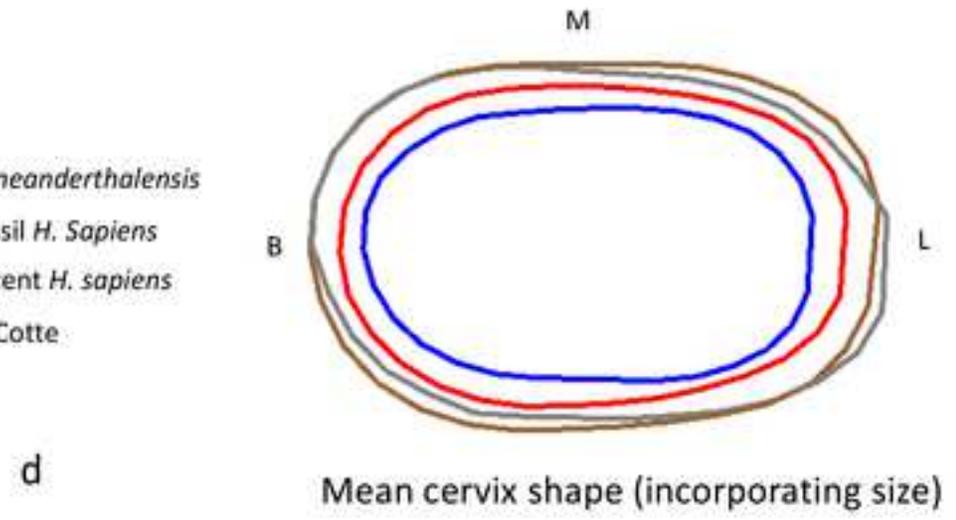
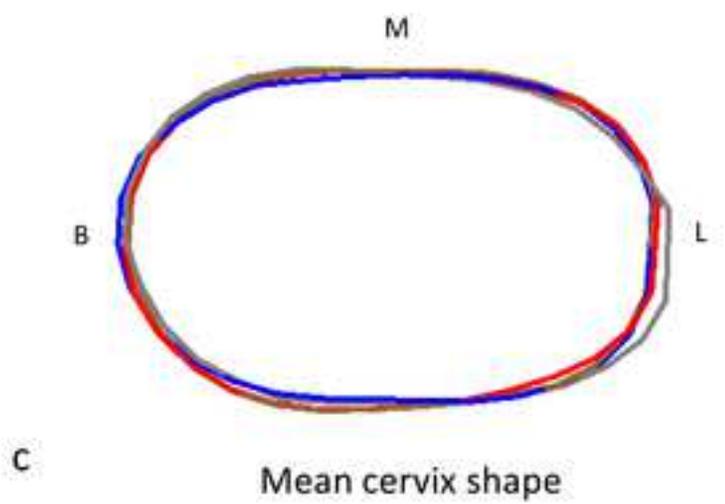
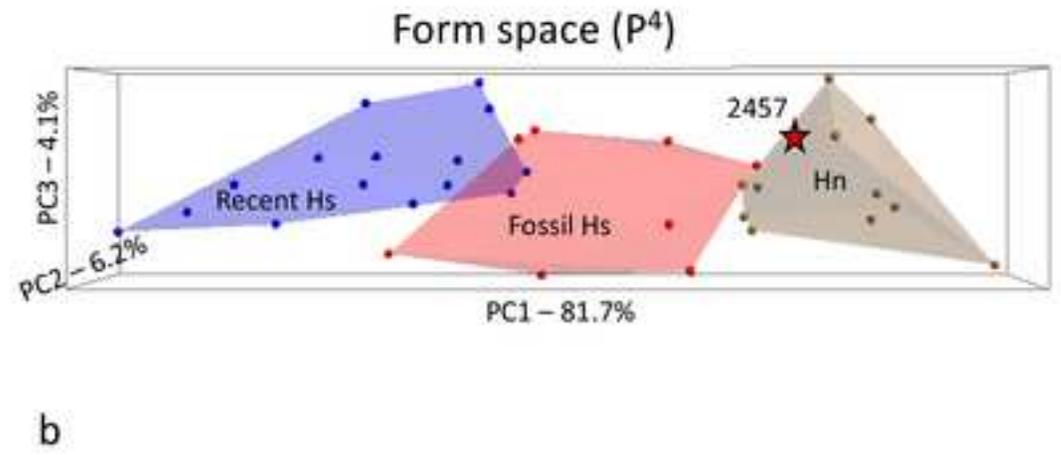
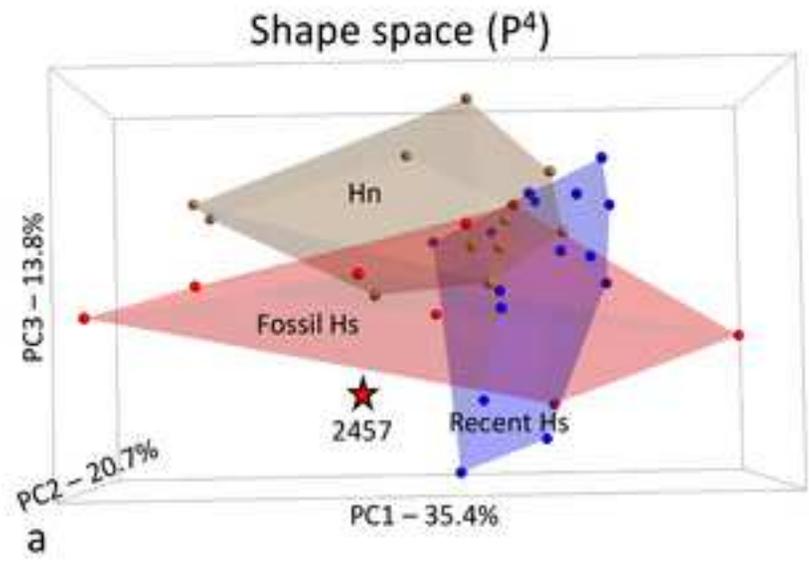


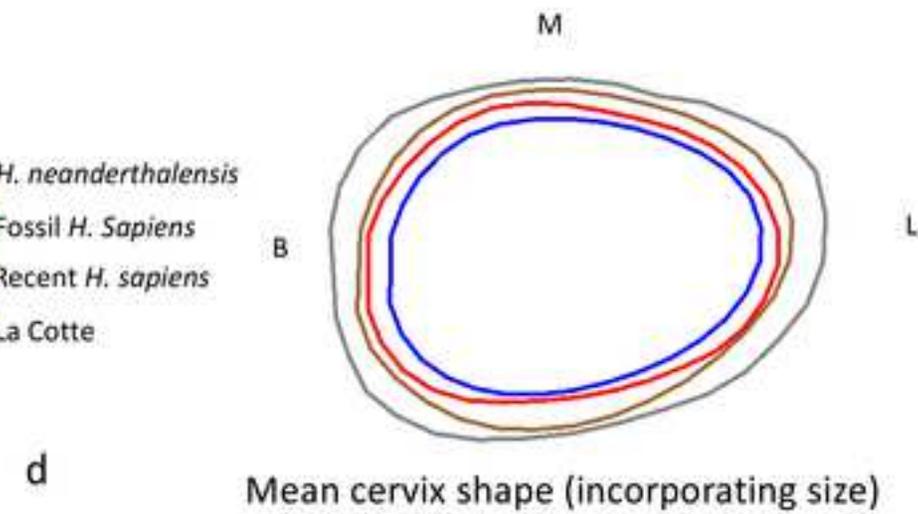
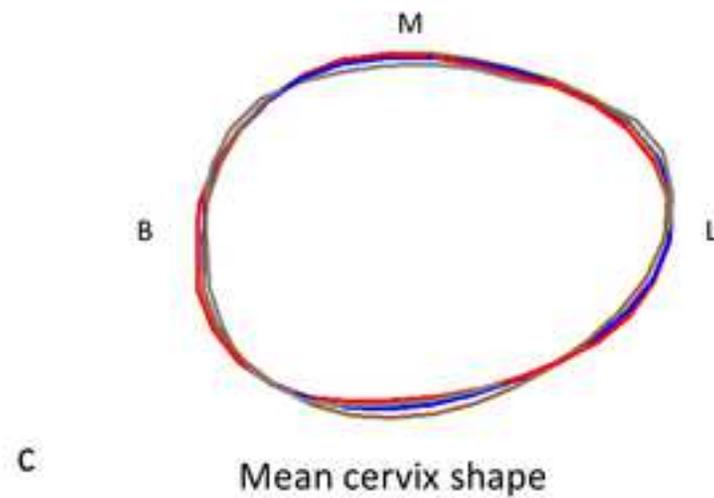
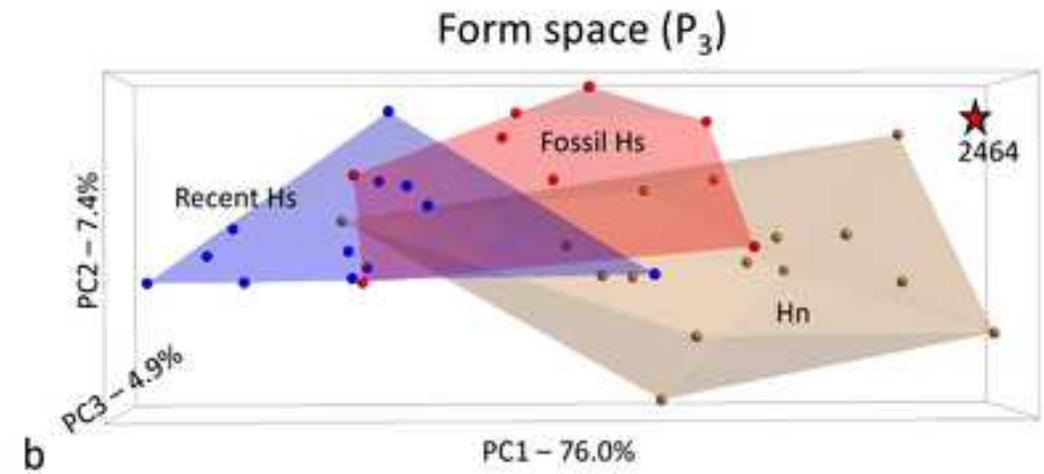
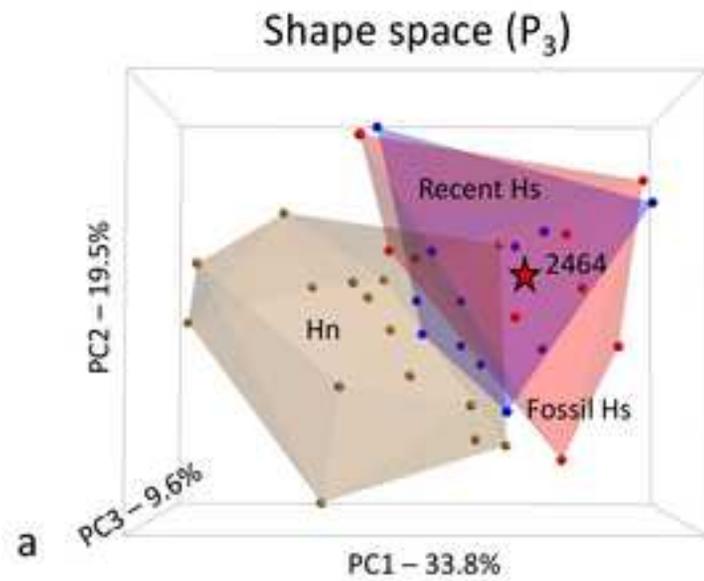
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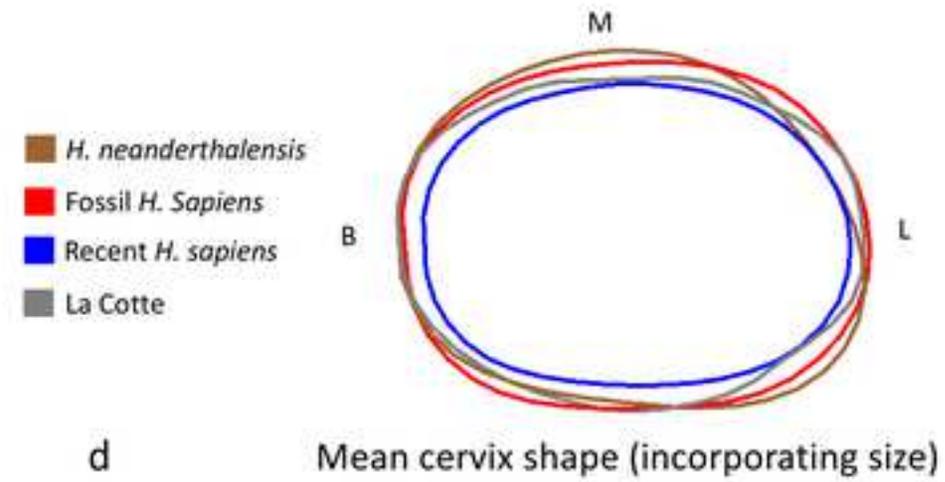
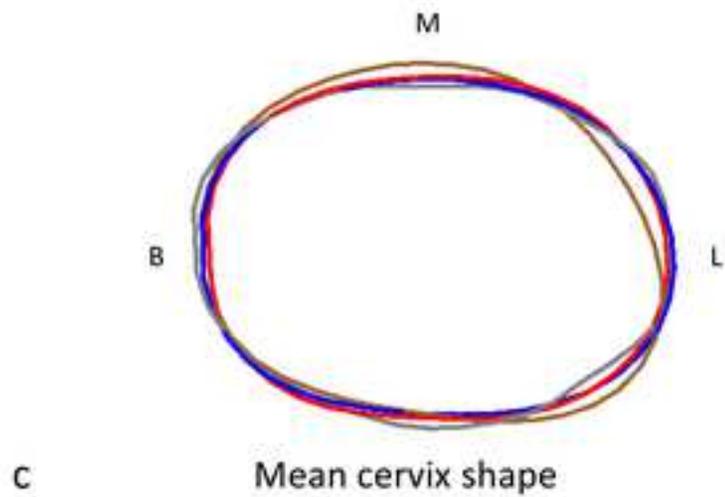
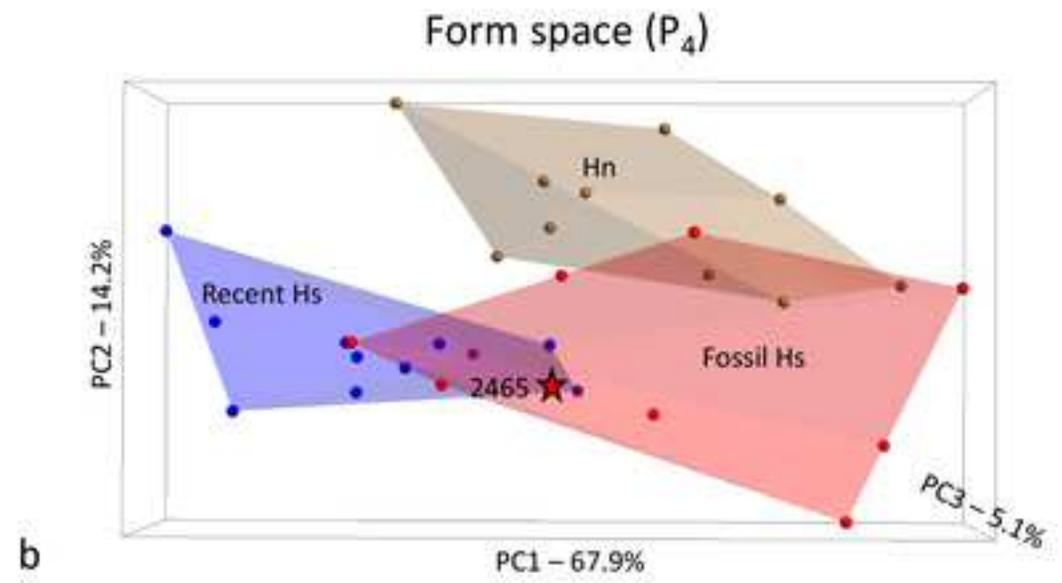
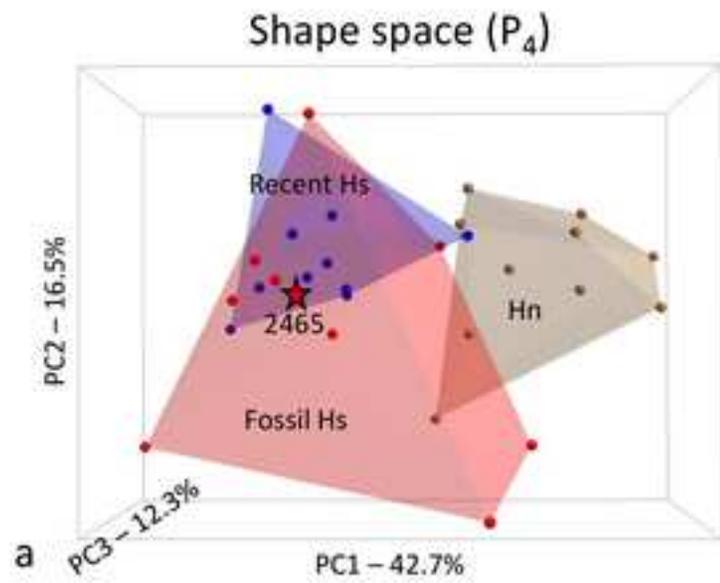


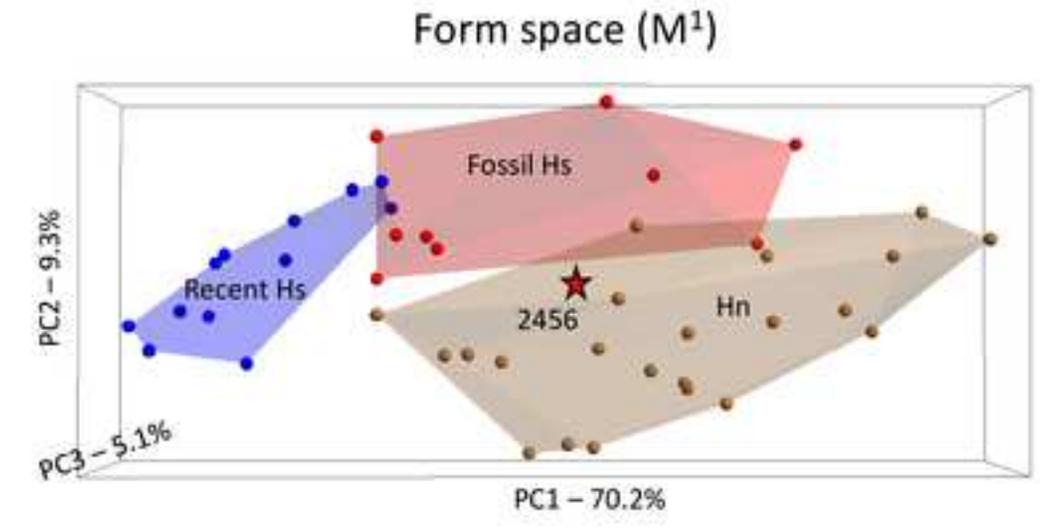
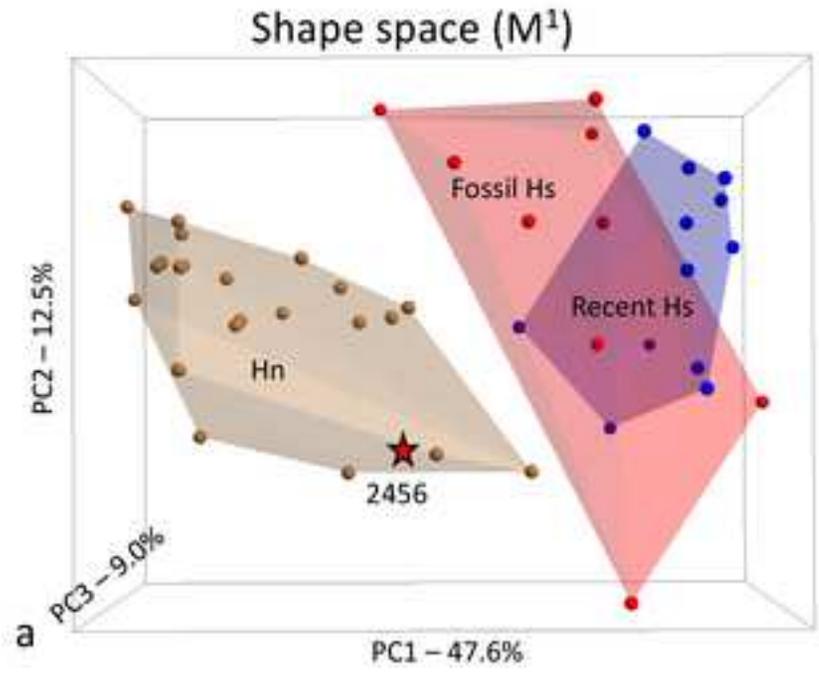




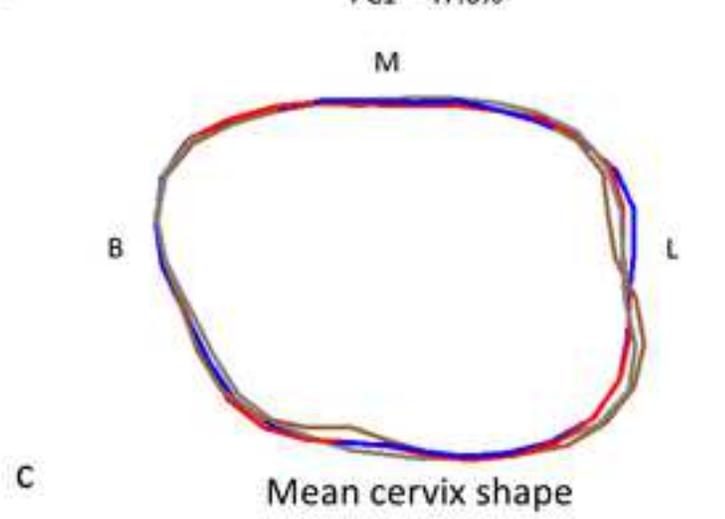






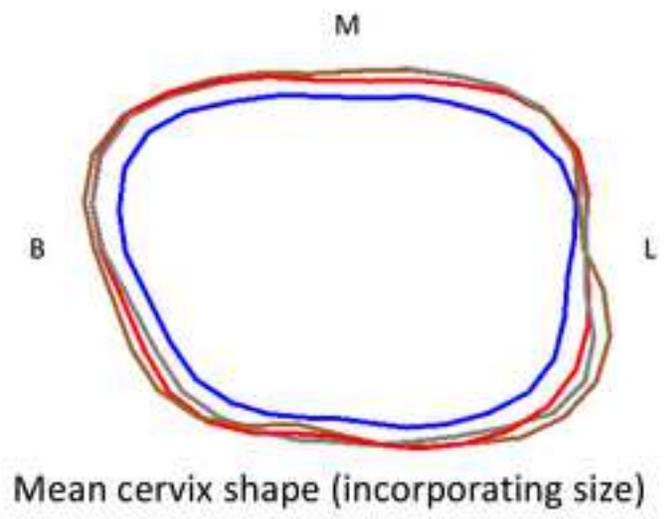


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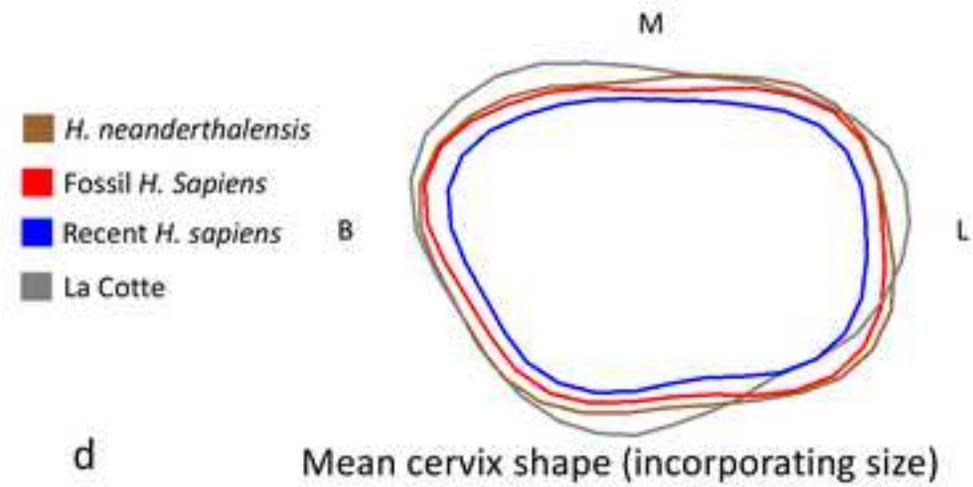
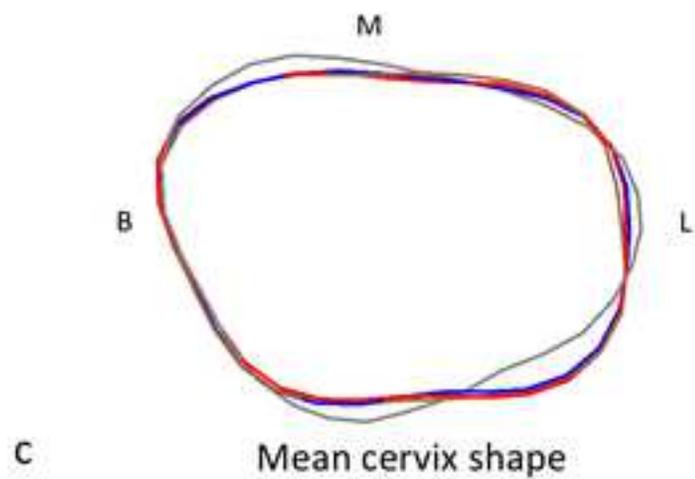
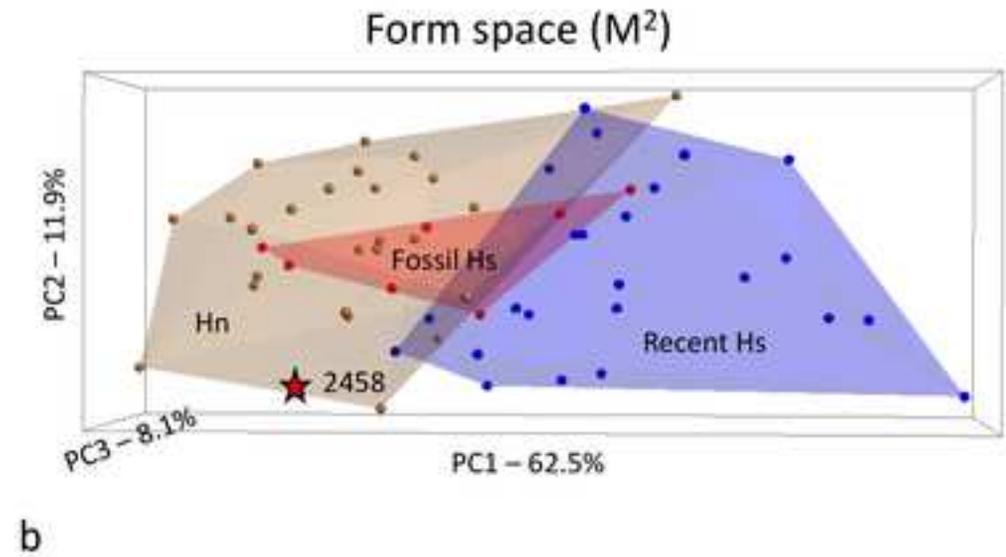
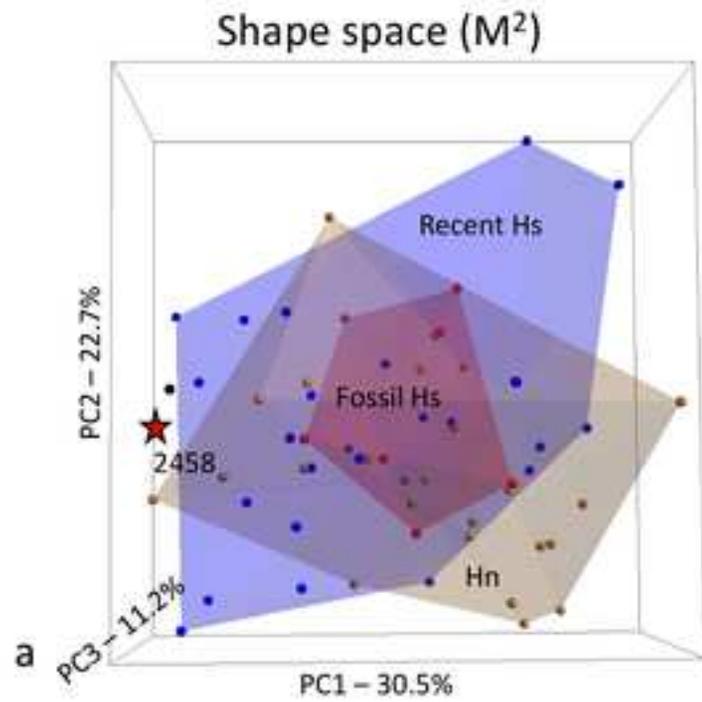


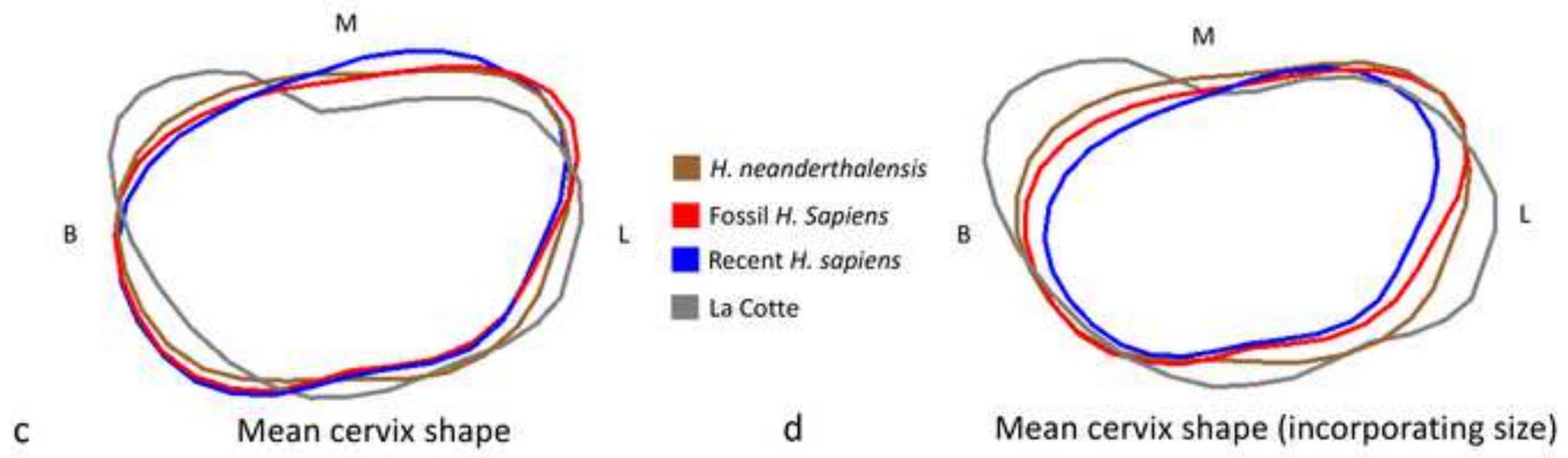
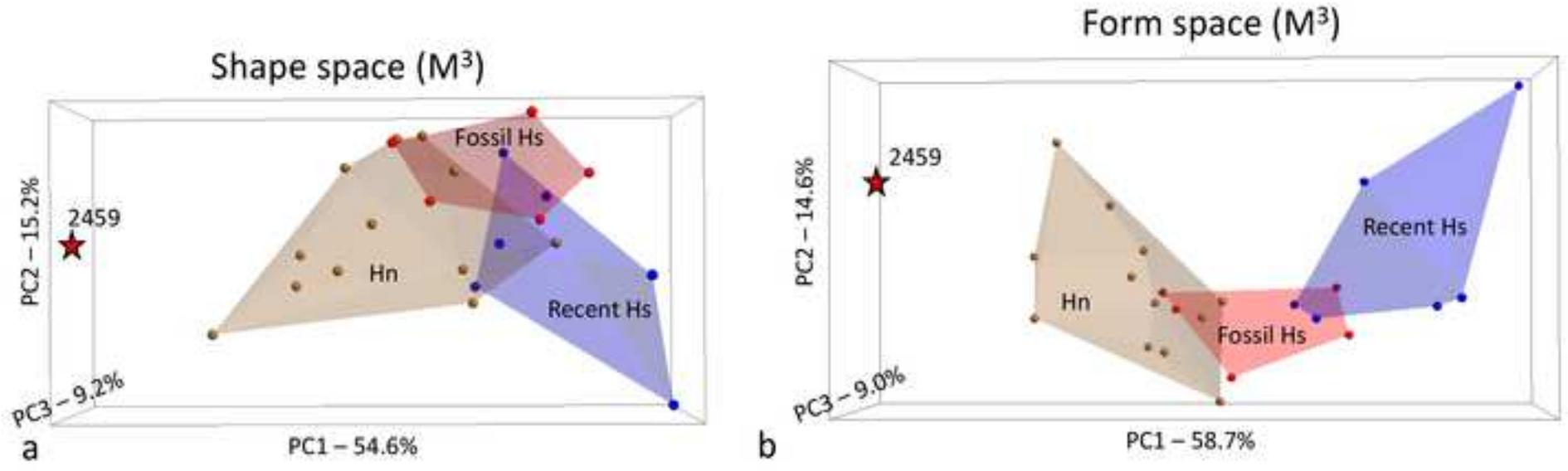
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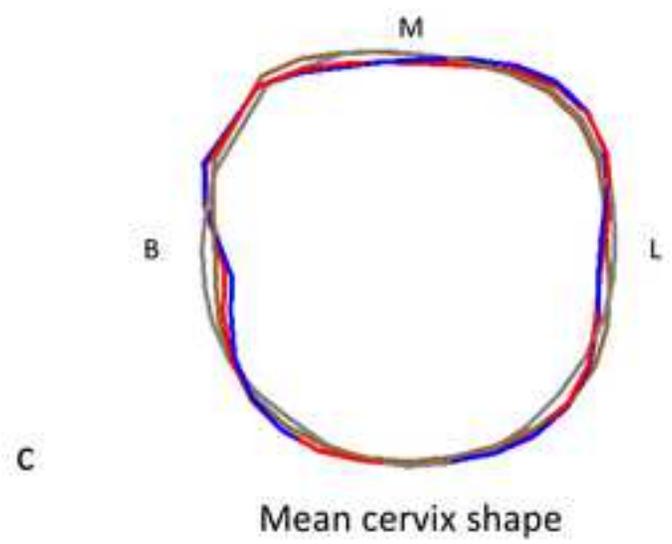
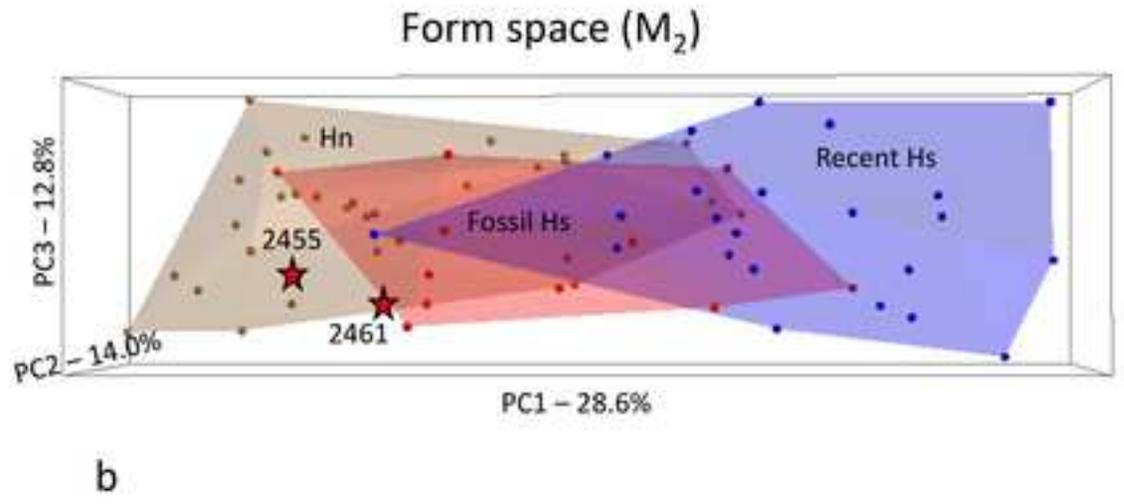
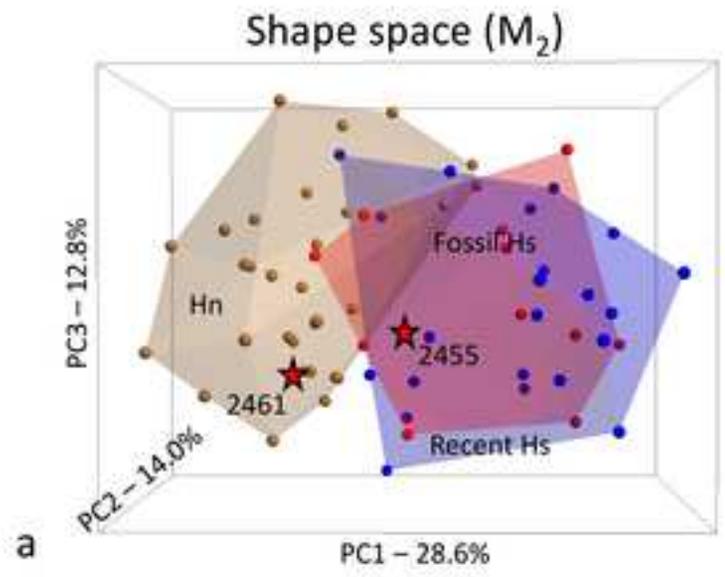
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- Recent *H. sapiens*
- La Cotte



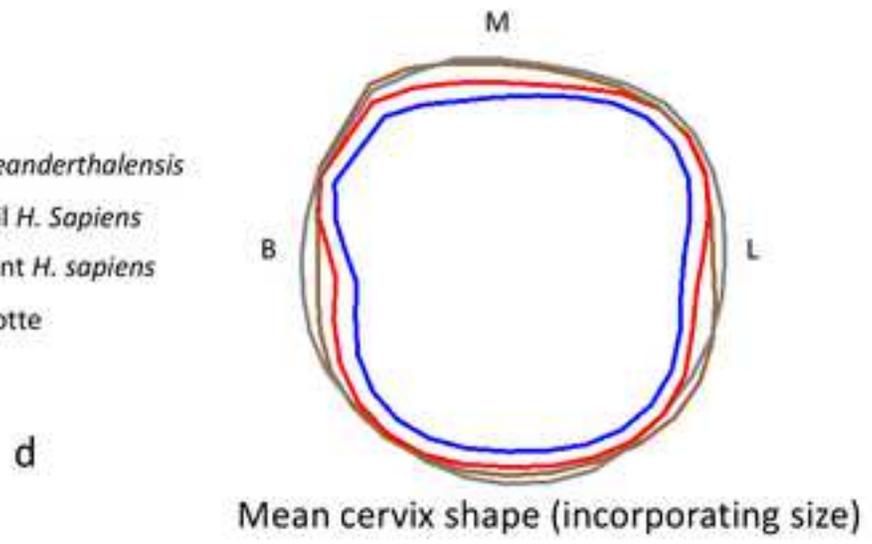
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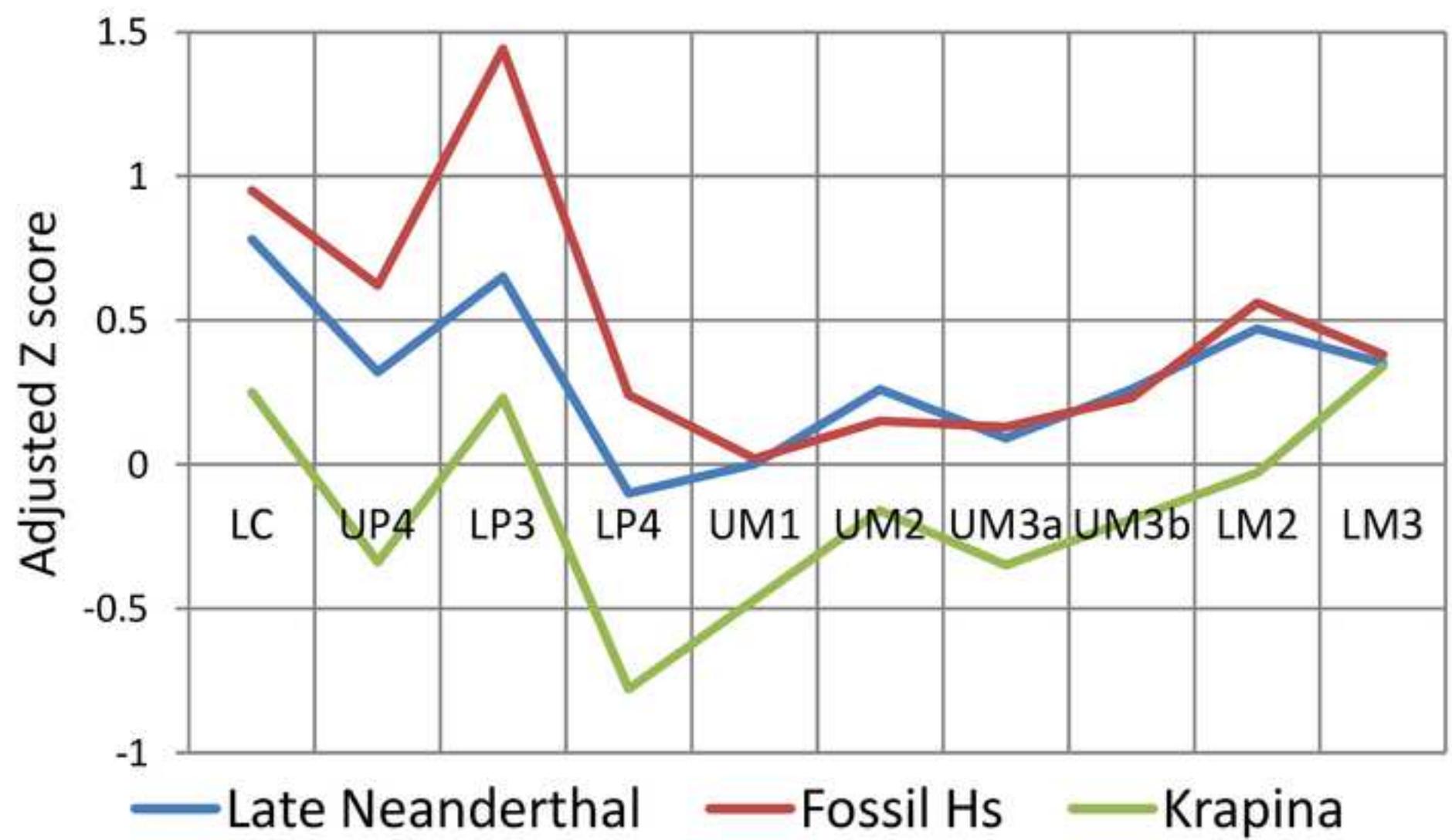






- *H. neanderthalensis*
- Fossil *H. sapiens*
- Recent *H. sapiens*
- La Cotte





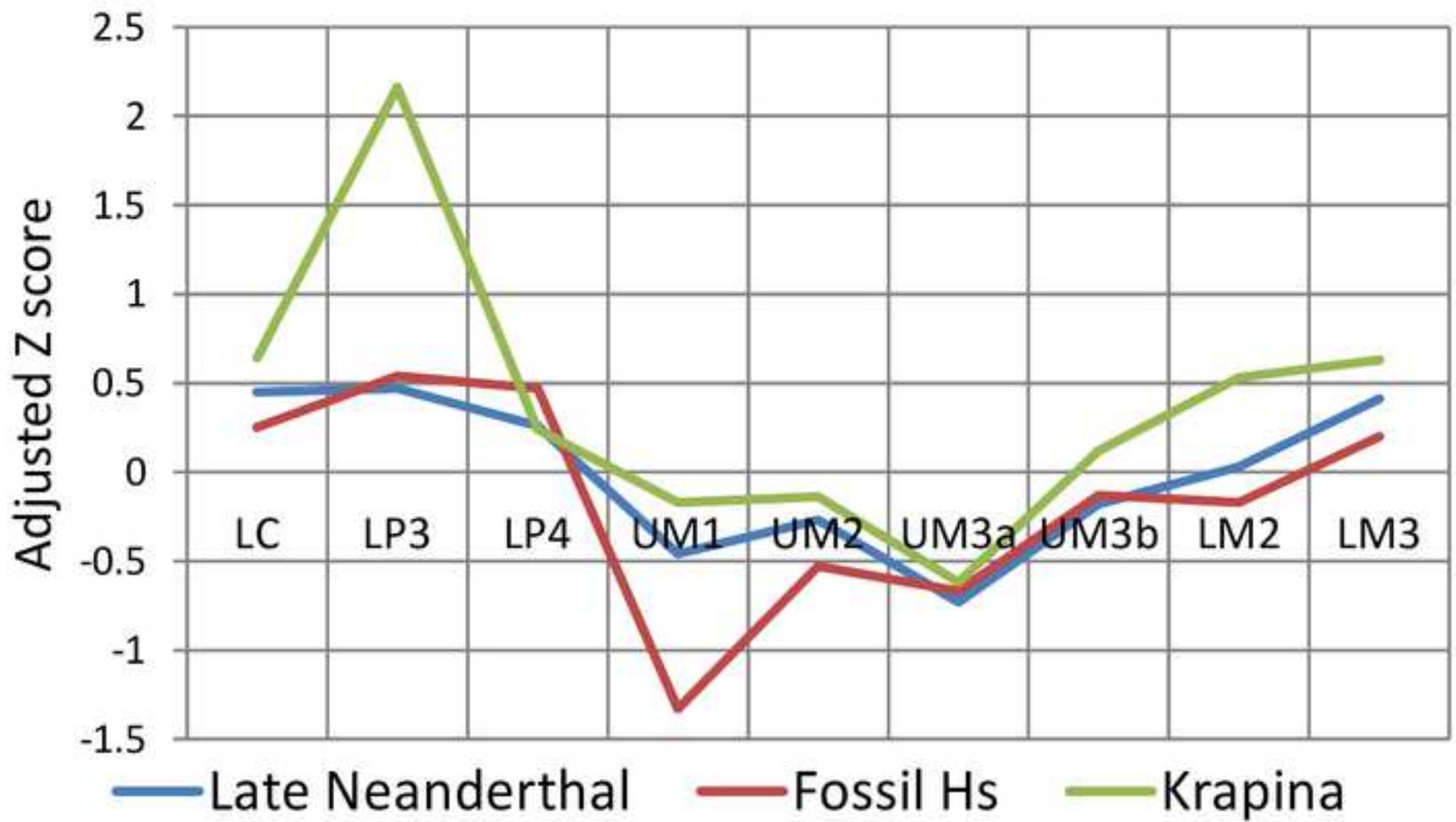


Table 1La Cotte de St Brelade site stratigraphy.^a

North ravine, central area (Zeuner, 1940; Callow, 1986c)		West ravine; north end (Burdo, 1960)		West ravine; railway section (Bates et al., 2013)		OSL	MIS
		A	Modern soil				
		B/C	Loess and loessic head				
		D	Fine gravel				
11	Loessic head	E–H	Loessic head ^b				
	Grey sand						
11	Pedogenesis						
11	Loessic deposit with anthropogenic material and Neanderthal teeth	1	Loessic head	Loessic head			
9.3	Ranker soil	2A	Humic granitic sand				
9.2	Granitic sand						
9.1	Ranker soil						
8.3	Fresh-water pond deposits	3B	White clay with rounded clasts				
				VII	Mid to dark brown clay-silt		
				VI	Grey brown sandy-silt	48.3 ± 3.0 ka	3
				XI	Dark brown to yellowish brown gravel	54.2 ± 9.9 ka	3
		5A	Coarse gritty sand	V	Mid brown to reddish brown sandy silt to silty sand	64.7 ± 7.7; 63.3 ± 11.2; 85.8 ± 12 ka	3/4 or 5A/5B
8.2		6	Peaty soil	IV	Very dark brown bedded clay-silt and sandy clay- silt	80.7 ± 6.5 ka	5A/5B

Abbreviations: MIS = marine isotope stage; OSL = optically stimulated luminescence dating.

^a Numbers/letters before descriptions are context identifiers.^b Level at which occipital fragment discovered.

Table 2

La Cotte de St Brelade dental measurements (in mm).

SJMJ identity	Tooth type	Year found	Wear grade	Crown length	Crown MD	Crown breadth	Crown height	Pulp chamber	Root trunk	Total Root length	Cervix MD	Cervix BL ^c
				MD ^c	corrected	BL		height	length	length		
2462 ^d	RI ₁	1910	4	5.75 ^a		7.0 ^a	>6.5 ^a			>14.0 ^a	5.0 ^a	7.1
2463	LC ₁	1910	4	8.1		10.0	>9.2			>17.6	6.7	10.1
2457	LP ⁴	1910	5	(6.0)	7.4	10.6	>6.2			>13.2	5.8	10.0
2464	LP ₃	1910	4	7.8	8.1	10.2	>5.9			>16.3	6.5	9.3
2465	LP ₄	1910	5	6.8	7.3	9.1	>4.5			>16.6	5.9	8.5
2456	RM ¹	1910	4	(11.0)	11.6	11.6	>5.3	5.9	9.0	>10.5	8.9	11.5
2458	LM ²	1910	3	10.8	11.1	12.4	>5.0	6.1	8.0	>14.5	9.2	12.1
2459	RM ³	1911	5	10.0		12.3	>5.0	4.9	8.5	>11.6	8.5	—
2467	LM ³	1911	2/3	10.3		11.5	>5.0 ^a	—	—	16.0 ^a	—	—
2461	RM ₂	1910	3	11.7	12.1	11.6	>5.1	5.5	7.0	>14.2	10.0	10.6
2455	LM ₂	1910	3	11.9	12.3	11.7	>4.9	—	7.0 ^a	>12.5 ^a	10.0 ^a	(11.0)
2460	RM ₃	1911	3	(12.0)	12.0	11.7	6.0 ^b	—	—	—	—	11.7

Abbreviations: BL = buccolingual; MD = mesiodistal; L = left; R = right.

^a Measurements from Keith and Knowles (1912).

^b Measured on lingual side of tooth.

^c Parentheses indicate tooth damaged.

^d SJMJ2462 considered to be non-hominin.

Table 3Canine discrete morphological traits.^a

Trait	La Cotte		Comparative material				95% confidence intervals
	de St Brelade	Grade (0 = absent)	Early and late Neanderthal %	No.	Fossil <i>H. sapiens</i> %	No.	
Lower canine	SJM2463						
Tuberculum dentale	Small cuspule	>0	48	12/25	59	10/17	
Shoveling	2	>0	100	25/25	88	15/17	
Distal accessory ridge	4	>0	78	14/18	42	5/12	DF

Abbreviations: No. = number of specimens with trait in sample / sample size; DF = confidence interval for difference in frequencies does not include zero.

^aData source: Martínón-Torres et al. (2012).

Table 4

Premolar discrete morphological traits.

Trait	La Cotte		Comparative material				
	de St	Grade	Early and late		Fossil <i>H. sapiens</i>		95%
	Brelade ^f	(0 = absent)	%	No.	%	No.	confidence intervals
Upper fourth premolar	SJMJ2457						
Buccal mesial accessory ridge	(0)	=0	83	10/12 ^e	40	8/20 ^e	DF
Buccal distal accessory ridge	(0)	=0	58	7/12 ^e	40	8/20 ^e	
Essential crest bifurcated	—	>0	67	10/15 ^b	36	4/11 ^b	
Transverse crest	0	>0	13	2/16 ^b	18	2/11 ^b	
Mesial/distal accessory cusps	(0 mesial)	>0	48	10/21 ^a	33	1/3 ^a	
Lower third premolar	SJMJ2464						
Buccal mesial accessory ridge	(1)	>0	24	4/17 ^a	13	1/8 ^a	
Buccal distal accessory ridge	(1)	>0	90	18/20 ^a	100	9/9 ^a	
Number of lingual cusps	3	>1	21	7/34 ^a	7	1/14 ^a	
Metaconid position mesial	Mesial	Mesial	6	2/32 ^a	20	3/15 ^a	
Transverse crest	0	=0	3	1/30 ^a	19	3/16 ^a	
Mesiolingual truncation (asymmetry)	0 (slight)	=0	6	1/18 ^a	44	7/16 ^a	DF
Mesial occlusolingual groove	0	>0	64	16/25 ^a	50	7/14 ^a	
Tomes' root	4	>3	12	2/17 ^c	38	5/13 ^d	
Taurodontism—BL widening	Present	>0	33	5/15 ^c	71	5/7 ^d	
Taurodontism—MD and BL	Present	>0	20	3/15 ^c	14	1/7 ^d	
Lower fourth premolar	SJMJ2465						
Buccal mesial accessory ridge	(0)	>0	13	2/16 ^a	0	0/7 ^a	

Buccal distal accessory ridge	(1)	>0	88	14/16 ^a	25	2/8 ^a	DF, SF
Number of lingual cusps	(3)	>1	94	29/31 ^a	50	8/16 ^a	DF, SF
Metaconid position mesial	Mesial	Mesial	97	31/32 ^a	73	11/15 ^a	DF
Transverse crest	0	=0	6	2/31 ^a	76	13/17 ^a	DF, SF
Mesiolingual truncation (asymmetry)	0 (very slight)	=0	6	2/31 ^a	67	8/12 ^a	DF, SF
Mesial occlusolingual groove	(0)	>0	8	2/25 ^a	0	0/12 ^a	
Tomes' root	0	>3	25	5/20 ^c	23	3/13 ^d	
Taurodontism–BL widening	Present	>0	50	8/16 ^c	50	4/8 ^d	
Taurodontism–MD and BL	Present	>0	19	3/16 ^c	38	3/8 ^d	

Abbreviations: BL = buccolingual; MD = mesiodistal; No. = number of specimens with trait in sample / sample size; DF = confidence interval for difference in frequencies does not include zero; SF = confidence intervals for sample frequencies do not overlap.

^a Data source: Bailey (2006a).

^b Data source: Martín-Torres et al. (2012).

^c Data source: Morphometrics comparative sample (SOM Table S1).

^d Data source: Morphometrics comparative sample (SOM Table S3).

^e Data source: Becam et al. (2019), sample under fossil *H. sapiens* is recent human.

^f Parentheses denote interpretation at enamel dentine junction.

Table 5Upper first molar occlusal polygons and relative cusp areas.^a

	La Cotte SJMJ2456	Early and late Neanderthal	Fossil <i>H. sapiens</i> ^b
Occlusal polygon angles °		X (SD)	X (SD)
<i>n</i>		17	5
Protocone	100	106.1 (5.2)	106.3 (4.4)
Paracone	68	66.7 (6.7)	71.1 (2.7)
Metacone	116	118.0 (10.0)	110.3 (4.9)
Hypocone	76	69.0 (6.1)	73.3 (4.8)
Relative cusp areas (%)			
<i>n</i>		21	15
Protocone	33	29.9 (2.4)	31.8 (1.5)
Paracone	27	25.8 (2.1)	25.7 (2.3)
Metacone	21	20.6 (1.8)	22.4 (1.7)
Hypocone	19	23.7 (2.1)	20.1 (3.0)
Ratio of occlusal polygon area to crown base area (%)			
<i>n</i>		17	5
Value	24	26.7 (1.8)	32.7 (1.9)

Abbreviation: X = sample mean.

^a Data sources: relative cusp areas from Quam et al. (2009), remainder from Bailey et al. (2008).

^b European Late Pleistocene.

Table 6

Upper molar discrete morphological traits.

Trait	La Cotte de St		Comparative material				
	Brelade ^c	Grade (0 = absent)	Early and late Neanderthal %	No.	Fossil <i>H.</i> <i>sapiens</i> %	No.	95% confidence intervals
Upper first molar	SJMJ 2456						
Cusp 5	(0)	>0	64	14/22 ^a	53	9/17 ^a	
Carabelli's trait	0	>2	68	17/25 ^a	40	8/20 ^a	
Mesial accessory cusps	(2)	>0	40	4/10 ^a	22	2/9 ^a	
Hypocone size (reduced)	5	<3	0	0/39 ^a	0	0/25 ^a	
Metacone size	5	>3	74	17/23 ^b	74	14/19 ^b	
Oblique ridge	2	>0	95	21/22 ^b	84	16/19 ^b	
Mesial transverse crest	(0)	>0	25	5/20 ^b	31	4/13 ^b	
Parastyle	0	>0	30	6/20 ^b	0	0/15 ^b	DF
Upper second molar	SJMJ 2458						
Cusp 5	2/3	>0	68	15/22 ^a	39	7/18 ^a	
Carabelli's trait	0	>2	50	11/22 ^a	16	3/19 ^a	DF
Mesial accessory cusps	(1)	>0	100	10/10 ^a	13	1/8 ^a	DF, SF
Hypocone size (reduced)	(1-2)	<3	6	2/33 ^a	15	3/20 ^a	
Metacone size	5	>3	48	10/21 ^b	33	4/12 ^b	
Oblique ridge	0	>0	71	15/21 ^b	58	7/12 ^b	
Mesial transverse crest	(0)	>0	24	4/17 ^b	22	2/9 ^b	
Parastyle	0	>0	0	0/19 ^b	0	0/10 ^b	

Upper third molar	SJMJ	SJMJ						
	2459	2467						
Cusp 5	—	0	>0	35	6/17 ^a	29	4/14 ^a	
Carabelli's trait	0	—	>2	14	2/14 ^a	25	3/12 ^a	
Mesial accessory cusps	(0)	—	>0	70	7/10 ^a	28	3/11 ^a	DF
Hypocone size (reduced)	(>2)	—	<3	68	13/19 ^a	57	8/14 ^a	
Metacone size	—	—	>3	17	3/18 ^b	0	0/10 ^b	
Oblique ridge	(0)	0	>0	29	5/17 ^b	20	2/10 ^b	
Mesial transverse crest	(0)	—	>0	7	1/14 ^b	22	2/9 ^b	
Parastyle	0	—	>0	13	2/16 ^b	0	0/9 ^b	

Abbreviations: No. = number of specimens with trait in sample / sample size; DF = confidence interval for difference in frequencies does not include zero; SF = confidence intervals for sample frequencies do not overlap.

^aData source: Bailey (2006a).

^bData source: Martín-Torres et al. (2012).

^cParentheses denote interpretation at enamel dentine junction.

Table 7

Lower molar discrete morphological traits.

Trait	La Cotte de St		Grade (0 = absent)	Comparative material				
	Brelade ^c			Early and late Neanderthal		Fossil <i>H.</i> <i>sapiens</i>		95% confidence intervals
				%	No.	%	No.	
Lower second molar	SJMJ 2455	SJMJ 2461						
Groove pattern	Y	Y	=Y	75	27/36 ^a	44	12/27 ^a	DF
Hypoconulid	5, D	5, D	>0	100	39/39 ^a	65	13/20 ^a	DF, SF
Deflecting wrinkle	(0)	(0)	>0	26	6/23 ^b	22	5/23 ^b	
Distal trigonid crest	(0)	0	>0	14	4/29 ^a	0	0/24 ^a	
Mid-trigonid crest	(0)	0	=0	4	1/26 ^a	96	23/24 ^a	DF, SF
Cusp 6	(0)	(1)	>0	50	11/22 ^a	24	4/17 ^a	
Cusp 7	(0)	(0)	>0	20	7/35 ^a	8	2/24 ^a	
Anterior fovea	(3/4)	(3/4)	>1	89	23/26 ^a	50	10/20 ^a	DF, SF
Protostylid	0	1(5)	>0	23	5/22 ^b	14	3/22 ^b	
Lower third molar	SJMJ 2460							
Groove pattern	X		=Y	41	7/17 ^a	56	10/18 ^a	
Hypoconulid	4, D		>0	100	23/23 ^a	68	13/19 ^a	DF, SF
Deflecting wrinkle	0		>0	7	1/15 ^b	13	2/15 ^b	
Distal trigonid crest	0		>0	11	2/19 ^a	0	0/16 ^a	
Mid-trigonid crest	0		=0	7	1/15 ^a	100	16/16 ^a	DF, SF
Cusp 6	1		>0	50	5/10 ^a	41	7/17 ^a	
Cusp 7	3		>0	40	6/15 ^a	17	3/18 ^a	

Anterior fovea	3	>1	93	13/14 ^a	47	7/15 ^a	DF
Protostylid	(6)	>0	39	5/13 ^b	12	2/17 ^b	

Abbreviations: D = distal; No. = number of specimens with trait in sample / sample size;

DF = confidence interval for difference in frequencies does not include zero; SF =

confidence intervals for sample frequencies do not overlap.

^aData source: Bailey (2006a).

^bData source: Martín-Torres et al. (2012).

^cParentheses denote interpretation at enamel dentine junction.

Table 8Comparative data for cervical dimensions (in mm).^a

Sample	Lower canine			Upper fourth			Lower third			Lower fourth			Upper first molar			Upper second			Lower second			
	SJMJ2463			premolar			premolar			premolar			SJMJ2456			molar			molar			
	<i>n</i>	MD	BL	<i>n</i>	MD	BL	<i>n</i>	MD	BL	<i>n</i>	MD	BL	<i>n</i>	MD	BL	<i>n</i>	MD	BL	<i>n</i>	MD	BL	
La Cotte de St Brevalde		6.7	10.1		5.8	10.0		6.5	9.3		5.9	8.5		8.9	11.5		9.2	12.1		10.0	10.6	
Neanderthal	X	16	5.8	8.9	9	5.3	9.0	12	5.5	7.8	16	5.8	8.2	7	8.7	11.2	7	8.8	11.5	9	10.3	9.8
	range		4.3–	7.5–		4.5–	8.0–		4.9–	6.9–		4.5–	7.3–		7.3–	10.5–		7.6–	10.3–		9.4–	8.3–
			6.4	10.5		6.0	10.0		6.0	9.4		7.1	8.9		10.4	12.1		10.1	12.5		11.6	11.6
	SD		0.5	0.7		0.5	0.7		0.3	0.7		0.7	0.5		1.1	0.7		1.1	0.9		0.7	0.9
	Azs ^b		0.8	0.8		0.4	0.6		1.5	1.0		0.1	0.3		0.1	0.2		0.2	0.3		-0.2	0.4
Fossil <i>H.</i> <i>sapiens</i>	X	22	5.7	8.1	15	5.1	8.6	24	5.2	7.3	20	5.2	7.3	20	8.3	11.0	18	7.8	10.9	28	9.3	9.1
	range		4.8–	6.7–		4.6–	7.9–		4.6–	5.8–		4.2–	6.4–		7.9–	9.9–		6.6–	8.8–		8.0–	7.6–
			6.6	9.7		5.9	10.4		6.0	8.4		6.6	9.7		9.4	12.6		9.1	13.2		10.7	11.0
	SD		0.5	0.8		0.4	0.7		0.4	0.6		0.5	0.7		0.4	0.6		0.6	1.0		0.6	0.8
	Azs ^b		1.0	1.2		0.8	0.9		1.6	1.6		0.7	0.8		0.7	0.4		1.1	0.6		0.6	0.9

Abbreviations: Azs = adjusted Z score; BL = buccolingual; MD = mesiodistal; X = sample mean.

^aData sources: Neanderthal C₁, Le Cabec (2013); Neanderthal remainder, see SOM Table S5; fossil *H. sapiens*, see SOM Table S3.

^b Values in bold: adjusted Z score $\geq \pm 1.0$.

Table 9

Summary of principal Neanderthal and modern human traits in La Cotte de St Brelade teeth.

Individual and group	SJMJ Identity	Tooth type	Neanderthal features	<i>H. sapiens</i> features	Attribution
A-1	2458	Left M ²	Mesial accessory cusp; cusp tips internally placed; roots taurodont; cervical measurements		N
	2461	Right M ₂	Root shape; roots taurodont; cervix shape	Mid-trigonid crest absent	N/Hs
	2455	Left M ₂	Root shape; roots taurodont; cervix shape	Mid-trigonid crest absent	N/Hs
	2460	Right M ₃	Multiple cusps and accessory crests	Mid-trigonid crest absent; metaconid dentine horn tip not centrally placed	N/H s
A-2	2463	Left C ₁	Large distal accessory ridge; root shape and robusticity; root canal form; crown area; cervical measurements		N
	2464	Left P ₃	Buccal cusp form; buccal cingulum at EDJ; root robusticity; root taurodont; crown area; cervical measurements	Transverse crest absent; mesiolingual truncation (asymmetry) absent; cervix shape	N/Hs
A-3	2456	Right M ¹	Cusp tips internally placed; distobuccal truncation; relative size and shape of occlusal polygon; roots	Relatively small hypocone and large hypocone angle	N/Hs

			taurodont; cervix shape;		
			crown index		
A-4	2467	Left M ³	Roots taurodont; root length		N
B-1	2457	Left P ⁴	Inclination of buccal surface; root robust and two-rooted; root taurodont	Cervix shape	N/Hs
	2465	Left P ₄	Three lingual cusps; root taurodont	Transverse crest absent; mesiolingual truncation (asymmetry) absent; cervix shape	N/Hs
B-2	2459	Right M ³	Inferred presence multiple distal cusps; roots taurodont; cervix shape		N

Abbreviations: Hs = *H. sapiens*; N = Neanderthal.



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