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1 Microevolution of outer and inner structures of upper molars in Late Pleistocene and Early
2 Holocene humans

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5 4 Microévolution des structures externe et interne des molaires supérieures chez les Hommes
6
7 5 *de la fin du Pléistocène et du début de l'Holocène*

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23 ABSTRACT

1 24

2 25 In this study, we investigate outer and inner variations of upper second molars (UM2) for Late
3 26 Pleistocene and Early Holocene modern humans, at a key-period in our evolutionary history
4 27 associated with major sociocultural, economic and environmental changes. Non-metric traits
5 28 have been recorded on 89 UM2 of 66 Upper Paleolithic, Mesolithic and Neolithic individuals,
6 29 and 40 UM2 have been microscanned to assess variations in enamel thickness (ET)
7 30 distribution and enamel-dentine junction (EDJ) shape. Major changes are found between
8 31 Mesolithic and Neolithic periods: a decrease of the metacone expression combined with an
9 32 increase of the hypocone development; an increase of the heterogeneity of ET distribution
10 33 between lingual and buccal cusps; and an increase of the development of the dentine horn tips
11 34 corresponding to the hypocone and, to a lesser extent, to the metacone. These morphological
12 35 modifications could be linked to the masticatory functional changes associated with the
13 36 transition to agriculture.

14 37

15 38 RÉSUMÉ

16 39

17 40 Dans cette étude, nous avons examiné les variations externes et internes des secondes
18 41 molaires supérieures (UM2) d'Hommes de la fin du Pléistocène et du début de l'Holocène,
19 42 période-clé de notre histoire évolutive associée à des changements socioculturels,
20 43 économiques et environnementaux majeurs. Les variations non-métriques ont été enregistrées
21 44 sur 89 UM2 de 66 individus paléolithiques, mésolithiques et néolithiques, et 40 UM2 ont été
22 45 scannées par microtomographie pour évaluer les variations de distribution d'épaisseur de
23 46 l'émail (EE) et de forme de la jonction émail-dentine (JED). Les changements majeurs sont
24 47 trouvés entre le Mésolithique et le Néolithique: diminution de l'expression du métacône
25 48 combinée à un hypocône plus développé; hétérogénéité accrue dans la distribution de l'EE
26 49 entre les cuspides linguales et buccales; et augmentation de taille des cornes de dentine
27 50 correspondant à l'hypocône et, dans une moindre mesure, au métacône. Ces modifications
28 51 morphologiques peuvent être liées aux changements fonctionnels masticatoires associés à la
29 52 transition vers l'agriculture.

30 53

54 **1. Introduction**

55
56 Documented since the apparition of the genus Homo, a reduction in tooth size together
57 with a morphological simplification have been reported (Brace, 1963, 1967; Frayer, 1977;
58 Wolpoff, 1971). This phenomenon accelerated at the end of the Pleistocene, and particularly
59 during the Upper Paleolithic (Brace et al., 1987; Calcagno, 1986; Frayer, 1977; Pinhasi and
60 Meiklejohn 2011). Among the most evoked factors, cultural and dietary changes (Brace,
61 1963), energetic demand (Jolly, 1970), competition during teeth development (Sofaer et al.,
62 1971), resistance to pathology (Calcagno, 1986), and demographic and societal changes
63 (Macchiarelli and Bondioli, 1986) have been proposed as having played an active role in
64 affecting this phenomenon. Based only on outer assessment of teeth, these explanatory
65 models are still discussed and no consensus has been reached on this dental structural
66 reduction.

67 Outer and inner structures of human teeth provide a wealth of information that is crucial
68 in both paleoanthropological and archaeological studies. Crown size and shape have been
69 largely used to estimate phylogenetic relationships, biological affinities and kinship (e.g.,
70 Bailey, 2000; Carter et al., 2014; Crubézy and Sellier, 1990a; Irish, 1997; Irish et al., 2014; Paul
71 and Stojanowski, 2015). Enamel thickness and dental tissue proportions have been
72 determinant to discuss taxonomy, phylogeny, developmental and dietary aspects (Bayle et al.,
73 2010; Fornai et al., 2014; Le Luyer et al., 2014; Mahoney, 2013; Martin, 1985; Molnar and
74 Gantt, 1977; Schwartz, 2000; Skinner et al., 2015; Smith et al., 2012; Zanolli, 2014). The
75 enamel-dentine junction (EDJ) is the developmental precursor and the primary contributor of
76 the outer enamel surface (OES) morphology (Guy et al., 2015; Morita et al., 2014; Skinner,
77 2008; Skinner et al., 2008a, 2010). While the OES and enamel thickness have been related to
78 dietary aspects and masticatory biomechanical constraints directly under selective pressures
79 (Hlusko et al., 2004; Horvath et al., 2014; Kelley and Swanson, 2008; Le Luyer et al., 2014;
80 Pampush et al., 2013), the EDJ has been considered as more conservative evolutionarily,
81 providing essential information about the developmental processes underlying teeth crown
82 growth and more reliable for assessing phylogenetic relationships (Braga et al., 2010;
83 Korenhof, 1961; Olejniczak et al., 2007; Pan et al., 2016; Skinner, 2008; Skinner et al.,
84 2008a). Thus, virtual dental anthropology brings highly relevant complementary evidences
85 (Macchiarelli et al., 2008, 2013), and studies integrating both outer and inner aspects of teeth
86 may provide greater opportunity to understand of human evolution.

87 Advanced virtual imaging techniques such as microtomography (microCT or μ CT)

88 allow non-invasive quantitative and qualitative characterizations of inner structures. Although
89 major sociocultural and economic changes occurred at the Pleistocene-Holocene boundary
90 (Bonsall et al., 2004; Langlais et al., 2012; Marchand and Perrin, 2015; Pinhasi and Stock,
91 2011; Richards et al., 2003; Valdeyron, 2014), representatives of the first human societies
92 have been poorly assessed by means of advanced virtual anthropology (but see Le Luyer,
93 2016; Le Luyer et al., 2014, 2016). This study aims to investigate outer and inner variations of
94 modern humans upper second molars dated from Late Pleistocene and Early Holocene from a
95 whole crown perspective, by assessing non-metric variation, enamel thickness and EDJ shape.

97 **2. Material and methods**

99 2.1. Samples

100
101 We analysed 89 second upper molars (UM2) of 66 adult and immature individuals
102 (Table 1) from French sites (Fig. 1) dated from the Upper Paleolithic (Middle and Upper
103 Magdalenian, Azilian/Laborian), the Mesolithic (Early and Late Mesolithic) and the Neolithic
104 (Early and Middle Neolithic). All the selected teeth are fully formed UM2 crowns, free of
105 damages or pathologies. From this sample, 40 unworn or slightly worn UM2 were
106 microscanned (μ CT, Table 1) for enamel thickness and EDJ analyses. UM2s have been
107 selected for this study for two reasons: they are often less worn than the first molars, and their
108 development is more stable than those of the third molars (Garn et al., 1962). Even if it was
109 not the purpose of the study, we primarily tested differences linked to sexual dimorphism.
110 When the hip bones were preserved, their morphology and morphometry were used to
111 determine the sex of the adult individuals (Bruzek, 2002; Murail et al., 2005). For all the
112 parameters assessed in this study, no significant differences were found between sexes.

114 2.2. Non-metric variations

115
116 Crown morphological variations were assessed by recording the number of cusps and
117 their development. Five non-metric traits (metacone, hypocone, metaconule, parastyle, and
118 Carabelli's trait) were scored using the Arizona State University Dental Anthropology System
119 (ASUDAS, Scott and Turner, 1997; Turner et al., 1991). For each individual, observations
120 were made on right and left antimeres if they were present. In case of asymmetry, the
121 antimere exhibiting the greatest degree of trait expression was selected prior to calculated

122 frequencies (Turner and Scott, 1977). The metacone, the hypocone and the parastyle have
123 been considered as present when their expression reached a fully formed cusp (i.e., score 3).
124 According to standard ASUDAS rank-scale trait breakpoint from Scott and Turner (1997), the
125 mecatonule has been recorded present from its first degree while the presence of the
126 Carabelli's trait was determined from the score 5. Fisher's exact test was used to compare
127 differences between adult and immature individuals, and between considered periods.

2.3. Microtomographic record

131 To assess the inner structural variation, 40 UM2 have been imaged by using the
132 Skyscan 1076 in vivo X-ray equipment set at the MRI platform (University Montpellier 2,
133 France). Scans were realized according to the following parameters: 100 kV voltage, 100 μ A
134 current, 1.0 mm aluminum filter and 0.20° rotation step. Using Nrecon 1.6 (Skyscan), the
135 final volumes were reconstructed with an isotropic voxel size ranging from 17.93 μ m for
136 isolated teeth to 36.18 μ m for jaw fragments. A semi-automatic threshold-based segmentation
137 (HMH, Coleman and Colbert, 2007; Spoor et al., 1993) was conducted using Avizo 9.0
138 (VSG) with manual corrections (Bayle et al., 2009, 2010; Kono, 2004; Macchiarelli et al.,
139 2006; Olejniczak et al., 2008a, b, c; Smith et al., 2005; Zanolli et al., 2010, 2014). Crowns
140 were digitally isolated from roots (Olejniczak et al., 2008a) and 3D surface models of the
141 OES and the EDJ were generated using a constrained smoothing algorithm (Kupczik and
142 Hublin, 2010).

2.4. Enamel thickness variations

146 Average enamel thickness (AET) and relative enamel thickness (RET) were calculated
147 in 2D and in 3D (Kono, 2004; Macchiarelli et al., 2006; Martin, 1985; Olejniczak et al.,
148 2008c; Skinner et al., 2015; Smith et al., 2012). For all worn teeth, enamel loss was virtually
149 reconstructed on the mesial sections prior to measure 2D enamel thicknesses (Smith et al.,
150 2012). Mann-Whitney U-tests were performed to detect potential significant differences in
151 enamel thickness between adult and immature individuals, and between periods. Three-
152 dimensional cartographies of the distribution of enamel thickness were created by measuring
153 the distance between the OES and EDJ (Macchiarelli et al., 2008). Also, using MPSAK v2.9
154 (developed by L. Bondioli, available in Dean and Wood, 2003), the topographical variation of
155 the standardized enamel thickness was measured from the cervix to the apex of the cusps, on

156 both lingual and buccal sides of the mesial sections (Le Luyer et al., 2014; Macchiarelli et al.,
157 2007). For the enamel thickness analyses, only unworn to slightly worn teeth (wear stage
158 inferior or equal to 4, Molnar, 1971) have been included. Two teeth (the Upper Magdalenian
159 of Le Morin and a Middle Neolithic one from Gurgy) exhibiting a wear stage of 5 (Molnar,
160 1971) are given separately for information purposes.

2.5. Enamel-dentine junction shape

Using the software Viewbox 4 (dHAL software) and a template specifically developed
to finely quantify variations at microevolutionary scale (Le Luyer et al., 2016), 114 landmarks
were digitized on the EDJ surface: five anatomical landmarks (four on the tip of the dentine
horn corresponding to protocone, paracone, metacone, hypocone and one on lowest point of
the occlusal basin), 52 curve semilandmarks, and 57 surface semilandmarks (Coquerelle et al.,
2011; Gunz and Mitteroecker, 2013; Gunz et al., 2005; Polychronis et al., 2013; Skinner et al.,
2008a, b). Extensively worn UM2 and those revealing homology issues (e.g., presence of
Carabelli's trait or a Hertwig's epithelial root sheath) were excluded for the EDJ analysis. For
five teeth exhibiting small dentine patches (stages 3 or 4, Molnar, 1971), reconstructions of
the apex of horn tips were made using Avizo 9.0 (VSG) and based on morphology observed
for preserved dentine horns. Using R software (R Development Core Team, 2016) and
packages Morpho (Schlager, 2016), shapes (Dryden, 2016) and scatterplot3d (Ligges and
Mächler, 2003), generalized procrustes analysis (GPA) and principal component analysis
(PCA) were carried out on the matrix of shape coordinates augmented by a column of the
natural logarithm of Centroid Size (LnCS), corresponding to a PCA in form space (Bookstein,
1996; Mitteroecker and Gunz, 2009; Mitteroecker et al., 2004; Rohlf and Slice, 1990).

3. Results

3.1. Outer morphology

Frequencies of non-metric traits are presented in Table 2. For all non-metric traits
considered, no significant differences were found between immature and adult individuals,
neither between the Upper Paleolithic, the Mesolithic and the Neolithic periods. The
metacone is always well-developed for the UM2 dated from the Middle Magdalenian to the
Late Mesolithic. The frequency of the metacone decreases with the Early Neolithic (Table 2),

190 revealing a lower expression of this cusp. For the hypocone, no clear trends were found when
191 we considered the sample by different chronocultures. When we combined the samples by
192 periods, an increase of the frequencies is shown for the hypocone, with 60.00% of presence
193 for the Upper Paleolithic, 66.67% for the Mesolithic and 82.93% for the Neolithic. This signal
194 reveals a high expression of the hypocone for Neolithic individuals. The metaconule also
195 exhibits various frequencies and is the most common in the Middle Neolithic molars, if the
196 only Late Mesolithic UM2 is put aside. The parastyle and Carabelli's trait are absent from the
197 whole sample (except the parastyle for one Early Neolithic molar). Indeed, their recorded
198 degrees of expression were too small to be considered as present. As a whole, even if no
199 significant differences were found between periods, the results of the study of non-metric
200 traits show a decrease in the frequencies of the metacone development combined with an
201 increase of the hypocone development from the Middle Magdalenian to the Neolithic, with
202 main differences observed between the Mesolithic and the Neolithic.

3.2. Inner morphology

Enamel thickness. Values of 2D and 3D average (AET) and relative (RET) enamel thickness are presented for each chronoculture in Table 3. On the whole sample, all the values are significantly higher for immature individuals compared to adult ones. However, this is directly linked to the more pronounced degrees of occlusal wear for adults, and the immature/adult ratios are comparable between periods ($\chi^2=2.447$; $df=2$; $p=0.294$). No significant differences were found between the considered periods, except for the RET2D which is significantly lower for Early Mesolithic molars than for Early Neolithic ones ($p=0.036$). A high range of variation is shown for the Middle Neolithic UM2s, which corresponds to the larger sample ($N=30$). The Middle Magdalenian tooth shows thick enamel, both in 2D and in 3D, and is situated in the high range of variation measured for the Neolithic molars. The 2D values of the Upper Magdalenian tooth are higher than the mean observed for Mesolithic and Neolithic samples (Table 3). On average, the Mesolithic teeth exhibit the thinnest enamel, and all the indices show an increase of enamel thickness from Early Mesolithic to Middle Neolithic.

When considering the distribution of enamel thickness on the whole crown for unworn UM2s, thicker enamel is found on the lingual cusps for all the specimens whatever their chronocultural context is (Fig. 2). The distribution is more homogeneous for the Upper Paleolithic and the Early Mesolithic teeth, while for the Neolithic, the enamel is particularly

224 thicker on the hypocone. Indeed, the heterogeneity of enamel thickness between buccal and
225 lingual cusps is accentuated for both Early and Middle Neolithic unworn UM2s.

226 Profiles of topographical variation of enamel thickness on the mesial sections show less
227 variability on the buccal side (Fig. 3, top) than on the lingual one (Fig. 3, bottom). The Upper
228 Paleolithic tooth exhibits the same pattern of thick enamel on both lingual and buccal aspects.
229 Enamel thicknesses are generally similar between Early Mesolithic and Neolithic UM2s on
230 the buccal side, while for the lingual side, the Neolithic molars have thicker enamel than
231 Mesolithic one. Indeed, the heterogeneity between lingual and buccal sides is pronounced for
232 the Neolithic teeth, and particularly for the Middle Neolithic UM2s.

233 Enamel-dentine junction shape. The EDJ shape has been assessed for 34 UM2 dated
234 from the Middle Magdalenian (La Marche), the Early Mesolithic (La Vergne and Les Perrats),
235 the Early Neolithic (Germignac, Les Bréguières) and the Middle Neolithic (Gurgy, Auneau,
236 La Lède du Gurg, Mykolas). The results of the PCA on form space (Fig. 4) show that the first
237 component (PC1) captures overall size variation as well as size-related shape variation
238 (allometry), whereas the other components (PC2 and PC3) contain residual, non-allometric,
239 shape variation. Along PC1 axis (which represents 29.51% of the overall variation), the
240 negative values correspond to a large EDJ with an important height of dentine horns, while
241 the positive values represent EDJ with a small size and a low height of dentine horns. Along
242 PC2 axis (15.87% of overall variation), the positive values show EDJ with high dentine horns
243 associated with large secondary basin, EDJ with low dentine horn tips and small secondary
244 basin are found in PC2 negative values. Along PC3 axis (12.50% of overall variation), the
245 negative values correspond to EDJ with an important height between cervical line and dentine
246 horn tips, while positive values for PC3 represent low height of EDJ associated to a
247 mesiodistal strengthening. A high variability is shown for the size and shape of EDJ, and
248 particularly for the Middle Neolithic molars (Fig. 4). The Upper Magdalenian and the Early
249 Mesolithic UM2s show relatively bigger EDJ with small dentine horn tips. As shown for
250 outer morphology on the larger sample, they exhibit lower development of the distolingual
251 horn tip. Even if there is no clear separation between the periods from this small EDJ sample
252 size, the oldest molars present an EDJ with the lowest development of dentin horns, and
253 particularly those corresponding to the hypocone.

254 255 **4. Discussion and conclusions**

257 The Late Pleistocene and Early Holocene periods were marked by major environmental,
1 258 cultural and biological changes (e.g., Brace, 1962, 1967; Greene et al., 1967; Langlais et al.,
2 3 259 2012; Marchand and Perrin, 2015; Pinhasi and Stock, 2011). A size reduction and a
4 5 260 morphological simplification of the teeth have been observed for these periods, and mainly
6 7 261 linked with cultural and dietary changes associated with the transition to agriculture (Brace,
8 9 262 1962; Brace et al., 1987; Calcagno, 1986; Frayer, 1977; Greene et al., 1967; Jolly, 1970;
10 263 Macchiarelli and Bondioli, 1986). Based on outer structures only, these dental modifications
11 12 264 have not been assessed for the inner structures neither from a whole crown perspective.

14 265 The crown morphology is determined by a morphodynamic interaction between
15 16 266 developmental genes and cusp morphogenesis (for a review, see Paul et al., 2016). The
17 18 267 patterning cascade model (Jernvall, 2000) predicts the future cusp number, size and shape,
19 20 268 and tooth sizes along the row, and minor changes during the developmental trajectory can
21 22 269 alter these features (Evans et al., 2016; Jernvall, 2000; Salazar-Ciudad and Jernvall, 2002).

23 270 Non-metric dental traits are under multiple controls, influenced by genetic, epigenetic and
24 25 271 environmental factors (overview in Hughes and Townsend, 2013; Townsend et al., 2012).
26 27 272 While the expression of the dental traits shows a high variability in modern humans (e.g.,
28 29 273 Hanihara et al., 2003; Irish, 1997; Scott and Turner, 1997), they are reliable markers for
30 31 274 estimate biological relationships between populations and kinship (Coppa et al., 2007;
32 33 275 Crubézy and Sellier, 1990a, b; Delgado-Burbano, 2007; Desideri, 2003; Irish, 1997, 2006,
34 35 276 2014; Turner, 1987; Ullinger et al., 2005).

36 277 Besides its relevance to discuss phylogenetic and taxonomic affinities, the inner tooth
37 38 278 structure, and particularly enamel thickness, has been of considerable interest to study dietary
39 40 279 regime and tooth function (Beynon and Wood, 1986; Lucas et al., 2008a, b; Martin, 1985;
41 42 280 Molnar and Gantt, 1977; Schwartz, 2000). It has been shown that the thickness of enamel is
43 44 281 selectively responsive to functionally-related dietary changes and occlusal wear (Hlusko et al.,
45 46 282 2004; Horvath et al., 2014; Kelley and Swanson, 2008; Le Luyer et al., 2014; Pampush et al.,
47 48 283 2013), and that, in hominoids, a thick enamel is a homoplastic trait (Horvath et al., 2014;
49 284 Pampush et al., 2013). Thus, the occlusal topographic features (grooves, crest, cusp
50 51 285 sharpness) might be more relevant than enamel thickness only to discuss biomechanical
52 53 286 implications (Benazzi et al., 2013; Berthaume, 2014).

54 287 Studies on EDJ have shown that, while differences in dentine horn height, crown height,
55 56 288 as well as in cervix shape, are more important between adjacent molars of the same taxon than
57 58 289 for the same molar between taxa (Skinner et al., 2008a), its morphology successfully
59 60 290 discriminate taxonomic and phylogenetic relationships (e.g., Bailey et al., 2011; Olejniczak et

291 al., 2007; Skinner et al., 2008a, b, 2009a, b). Recently explored at a microevolutionary scale
1 292 in a Middle Neolithic sample (Le Luyer et al., 2016), the EDJ shape has been suggesting as a
2 293 reliable proxy to track individuals sharing similar cultural and burial practices.

3 294 In this study, even though it should be noted that our results could be affected by a bias
4 295 due to a small sample, particularly for the inner structure, and the heterogeneity of the sample
5 296 size between the periods, the upper molars from Late Pleistocene to Early Holocene human
6 297 individuals tend to show a reduction of the metacone combined with a more developed
7 298 hypocone, and even if no statistically significant difference has been found, this tendency is
8 299 particularly marked since the beginning of the Neolithic. Even if an overlap is shown for the
9 300 samples from all the periods, the EDJ morphology shows an increase of the height of the
10 301 dentine horn tips from Magdalenian to Middle Neolithic, and particularly for those
11 302 corresponding to the hypocone cusp. Thus, this EDJ signal is consistent with the data we
12 303 obtained from the study of non-metric variations on a larger sample, and allow to quantify
13 304 these morphological changes. Average and relative enamel thicknesses have been found to be
14 305 higher in Upper Paleolithic teeth and smaller in Early Mesolithic teeth, then increasing from
15 306 Mesolithic to Middle Neolithic individuals. Whatever period is considered, systematically,
16 307 enamel thickness distribution is asymmetric between the functional and the non-functional
17 308 cusps of the UM2s, with thicker enamel on the lingual cusps. While the distribution of enamel
18 309 is more homogeneous for the Upper Paleolithic and the Mesolithic teeth in our sample, it is
19 310 noteworthy that the Neolithic individuals show an increase of the heterogeneity of enamel
20 311 thickness distribution.

21 312 Major changes in outer and inner structural morphology from Late Pleistocene to Early
22 313 Holocene human individuals are found for the functional cusps (e.g., Kay and Hiiemae, 1974;
23 314 Macho and Berner, 1994), and particularly the hypocone. These results are consistent with
24 315 previous studies showing that mesial cusps of upper molars are more stable in modern human
25 316 populations (Macho and Moggi-Cecchi, 1992) while distal cusps are more plastic to
26 317 environmental stress (e.g., Riga et al., 2014; Scott and Turner, 1997). According to the
27 318 patterning cascade model of development (Salazar-Ciudad and Jernvall, 2002), initial
28 319 differences (even small) during development will have cumulative effects on the later-forming
29 320 cusps, reducing or deleted them (Jernvall and Jung, 2000; Paul et al., 2016; Skinner and Gunz,
30 321 2010). However, the complete or near-complete loss of the hypocone (three-cusped UM2s)
31 322 occurs in relatively low frequencies (0-33.7%) in all recent human populations (Scott and
32 323 Turner, 1997; Irish, 2016). The study of Bailey (2000) reported the lowest hypocone
33 324 frequency for Upper Paleolithic Central European specimens. While no complete loss of the

325 hypocone was found in later fossil Homo, Bailey and Hublin (2013) observed four Upper
326 Paleolithic UM2s with a hypocone reduced to the point of a small cusplule. This is consistent
327 with the results of our study of the Magdalenian specimens at outer and inner levels.

328 Considering enamel thickness, our Late Pleistocene/Early Holocene specimens show
329 substantial differences with the mean enamel thicknesses reported for 46 extant humans
330 (African, Asian, European, and Northern Americans) that range from 1.27 mm to 1.40 mm for
331 AET2D, and from 20.00 to 21.64 for RET2D (Grine, 2005; Kono, 2004; Smith et al., 2012;
332 Olejniczak et al., 2008a, b). Notably, the Magdalenian specimens exhibit thicker enamel
333 while the Mesolithic individuals have particularly thinner enamel compared to the extant
334 human conditions. The increase of the heterogeneity in its distribution, combined with higher
335 EDJ horn tips for the thickest cusps, could reveal differences in masticatory biomechanical
336 constraints. Indeed, significant functional links have been found between enamel thickness,
337 tooth form and diet (Lucas et al., 2008a, b; Mahoney, 2013; Molnar and Gantt, 1977; Molnar
338 and Ward, 1977; Schwartz, 2000). Also, thick enamel exhibited on the lingual cusps could be
339 an adaptation to increase resistance and attritional longevity in response to abrasive diet (Le
340 Luyer et al., 2014; Lucas et al., 2008b). This suggestion is strengthened by the occlusal wear
341 differences that have been reported between these populations (Le Luyer, 2016): while Upper
342 Paleolithic and Mesolithic individuals show a flatter wear associated with a homogenous
343 distribution of the enamel thickness, the Neolithic molars present an oblique wear direction
344 combined with a heterogeneous enamel thickness distribution (see also Le Luyer et al., 2014).
345 This ubiquitous oblique wear direction has been linked to more refined and grinded foodstuffs
346 with a more abrasive impact (Brace, 1962; Greene et al., 1967; Smith, 1984). Thus, the outer
347 and inner dental modifications that we observed between these Late Pleistocene and Early
348 Holocene populations are probably primarily linked with the functional constraints of the
349 mastication of different dietary items, as major changes in subsistence strategies occurred
350 between these periods (Bonsall et al., 2004, 2009; Drucker and Henry-Gambier, 2005;
351 Richards et al., 2003; Schulting and Richards, 2001).

352 Even if environmental and/or developmental aspects may have played a role in the
353 morphological changes observed in these Late Pleistocene and Early Holocene human molars,
354 we suggest that the development of the hypocone combined with a reinforcement of its
355 enamel thickness is a functionally-related adaptive modification, linked to dietary changes
356 associated with the transition to agriculture. Furthermore, considering recent study combining
357 outer and inner crown assessment on a larger sample of both deciduous and permanent teeth
358 (Le Luyer, 2016), discontinuities found between Late Pleistocene and Early Holocene human

359 groups suggest that environmentally-driven modifications beginning at the Holocene had a
360 major impact on dental size reduction, while Neolithic cultural changes had mostly affected
361 enamel distribution (Le Luyer, 2016). Explanatory models proposed and discussed so far do
362 not explain all the inner modifications, but some models can help to interpret some
363 differences. Thus, a reappraisal in a whole crown perspective is needed for the interpretation
364 of the time-related trend of dental structural reduction. Further studies on a larger sample will
365 track the underlying factors and the microevolutionary mechanisms having affected dental
366 evolution, notably across the key-period of the Pleistocene-Holocene transition.

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382 383 **References**

- 384
385 Bailey, S.E., 2000. Dental morphological affinities among late Pleistocene and recent
386 humans. *Dent. Anthropol.* 14, 1-8.
387 Bailey, S.E., Hublin, J.-J., 2013. What does it mean to be dentally "modern"? In: Scott, G.R.,
388 Irish, J.D. (Eds.), *Anthropological Perspectives on Tooth Morphology: Genetics,
389 Evolution, Variation*. Cambridge University Press, Cambridge, pp. 222-249.
390 Bailey, S.E., Skinner, M.M., Hublin, J.-J., 2011. What lies beneath? An evaluation of lower
391 molar trigonid crest patterns based on both dentine and enamel expression. *Am. J. Phys.
392 Anthropol.* 145, 505-518.

- 393 Barral, L., 1958. Contribution à la connaissance des populations néo-énéolithiques de Basse-
 1 394 Provence. L'homme cardial de Castellar, abri Pendimoun (A.-M.). Bull. Musée
 2 395 Anthropol. Préhist. Monaco 5, 135-164.
- 3 396 Barshay-Szmidt, C., Costamagno, S., Henry-Gambier, D., Laroulandie, V., Pétilion, J.-M.,
 4 397 Boudadi-Maligne, M., Kuntz, D., Langlais, M., Mallye, J.-B., 2016. New extensive
 5 398 focused AMS ¹⁴C dating of the Middle and Upper Magdalenian of the western
 6 399 Aquitaine/Pyrenean region of France (ca. 19-14 ka cal BP): Proposing a new model for
 7 400 its chronological phases and for the timing of occupation. *Quat. Int.* 414, 62-91.
- 8 401 Bayle, P., Braga, J., Mazurier, A., Macchiarelli, R., 2009. Brief communication. High-
 9 402 resolution assessment of the dental developmental pattern and characterization of tooth
 10 403 tissue proportions in the late Upper Paleolithic child from La Madeleine, France. *Am. J.*
 11 404 *Phys. Anthropol.* 138, 493-498.
- 12 405 Bayle, P., Macchiarelli, R., Trinkaus, E., Duarte, C., Mazurier, A., Zilhão, J., 2010. Dental
 13 406 maturational sequence and dental tissue proportions in the early Upper Paleolithic child
 14 407 from Abrigo do Lagar Velho, Portugal. *Proc. Natl. Acad. Sci. USA* 107, 1338-1342.
- 15 408 Benazzi, S., Nguyer, H.N., Kullmer, O., Hublin, J.J., 2013. Unravelling the functional
 16 409 biomechanics of dental features and tooth wear. *PLoS ONE* 8, e69990 (doi:
 17 410 10.1371/journal.pone.0069990).
- 18 411 Berthaume, M.A., 2014. Tooth cusp sharpness as a dietary correlate in great apes. *Am. J.*
 19 412 *Phys. Anthropol.* 153, 226-235.
- 20 413 Beynon, A.D., Wood, B., 1986. Variations in enamel thickness and structure in East African
 21 414 hominids. *Am. J. Phys. Anthropol.* 70, 177-193.
- 22 415 Binder, D., Sénépart, I., 2010. La séquence de l'Impresso-Cardial de l'abri Pendimoun et
 23 416 l'évolution des assemblages céramiques en Provence. In: Manen, C., Convertini, F.,
 24 417 Binder, D., Sénépart, I. (Eds.), *Premières Sociétés Paysannes de Méditerranée*
 25 418 *Occidentale: Structure des Productions Céramiques*. Société Préhistorique Française,
 26 419 *Mémoire 51 Paris*, pp. 149-167.
- 27 420 Blanchard, J., 1934. Une nouvelle lampe paléolithique (Saint-Cirq-Madelon). *Bull. Soc.*
 28 421 *Préhist. Fr.* 31, 515.
- 29 422 Bonsall, C., Cook, G., Hedges, R.E.M., Higham, T., Pickard, C., Radovanovic, I., 2004.
 30 423 Radiocarbon and stable isotope evidence of dietary change from the Mesolithic to the
 31 424 Middle Ages in the Iron Gates: new results from Lepenski Vir. *Radiocarb.* 46, 293-300.
- 32 425 Bonsall, C., Cook, G., Pickard, C., McSweeney, K., Bartosiewicz, L., 2009. Dietary trends at
 33 426 the Mesolithic-Neolithic transition in North-West Europe. In: Crombé, P., Van

- 427 Strydonck, M., Sergant, J., Boudin, M., Bats, M. (Eds.), *Chronology and Evolution*
1 428 *within the Mesolithic of North-West Europe. Proc. Int. Meet., Brussels, May 30th-June*
2
3 429 *1st 2007. Cambridge Scholars Publishing, Cambridge, pp. 517-539.*
4
- 5 430 Bookstein, F.L., 1996. Combining the tools of geometric morphometrics. In: Marcus, F.,
6
7 431 Corti, M., Loy, A., Naylor, G.J.P., Slice, D.E. (Eds.), *Advances in Morphometrics.*
8
9 432 *Plenum Press, New York, pp. 131-151.*
- 10 433 Boulestin, B., 1999. *Approche taphonomique des restes humains. Le cas des mésolithiques de*
11
12 434 *la grotte des Perrats et le problème du cannibalisme en Préhistoire récente européenne.*
13
14 435 *Publishers of British Archaeological Reports, Oxford, 276 p.*
15
- 16 436 Brace, C.L., 1962. Cultural factors in the evolution of the human dentition. In: Montagu,
17
18 437 M.F.A. (Ed.), *Culture and the Evolution of Man. Oxford University Press, New York,*
19
20 438 *pp. 343-354.*
- 21 439 Brace, C.L., 1963. Structural reduction in evolution. *Amer. Nat.* 97, 39-49.
- 22 440 Brace, C.L., 1967. Environment, tooth form and size in the Pleistocene. *J. Dent. Res.* 46, 809-
23
24 441 816.
25
- 26 442 Brace, C.L., Rosenberg, K.R., Hunt, K.D., 1987. Gradual change in human tooth size in the
27
28 443 *Late Pleistocene and Post-Pleistocene. Evolution* 41, 705-720.
- 29 444 Braga, J., Thackeray, J.F., Subsol, G., Kahn, J.L., Maret, D., Treil, J., Beck, A., 2010. The
30
31 445 *enamel-dentine junction in the postcanine dentition of Australopithecus africanus: intra-*
32
33 446 *individual metameric and antimeric variation. J. Anat.* 216, 62-79.
- 34 447 Brun, V., 1867. *Abris et cavernes de Bruniquel. Fouilles paléontologiques de l'âge de pierre.*
35
36 448 *Recueil Acad. Montauban* 1, 329-353.
37
- 38 449 Bruzek, J., 2002. A method for visual determination of sex, using the human hip bone. *Am. J.*
39
40 450 *Phys. Anthropol.* 117, 157-168.
- 41 451 Calcagno, J.M., 1986. Dental reduction in post-Pleistocene Nubia. *Am. J. Phys. Anthropol.*
42
43 452 70, 349-363.
- 44 453 Carter, K., Worthington, S., Smith, T.M., 2014. News and views: Non-metric dental traits and
45
46 454 *hominin phylogeny. J. Hum. Evol.* 69, 123-128.
- 47 455 Célérier, G., Chollet, A., Hanai, A., 1997. Nouvelles observations sur l'évolution de l'Azilien
48
49 456 *dans les gisements de Bois-Ragot (Vienne) et de Pont-d'Ambon (Dordogne). Bull. Soc.*
50
51 457 *Préhist. Fr.* 94, 331-336.
- 52 458 Chancerel, A., Courtaud, P., Bessou, M., Ferrier, C., Pelegrin, J., Plisson, H., Chancerel, G.,
53
54 459 *Servelle, C., Ganne, A., 2011. La grotte Mykolas. Commune du Bugue (Dordogne).*
55
56 460 *Rapport de Fouille Programmée, 57 p.*
57
58
59
60
61
62
63
64
65

- 461 Chancerel, A., Courtaud, P., M'Trengoueni, M., 2007. La grotte du Piale (dite Mykolas).
 1 462 Commune du Bugue (Dordogne). Rapport de Fouille Programmée, 27 p.
 2
 3 463 Coleman, M.N., Colbert, M.W., 2007. Technical note. CT thresholding protocols for taking
 4
 5 464 measurements on three-dimensional models. *Am. J. Phys. Anthropol.* 133, 723-725.
 6
 7 465 Coppa, A., Cucina, A., Lucci, M., Mancinelli, D., Vargiu, R., 2007. Origins and spread of
 8
 9 466 agriculture in Italy: a nonmetric dental analysis. *Am. J. Phys. Anthropol.* 133, 918-930.
 10
 11 467 Coquerelle, M., Bookstein, F.L., Braga, J., Halazonetis, D.J., Weber, G.W., Mitteroecker, P.,
 12
 13 468 2011. Sexual dimorphism of the human mandible and its association with dental
 14
 15 469 development. *Am. J. Phys. Anthropol.* 145, 192-202.
 16
 17 470 Coste, A., Duday, H., Gurtherz, X., Roudil, J.-L., 1987. Les sépultures de la Baume Bourbon
 18
 19 471 à Cabrières (Gard). In: Guilaine, J., Roudil, J.-L., Vernet, J.-L. (Eds.), *Premières*
 20
 21 472 *Communautés Paysannes en Méditerranée Occidentale*. Actes Colloque Internat.,
 22
 23 473 CNRS Editions, Montpellier, pp. 531-535.
 24
 25 474 Courtaud, P., Duday, H., 1995. Découverte d'une nécropole mésolithique à La Vergne
 26
 27 475 (Charente-Maritime). *Bull. Mém. Soc. Anthropol. Paris* 7, 181-184.
 28
 29 476 Crubézy, É., Sellier, P., 1990a. Caractères discrets et "recrutement" des ensembles sépulcraux.
 30
 31 477 *Bull. Mém. Soc. Anthropol. Paris* 2, 171-177.
 32
 33 478 Crubézy, É., Sellier, P., 1990b. Liens de parenté et populations inhumées. *Nouv. Archéol.* 40,
 34
 35 479 35-37.
 36
 37 480 Dean, M.C., Wood, B., 2003. A digital radiographic atlas of great apes skull and dentition. In:
 38
 39 481 Bondioli, L., Macchiarelli, R. (Eds.), *Digital Archives of Human Paleobiology*. ADS
 40
 41 482 Solutions, Milan (CD-ROM).
 42
 43 483 Deffarge, R., 1956. Le gisement du Morin à Pessac-sur-Dordogne. *Rev. Hist. Archéo.*
 44
 45 484 *Libournais* 26, 68-69.
 46
 47 485 Delgado-Burbano, M.E., 2007. Population affinities of African Colombians to Sub-Saharan
 48
 49 486 Africans based on dental morphology. *Homo* 58, 329-356.
 50
 51 487 Desideri, J., 2003. Les traits non métriques dentaires sont-ils de bons indicateurs des distances
 52
 53 488 biologiques entre les populations? In: Besse, M., Stahl, G., Laurence, I., Curdy, P.
 54
 55 489 (Eds.), *Constellation. Hommage à Alain Gallay*. Cahiers Archéol. Romande, Lausanne,
 56
 57 490 pp. 447-462.
 58
 59 491 Drucker, D.G., Henry-Gambier, D., 2005. Determination of the dietary habits of a
 60
 61 492 Magdalenian woman from Saint-Germain-la-Rivière in southwestern France using
 62
 63 493 stable isotopes. *J. Hum. Evol.* 49, 19-35.
 64
 65 494 Dryden, I.L., 2016. *Shapes: Statistical Shape Analysis*. R package version 1.1-13

- 495 (<https://CRAN.R-project.org/package=shapes>).
- 1
2 496 Dubois, J.-P., Duday, H., Villes, A., 1986. Auneau (Eure-et-Loir), “Le parc du château”. Rev.
3
4 497 Archéol. Centre France 25, 102-103.
- 5 498 Duday, H., Courtaud, P., Robin, K., Dujardin, V., Gruet, Y., Gouraud, G., Martin, H., San
6
7 499 Juan-Foucher, C., 1998. La Vergne, La Grande Pièce. (Déviation de Saint-Jean
8
9 500 d'Angély, Charente-Maritime). Bull. Soc. Préhist. Fr. 95, 433-434.
- 10
11 501 Evans, A.R., Daly, E.S., Catlett, K.K., Paul, K.S., King, S.J., Skinner, M.M., Nesse, H.P.,
12
13 502 Hublin, J.-J., Townsend, G.C., Schwartz, G.T., Jernvall, J., 2016. A simple rule governs
14
15 503 the evolution and development of hominin tooth size. Nature 530, 477-480.
- 16 504 Evin, J.-M., Pachiardi, C., 1979. Lyon natural radiocarbon measurements VIII. Radiocarb.
17
18 505 21, 439.
- 19
20 506 Fornai, C., Benazzi, S., Svoboda, J., Pap, I., Harvati, K., Weber, G.W., 2014. Enamel
21
22 507 thickness variation of deciduous first and second upper molars in modern humans and
23
24 508 Neanderthals. J. Hum. Evol. 76, 83-91.
- 25 509 Frayer, D.W., 1977. Metric dental change in the European Upper Paleolithic and Mesolithic.
26
27 510 Am. J. Phys. Anthropol. 46, 109-120.
- 28
29 511 Gaillard, J., Taborin, Y., Gomez de Soto, J., 1984. La tombe néolithique de Germignac. Gallia
30
31 512 Préhist. 27, 97-119.
- 32
33 513 Gambier, D., Valladas, H., Tisnérat-Laborde, N., Arnold, M., Bresson, F., 2000. Datation de
34
35 514 vestiges humains présumés du Paléolithique supérieur par la méthode du Carbone 14 en
36
37 515 spectrométrie de masse par accélérateur. Paleo 12, 201-212.
- 38 516 Garn, S.M., Lewis, A.B., Bonné, B., 1962. Third molar formation and its development course.
39
40 517 Angle Orthodont. 32, 270-279.
- 41
42 518 Gomez de Soto, J., Boulestin, B., 1996. La grotte des Perrats à Agris (Charente): 1981-1994,
43
44 519 étude préliminaire. Chauvigny: Association Publications Chauvinoises, Dossier du Pays
45
46 520 Chauvinois 4, 139 p.
- 47 521 Greene, D.L., Ewing, G.H., Armelagos, G.J., 1967. Dentition of Mesolithic population from
48
49 522 Wadi Halfa, Sudan. Am. J. Phys. Anthropol. 27, 41-56.
- 50
51 523 Grine, F.E., 2005. Enamel thickness of deciduous and permanent molars in modern Homo
52
53 524 sapiens. Am. J. Phys. Anthropol. 126, 14-31.
- 54
55 525 Gunz, P., Mitteroecker, P., 2013. Semilandmarks: a method for quantifying curves and
56
57 526 surfaces. Hystrix 24, 103-109.
- 58 527 Gunz, P., Mitteroecker, P., Bookstein, F., 2005. Semilandmarks in three dimensions. In: Slice,
59
60 528 D.E. (Ed.), Modern Morphometrics in Physical Anthropology. Kluwer Academic-

529 Plenum, New York, pp. 73-98.

- 1
2 530 Guy, F., Lazzari, V., Gilissen, E., Thiery, G., 2015. To what extent is primate second molar
3 531 enamel occlusal morphology shaped by the enamel-dentine junction? PLoS ONE 10,
4 e0138802 (doi: 10.1371/journal.pone.0138802).
5 532
6
7 533 Hanihara, T., Ishida, H., Dodo, Y., 2003. Characterization of biological diversity through
8 analysis of discrete cranial traits. *Am. J. Phys. Anthropol.* 121, 241-251.
9 534
10
11 535 Hedges, R.E.M., Pettitt, P.B., Bronk Ramsey, C., van Klinken, G.J., 1997. Radiocarbon dates
12 from the Oxford AMS system: Archaeometry datelist 24. *Archaeom.* 39, 445-471.
13 536
14 537 Hlusko, L.J., Suwa, G., Kono, R.T., Mahaney, M.C., 2004. Genetics and the evolution of
15 primate enamel thickness: a baboon model. *Am. J. Phys. Anthropol.* 124, 223-233.
16 538
17
18 539 Horvath, J.E., Ramachandran, G.L., Fedrigo, O., Nielsen, W.J., Babbitt, C.C., St Clair, E.M.,
19 540 Pfefferle, L.W., Jernvall, J., Wray, G.A., Wall, C.E., 2014. Genetic comparisons yield
21 insight into the evolution of enamel thickness during human evolution. *J. Hum. Evol.*
22 541 73, 75-87.
23 542
24
25 543 Hughes, T.E., Townsend, G.C., 2013. Twin and family studies of human dental crown
26 morphology: genetic, epigenetic, and environmental determinants of the modern human
27 544 dentition. In: Scott, G.R., Irish, J.D. (Eds.), *Anthropological Perspectives on Tooth*
28 545 *Morphology: Genetics, Evolution, Variation*. Cambridge University Press, Cambridge,
29 546 pp. 31-68.
30 547
31
32 548 Irish, J.D., 1997. Ancestral dental traits in recent Sub-Saharan Africans and the origins of
33 549 modern humans. *J. Hum. Evol.* 34, 81-98.
34 550
35
36 551 Irish, J.D., 2006. Who were the ancient Egyptians? Dental affinities among Neolithic through
37 552 postdynastic peoples. *Am. J. Phys. Anthropol.* 129, 529-543.
38 553
39
40 554 Irish, J.D., 2014. Questions of Khoesan continuity: Dental affinities among the indigenous
41 555 Holocene peoples of South Africa. *Am. J. Phys. Anthropol.* 155, 33-44.
42 556
43
44 557 Irish, J.D., 2016. Assessing dental nonmetric variation among populations. In; Irish, J.D. and
45 558 Scott, G.R. (Eds.), *A Companion in Dental Anthropology*. Wiley-Blackwell, Chichester,
46 559 pp. 265-286.
47 560
48
49 561 Irish, J.D., Guatelli-Steinberg, D., Legge, S.S., de Ruiter, D.J., Berger, L.R., 2014. News and
50 562 views. Response to 'Non-metric dental traits and hominin phylogeny' by Carter et al.,
51 563 with additional information on the Arizona State University Dental Anthropology
52 564 System and phylogenetic 'place' of *Australopithecus sediba*. *J. Hum. Evol.* 69, 129-134.
53 565
54
55 566 Jernvall, J., 2000. Linking development with the generation of novelty in mammalian teeth.
56 567 *Proc. Natl. Acad. Sci. USA* 97, 2641-2645.
57 568
58
59
60
61
62
63
64
65

- 563 Jernvall, J., Jung, H.-S., 2000. Genotype, phenotype and developmental biology of molar
1 564 tooth characters. *Yearb. Phys. Anthropol.* 43, 171-190.
- 3 565 Jolly, C.J., 1970. The seed-eaters: A new model of hominid differentiation based on a baboon
4 566 analogy. *Man* 5, 5-26.
- 7 567 Jude, P.-É., 1960. *La Grotte de Rochereil, Station Magdalénienne et Azilienne*. Masson et Cie,
8 568 Paris, 76 p.
- 10 569 Kay, R.F., Hiiemae, K.M., 1974. Jaw movement and tooth use in recent and fossil primates.
11 570 *Am. J. Phys. Anthropol.* 40, 227-256.
- 14 571 Kelley, J.L., Swanson, W.J., 2008. Dietary change and adaptive evolution of enamelin in
15 572 humans and among primates. *Genetics* 178, 1595-1603.
- 18 573 Kono, R.T., 2004. Molar enamel thickness and distribution patterns in extant great apes and
19 574 humans: new insights based on a 3-dimensional whole crown perspective. *Anthropol.*
20 575 *Sci.* 112, 121-146.
- 23 576 Korenhof, C.A.W., 1961. The enamel-dentine border: a new morphological factor in the study
24 577 of the (human) molar pattern. In: *Proceeding of the Koninklijke Nederlandse Akademie*
25 578 *van Wetenschappen*, Amsterdam. pp. 639-664.
- 29 579 Kupczik, K., Hublin, J.J., 2010. Mandibular molar root morphology in Neanderthals and Late
30 580 Pleistocene and recent *Homo sapiens*. *J. Hum. Evol.* 59, 525-541.
- 32 581 Lacam, R., Niederlender, A., Vallois, H.-V., 1944. *Le Gisement Mésolithique du Cuzoul de*
33 582 *Gramat*. Masson et Cie, Paris, 92 p.
- 36 583 Langlais, M., Costamagno, S., Laroulandie, V., Pétilion, J.-M., Discamps, E., Mallye, J.-B.,
37 584 Cochard, D., Kuntz, D., 2012. The evolution of Magdalenian societies in South-West
38 585 France between 18,000 and 14,000 calBP: Changing environments, changing tool kits.
39 586 *Quat. Int.* 272-273, 138-149.
- 43 587 Laporte, L., Gomez de Soto, J., 2001. *Germignac et Lamérac: perles discoïdes et anneaux-*
44 588 *disques dans le Centre-Ouest de la France*. *Rev. Archéol. Ouest* 18, 13-26.
- 47 589 Le Luyer, M., 2016. *Évolution dentaire dans les populations humaines de la fin du Pléistocène*
48 590 *et du début de l'Holocène (19000-5500 cal. BP): une approche intégrée des structures*
49 591 *externe et interne des couronnes pour le Bassin aquitain et ses marges*. PhD dissertation.
50 592 *Université de Bordeaux, Bordeaux*, 456 p.
- 54 593 Le Luyer, M., Rottier, S., Bayle, P., 2014. Brief communication: Comparative patterns of
55 594 enamel thickness topography and oblique molar wear in two Early Neolithic and
56 595 medieval population samples. *Am. J. Phys. Anthropol.* 155, 162-172.
- 59 596 Le Luyer, M., Coquerelle, M., Rottier, S., Bayle, P., 2016. Internal tooth structure and burial
60 61 62 63 64 65

- 597 practices: insights into the Neolithic necropolis of Gurgy (France, 5100-4000 cal. BC).
1 598 PLoS ONE 11, e0159688 (doi: 10.1371/journal.pone.0159688).
2
3 599 Lenoir, M., 1983. Le Paléolithique des Basses Vallées de la Dordogne et de la Garonne. PhD
4
5 600 dissertation. Université Bordeaux 1, Bordeaux, 696 p.
6
7 601 Lepront, R., Mirande, H., 1933. Le gisement de Saint-Germain-la-Rivière (sa découverte).
8
9 602 Rev. Hist. Archéo. Libournais 36, 197-209.
10
11 603 Ligges, U., Mächler, M., 2003. Scatterplot 3d - An R package for visualizing multivariate
12
13 604 data. J. Stat. Softw. 8, 1-20.
14
15 605 Lucas, P.W., Constantino, P.J., Wood, B.A., 2008a. Inferences regarding the diet of extinct
16
17 606 hominins: Structural and functional trends in dental and mandibular morphology within
18
19 607 the hominin clade. J. Anat. 212, 486-500.
20
21 608 Lucas, P.W., Constantino, P.J., Wood, B.A., Lawn, B., 2008b. Dental enamel as a dietary
22
23 609 indicator in mammals. Bioessays 30, 374-385.
24
25 610 Macchiarelli, R., Bayle, P., Bondioli, L., Mazurier, A., Zanolli, C., 2013. From outer to inner
26
27 611 structural morphology in dental anthropology. The integration of the third dimension in
28
29 612 the visualization and quantitative analysis of fossil remains. In: Scott, R.G., Irish, J.D.
30
31 613 (Eds.), Anthropological Perspectives on Tooth Morphology: Genetics, Evolution,
32
33 614 Variation. Cambridge University Press, Cambridge, pp. 250-277.
34
35 615 Macchiarelli, R., Bondioli L., 1986. Post-Pleistocene reductions in human dental structure: A
36
37 616 reappraisal in terms of increasing population density. Hum. Evol. 1, 405-418.
38
39 617 Macchiarelli, R., Bondioli, L., Débénath, A., Mazurier, A., Tournepiche, J.-F., Birch, W.,
40
41 618 Dean, M.C., 2006. How Neanderthal molar teeth grew. Nature 444, 748-751.
42
43 619 Macchiarelli, R., Bondioli, L., Mazurier, A., 2008. Virtual dentitions: Touching the hidden
44
45 620 evidence. In: Irish, J.D., Nelson, G.C. (Eds.), Technique and Application in Dental
46
47 621 Anthropology. Cambridge University Press, Cambridge, pp. 426-448.
48
49 622 Macchiarelli, R., Mazurier, A., Volpato, V., 2007. L'apport des nouvelles technologies à
50
51 623 l'étude des Néandertaliens. In: Vandermeersch, B., Maureille, B. (Eds.), Les
52
53 624 Néandertaliens. Biologie et Cultures. Comité Travaux Historiques Scientifiques, Paris,
54
55 625 pp. 169-179.
56
57 626 Macho, G.A., Berner, M., 1994. Enamel thickness and the helicoidal occlusal plane. Am. J.
58
59 627 Phys. Anthropol. 94, 327-337.
60
61 628 Macho, G.A., Moggi-Cecchi, J., 1992. Reduction of maxillary molars in Homo sapiens
62
63 629 sapiens: A different perspective. Am. J. Phys. Anthropol. 87, 151-159.
64
65 630 Mahoney, P., 2013. Testing functional and morphological interpretations of enamel thickness

- 631 along the deciduous tooth row in human children. *Am. J. Phys. Anthropol.* 151, 518-
632 525.
- 633 Marchand, G., Perrin, T., 2015. Why this revolution? Explaining the major technical shift in
634 Southwestern Europe during the 7th millennium cal. BC. *Quat. Int.*, in press (doi:
635 <http://dx.doi.org/10.1016/j.quaint.2015.07.059>).
- 636 Martin, L., 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314, 260-
637 263.
- 638 Mitteroecker, P., Gunz, P., 2009. Advances in geometric morphometrics. *Evol. Biol.* 36, 235-
639 247.
- 640 Mitteroecker, P., Gunz, P., Bernhard, M., Schaefer, K., Bookstein, F.L., 2004. Comparison of
641 cranial ontogenetic trajectories among great apes and humans. *J. Hum. Evol.* 46, 679-
642 697.
- 643 Molnar, S., 1971. Human tooth wear, tooth function and cultural variability. *Am. J. Phys.*
644 *Anthropol.* 34, 175-190.
- 645 Molnar, S., Gantt, D.G., 1977. Functional implications of primate enamel thickness. *Am. J.*
646 *Phys. Anthropol.* 46, 447-454.
- 647 Molnar, S., Ward, S.C., 1977. On the hominid masticatory complex: Biomechanical and
648 evolutionary perspectives. *J. Hum. Evol.* 6, 557-568.
- 649 Morita, W., Yano, W., Nagaoka, T., Abe, M., Ohshima, H., Nakatsukasa, M., 2014. Patterns
650 of morphological variation in enamel-dentin junction and outer enamel surface of
651 human molars. *J. Anat.* 224, 669-680.
- 652 Murail, P., Bruzek, J., Houët, F., Cunha, E., 2005. DSP: A tool for probabilistic sex diagnosis
653 using worldwide variability in hip-bone measurements. *Bull. Mém. Soc. Anthropol.*
654 *Paris* 17, 167-176.
- 655 Olejniczak, A.J., Gilbert, C.C., Martin, L.B., Smith, T.M., Ulhaas, L., Grine, F.E., 2007.
656 Morphology of the enamel-dentine junction in sections of anthropoid primate maxillary
657 molars. *J. Hum. Evol.* 53, 292-301.
- 658 Olejniczak, A.J., Smith, T.M., Feeney, R.N., Macchiarelli, R., Mazurier, A., Bondioli, L.,
659 Rosas, A., Fortea, J., de la Rasilla, M., Garcia-Taberner, A., Radovic, J., Skinner,
660 M.M., Toussaint, M., Hublin, J.-J., 2008c. Dental tissue proportions and enamel
661 thickness in Neandertal and modern human molars. *J. Hum. Evol.* 55, 12-23.
- 662 Olejniczak, A.J., Smith, T.M., Skinner, M.M., Grine, F.E., Feeney, R.N., Thackeray, J.F.,
663 Hublin, J.-J., 2008b. Three-dimensional molar enamel distribution and thickness in
664 *Australopithecus* and *Paranthropus*. *Biol. Lett.* 4, 406-410.

- 665 Olejniczak, A.J., Tafforeau, P., Feeney, R.N., Martin, L.B., 2008a. Three-dimensional primate
1 666 molar enamel thickness. *J. Hum. Evol.* 54, 187-195.
- 3 667 Pampush, J.D., Duque, A.C., Burrows, B.R., Daegling, D.J., Kenney, W.F., McGraw, W.S.,
4 668 2013. Homoplasy and thick enamel in primates. *J. Hum. Evol.* 64, 216-224.
- 7 669 Pan, L., Dumoncel, J., de Beer, F., Hoffman, J., Thackeray, J.F., Duployer, B., Tenailleau, C.,
8 670 Braga, J., 2016. Further morphological evidence on South African earliest *Homo* lower
9 671 postcanine dentition: Enamel thickness and enamel dentine junction. *J. Hum. Evol.* 96,
10 672 82-96.
- 14 673 Paul, K.S., Astorino, C.M., Bailey, S.E., 2016. The Patterning Cascade Model and Carabelli's
15 674 trait expression in metameres of the mixed human dentition: Exploring a morphogenetic
16 675 model. *Am. J. Phys. Anthropol.*, in press (doi: 10.1002/ajpa.23080).
- 20 676 Paul, K.S., Stojanowski, C.M., 2015. Performance analysis of deciduous morphology for
21 677 detecting biological siblings. *Am. J. Phys. Anthropol.* 157, 615-629.
- 23 678 Péquart, M., Péquart, S.-J., 1929. La nécropole mésolithique de Tévéc (Morbihan).
24 679 *L'Anthropol.* 39, 373-400.
- 27 680 Périscard, L., Lwoff, S., 1940. La Marche, commune de Lussac-les-Châteaux (Vienne):
28 681 premier atelier de Magdalénien III à dalles gravées mobiles (campagnes de fouilles
29 682 1937-1938). *Bull. Soc. Préhist. Fr.* 37, 155-180.
- 32 683 Pinhasi, R., Meiklejohn, C., 2011. Dental reduction and the transition to agriculture in
34 684 Europe. In: Pinhasi, R., Stock, J.T. (Eds.), *Human Bioarchaeology of the Transition to*
35 685 *Agriculture*. John Wiley & Sons, Chichester, pp. 421-474.
- 38 686 Pinhasi, R., Stock, J.T., 2011. *Human Bioarchaeology of the Transition to Agriculture*. John
39 687 Wiley & Sons, Chichester, 484 p.
- 41 688 Polychronis, G., Christou, P., Mavragani, M., Halazonetis, D.J., 2013. Geometric
42 689 morphometric 3D shape analysis and covariation of human mandibular and maxillary
43 690 first molars. *Am. J. Phys. Anthropol.* 152, 186-196.
- 47 691 Provost, S., 2013. La galerie sépulcrale des Bréguières (Mougins, Alpes-Maritimes):
48 692 paramètres quantitatifs et fonctionnement d'une sépulture collective entre le VI^e et le Ve
49 693 millénaire avant J.-C. Mémoire Master 2, Université de Bordeaux, Bordeaux, 70 p.
- 52 694 Provost, S., Binder, D., Castex, D., Delhon, C., Duday, H., Durrenmath, G., Gentile, I.,
53 695 Goude, G., Gourichon, L., Vuillien, M., Zémour A., 2014. Contribution 11 : Mougins-
54 696 Bréguières (Alpes-Maritimes): une sépulture collective à la transition des 6^{ème} et 5^{ème}
55 697 millénaires cal BCE. In: Collectif, *Projet collectif de recherche ETICALP « Évolutions,*
56 698 *transferts, Interculturalités dans l'arc liguro-provençal: Matières premières, productions,*
57 699

- 699 usages, du Paléolithique supérieur à l'âge du Bronze ancien », Rapport 2014, Service
1 régional de l'Archéologie Provence-Alpes-Côte d'Azur, pp. 197-212.
2
- 3 701 R Development Core Team, 2016. R: A Language and Environment for Statistical
4 Computing. R Foundation for Statistical Computing, Vienna, Austria.
5
- 6 702
7 703 Richards, M.P., Schulting, R.J., Hedges, R.E.M., 2003. Sharp shift in diet at onset of
8 Neolithic. *Nature* 425, 365-366.
9
- 10 704
11 705 Riga, A., Belcastro, M.G., Moggi-Cecchi, J., 2014. Environmental stress increases variability
12 in the expression of dental cusps. *Am. J. Phys. Anthropol.* 153, 397-407.
13
- 14 706
15 707 Rivollat, M., Mendisco, F., Pemonge, M.-H., Safi, A., Saint-Marc, D., Bremond, A., Couture-
16 Veschambre, C., Rottier, S., Deguilloux, M.-F., 2015. When the waves of European
17 neolithization met: First paleogenetic evidence from early farmers in the southern Paris
18 Basin. *PLoS ONE* 10, e0125521 (doi: 10.1371/journal.pone.0125521).
19
- 20 710
21 711 Rohlf, F.J., Slice, D.E., 1990. Extensions of the Procrustes method for the optimal
22 superimposition of landmarks. *Syst. Biol.* 39, 40-59.
23
- 24 712
25 713 Rottier, S., Mordant, C., Chambon, P., Thevenet, C., 2005. Découverte de plus d'une centaine
26 de sépultures du Néolithique moyen à Gurgy, les Noisats (Yonne). *Bull. Soc. Préhist.*
27 *Fr.* 102, 641-645.
28
- 29 714
30 715
31 716 Roussot-Larroque, J., 1977. Néolithisation et Néolithique ancien d'Aquitaine. *Bull. Soc.*
32 *Préhist. Fr.* 74, 559-582.
33
- 34 717
35 718 Salazar-Ciudad, I., Jernvall, J., 2002. A gene network model accounting for development and
36 evolution of mammalian teeth. *Proc. Natl. Acad. Sci. USA* 99, 8116-8120.
37
- 38 719
39 720 Schlager, S., 2016. Morpho: Calculations and Visualisations Related to Geometric
40 Morphometrics. R package version 2.4.1.1. ([https://CRAN.R-](https://CRAN.R-project.org/package=Morpho)
41 [project.org/package=Morpho](https://CRAN.R-project.org/package=Morpho)).
42
- 43 721
44 722 Schulting, R.J., Richards, M.P., 2001. Dating women and becoming farmers: New
45 palaeodietary and AMS dating evidence from the Breton Mesolithic cemeteries of
46 Tévéc and Hoëdic. *J. Anthropol. Archaeol.* 20, 314-344.
47
- 48 723
49 724
50 725 Schwartz, G.T., 2000. Taxonomic and functional aspects of the patterning of enamel
51 thickness distribution in extant large-bodied hominoids. *Am. J. Phys. Anthropol.* 111,
52 211-244.
53
- 54 726
55 727
56 728 Scott, G.R., Turner, C.G., 1997. *The Anthropology of Modern Human Teeth. Dental*
57 *Morphology and its Variation in Recent Human Populations.* Cambridge University
58 Press, Cambridge, 382 p.
59
- 60 729
61 730
62 731
63 732 Skinner, M., 2008. Enamel-Dentine Junction Morphology of Extant Hominoid and Fossil
64
65

- 733 Hominin Lower Molars. PhD dissertation. George Washington University, Washington,
1 734 202 p.
2
- 3 735 Skinner, M.M., Alemseged, Z., Gaunitz, C., Hublin, J.J., 2015. Enamel thickness trends in
4
5 736 Plio-Pleistocene hominin mandibular molars. *J. Hum. Evol.* 85, 35-45.
6
- 7 737 Skinner, M.M., Evans, A., Smith, T., Jernvall, J., Tafforeau, P., Kupczik, K., Olejniczak, A.J.,
8
9 738 Rosas, A., Radovicic, J., Thackeray, J.F., Toussaint, M., Hublin, J.J., 2010. Brief
10
11 739 communication. Contributions of enamel-dentine junction shape and enamel deposition
12
13 740 to primate molar crown complexity. *Am. J. Phys. Anthropol.* 142, 157-163.
- 14 741 Skinner, M.M., Gunz, P., 2010. The presence of accessory cusps in chimpanzee lower molars
15
16 742 is consistent with a patterning cascade model of development. *J. Anat.* 217, 245-253.
17
- 18 743 Skinner, M.M., Gunz, P., Wood, B.A., Hublin, J.J., 2008a. Enamel-dentine junction (EDJ)
19
20 744 morphology distinguishes the lower molars of *Australopithecus africanus* and
21
22 745 *Paranthropus robustus*. *J. Hum. Evol.* 55, 979-988.
- 23 746 Skinner, M.M., Gunz, P., Wood, B.A., Hublin, J.-J., 2009a. How many landmarks? Assessing
24
25 747 the classification accuracy of Pan lower molars using a geometric morphometric
26
27 748 analysis of the occlusal basin as seen at the enamel-dentine junction. *Front. Oral Biol.*
28
29 749 13, 23-29.
30
- 31 750 Skinner, M.M., Gunz, P., Wood, B.A., Boesch, C., Hublin, J.J., 2009b. Discrimination of
32
33 751 extant Pan species and subspecies using the enamel-dentine junction morphology of
34
35 752 lower molars. *Am. J. Phys. Anthropol.* 140, 234-243.
- 36 753 Skinner, M.M., Wood, B.A., Boesch, C., Olejniczak, A.J., Rosas, A., Smith, T.M., Hublin,
37
38 754 J.J., 2008b. Dental trait expression at the enamel-dentine junction of lower molars in
39
40 755 extant and fossil hominoids. *J. Hum. Evol.* 54, 173-186.
- 41
42 756 Smith, B.H., 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J.*
43
44 757 *Phys. Anthropol.* 63, 39-56.
- 45 758 Smith, T.M., Olejniczak, A.J., Martin, L.B., Reid, D.J., 2005. Variation in hominoid molar
46
47 759 enamel thickness. *J. Hum. Evol.* 48, 575-592.
- 48
49 760 Smith, T.M., Olejniczak, A.J., Zermeno, J.P., Tafforeau, P., Skinner, M.M., Hoffmann, A.,
50
51 761 Radovicic, J., Toussaint, M., Kruszynski, R., Menter, C., Moggi-Cecchi, J., Glasmacher,
52
53 762 U.A., Kullmer, O., Schrenk, F., Stringer, C., Hublin, J.-J., 2012. Variation in enamel
54
55 763 thickness within the genus *Homo*. *J. Hum. Evol.* 62, 395-411.
- 56 764 Sofaer, J.A., Bailit, H.L., MacLean, C.J., 1971. A developmental basis for differential tooth
57
58 765 reduction during hominid evolution. *Evolution* 25, 509-517.
59
- 60 766 Spoor, F., Zonneveld, F., Macho, G.A., 1993. Linear measurements of cortical bone and
61
62
63
64
65

- 767 dental enamel by computed tomography: Applications and problems. *Am. J. Phys.*
1 768 *Anthropol.* 91, 469-484.
- 3 769 Townsend, G., Bockmann, M., Hughes, T., Brook, A., 2012. Genetic, environmental and
4 770 epigenetic influences on variation in human tooth number, size and shape. *Odontology*
5 771 100, 1-9.
- 7 772 Turner, C.G., 1987. Late Pleistocene and Holocene population history of East Asia based on
8 773 dental variation. *Am. J. Phys. Anthropol.* 73, 305-321.
- 10 774 Turner, C.G., Nichol, C.R., Scott, G.R., 1991. Scoring procedures for key morphological
11 775 traits of the permanent dentition: The Arizona State University Dental Anthropology
12 776 System. In: Kelly, M., Larsen, C.S. (Eds.), *Advances in Dental Anthropology*. Wiley-
13 777 Liss, Inc., New-York, pp. 13-31.
- 15 778 Turner, C.G., Scott, G.R., 1977. Dentition of Easter Islanders. In: Dahlberg, A.A., Graber,
16 779 T.M. (Eds.), *Orofacial Growth and Development*. Mouton Publishers, The Hague, pp.
17 780 229-249.
- 19 781 Ullinger, J.M., Sheridan, S.G., Hawkey, D.E., Turner, C.G., Cooley, R., 2005.
20 782 Bioarchaeological analysis of cultural transition in the southern Levant using dental
21 783 nonmetric traits. *Am. J. Phys. Anthropol.* 128, 466-476.
- 23 784 Valdeyron, N., 2014. Le Mésolithique, une révolution verte au coeur de l'Europe des forêts?
24 785 Éléments pour une amorce de réflexion. In: Henry, A., Marquebielle, B., Chesnaux, L.,
25 786 Michel, S. (Eds.), *Des Techniques aux Territoires: Nouveaux Regards sur les Cultures*
26 787 *Mésolithiques*. Maison de la Recherche, Toulouse. *P@lethnology* 6, 84-88.
- 28 788 Verjux, C., 1999. Chronologie des rites funéraires mésolithiques à Auneau (Eure-et-Loir,
29 789 France). In: Bintz, P. (Ed.), *L'Europe des Derniers Chasseurs: Épipaléolithique et*
30 790 *Mésolithique*. Actes du 5e Colloque Internat. UISPP, Grenoble, pp. 293-202.
- 32 791 Vilain, R., 1961. Culoz (Ain): un gisement mésolithique avec sépulture dans le Bugey (notes
33 792 préliminaires). *Bull. Soc. Préhisto. Fr.* 58, 540-461.
- 35 793 Wolpoff, M.H., 1971. *Metric Trends in Hominid Dental Evolution*. Press of Case Western
36 794 Reserve University, Cleveland, 244 p.
- 38 795 Zanolli, C., 2014. Molar crown inner structural organization in Javanese *Homo erectus*. *Am.*
39 796 *J. Phys. Anthropol.* 156, 148-157.
- 41 797 Zanolli, C., Bayle, P., Macchiarelli, R., 2010. Tissue proportions and enamel thickness
42 798 distribution in the early Middle Pleistocene human deciduous molars from Tighenif,
43 799 Algeria. *C.R. Palevol* 9, 341-348.
- 45 800 Zanolli, C., Bondioli, L., Coppa, A., Dean, M.C., Bayle, P., Candilio, F., Capuani, S., Dreossi,

801 D., Fiore, I., Frayer, D.W., Libsekal, Y., Mancini, L., Rook, L., Medin Tekle, T., Tuniz,
1 802 C., Macchiarelli, R., 2014. The late Early Pleistocene human dental remains from Uadi
2 803 Aalad and Mulhuli-Amo (Buia), Eritrean Danakil: Macromorphology and
3
4 804 microstructure. *J. Hum. Evol.* 74, 96-113.
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806 **Captions**

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3 808 **Table 1**

5 809 List of specimens and number of teeth used in this study for outer (N) and inner (μ CT)
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7 810 aspects.

9 811 **Tableau 1**

11 812 Liste des spécimens et nombre de dents utilisées dans cette étude pour les aspects externes
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13 813 (N) et internes (μ CT).

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16 815 **Table 2**

18 816 Results of the study for outer morphology and frequencies of non-metric dental variations.

20 817 **Tableau 2**

22 818 Résultats de l'étude morphologique externe et fréquences des variations non-métriques
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24 819 dentaires.

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27 821 **Table 3**

29 822 Descriptive statistics for 2D and 3D average (AET) and relative (RET) enamel thickness
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31 823 values. sd = standard deviation; min = minimum; max = maximum.

33 824 **Tableau 3**

35 825 Statistiques descriptives pour les valeurs 2D et 3D d'épaisseurs moyenne (AET) et relative
36
37 826 (RET) de l'émail. sd = déviation standard; min = minimum; max = maximum.

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40 828 **Fig. 1.** Map showing the location of the sites studied.

42 829 **Fig. 1.** Carte montrant la localisation des sites étudiés.

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45 831 **Fig. 2.** Comparative cartographies of the distribution of enamel thickness for unworn upper
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47 832 second molars. All teeth are shown as left, in occlusal (O), mesial (M), distal (D), buccal (B)
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49 833 and lingual (L) views. The pseudo-colour scale (in mm), ranging from dark blue (thin enamel)
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51 834 to red (thick enamel), is specific to each tooth (see right).

53 835 **Fig. 2.** Cartographies comparatives de la distribution de l'épaisseur de l'émail pour les
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55 836 secondes molaires supérieures non usées. Toutes les dents sont montrées comme étant des
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57 837 gauches, en vues occlusale (O), mésiale (M), distale (D), buccale (B) et linguale (L).
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59 838 L'échelle colorimétrique (en mm), allant du bleu foncé (émail fin) au rouge (émail épais), est
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61 839 spécifique à chaque dent (voir à droite).

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2 841 **Fig. 3.** Topographical variation of standardized enamel thickness measured on the buccal
3 842 (top) and lingual (bottom) sides of the mesial sections. sd = standard deviation.

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5 843 **Fig. 3.** Variation topographique de l'épaisseur standardisée de l'émail mesurée sur les côtés
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7 844 buccal (en haut) et lingual (en bas) des sections mésiales. sd = déviation standard.

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11 846 **Fig. 4.** Results of PCA on the EDJ shape on form space according to the chronocultural
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13 847 periods and EJD shape variation (in occlusal view, top right) along the first three principal
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15 848 components (PC).

16 849 **Fig. 4.** Résultats de l'ACP en espace de forme pour la JED des UM2 selon les différentes
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18 850 périodes chronoculturelles et variation de la JED (en vue occlusale, en haut à droite) le long
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20 851 des trois premières composantes principales (PC).

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Table 1

| Chronoculture | Site | Excavation reference | Specimen(s) | Age of specimen(s) | UM2 | μ CT |
|--------------------|--------------------------|-----------------------------------|--|---|-----|----------|
| Middle Magdalenian | Saint-Germain-la-Rivière | Lepront and Mirande, 1933 | STG1 | 15780 \pm 200 BP (GifA-95456) ^a | 2 | |
| | Lafaye | Brun, 1867 | LF24 | 15290 \pm 150 BP (GifA-95047) ^a | 1 | |
| | La Marche | Péricard and Lwoff, 1940 | LMR5, LMR6, LMR7 | *14685 \pm 75 BP (OxA-30980) ^b | 3 | 1 |
| Upper Magdalenian | Le Morin | Deffarge, 1956 | A4 | 12275 \pm 60 (OxA-28122) ^b | 1 | 1 |
| Azilian/Laborian | Roc de Cave | Blanchard, 1934 | 1 | 11210 \pm 140 BP (GifA-95047) ^a | 1 | |
| | Rochereil | Jude, 1960 | R1 | not available | 2 | |
| | Pont d'Ambon | Célérier et al., 1997 | n°4-I9 | not available | 1 | |
| Early Mesolithic | Houleau 2 | Lenoir, 1983 | H2-R19 | *9250 \pm 80 BP (Ly-173/ OxA-5683) ^c | 1 | |
| | La Vergne | Courtaud and Duday, 1995 | LV87-St7 | 9070 \pm 70 BP (Ly-369/OxA-6699) ^d | 1 | 1 |
| | Culoz sous Balme | Vilain, 1961 | 2 | 8640 \pm 380 BP (Ly-1668) ^e | 2 | |
| | Les Perrats | Gomez de Soto and Boulestin, 1996 | PER-C20, PER08-3021 | 8175 \pm 40 BP (Ly-5194/GrA) ^f 8100 \pm 90 BP (Gif-95476) ^f | 2 | 2 |
| Late Mesolithic | Cuzoul de Gramat | Lacam et al., 1944 | 1 | not available | 2 | |
| | Téviec | Péquart and Péquart, 1929 | T3, T4 | not available | 4 | |
| Early Neolithic | Pendimoun | Barral, 1958 | H2, F1 | H2: 6450 \pm 40 BP (GrA-32061) ^g F1: 6445 \pm 40 BP (GrA-26893) ^g | 4 | 2 |
| | Les Bréguières | Provost, 2013 | BRE7, 3218, 3269, 3354, 3404, 3479, 3428, 6302, 6303, 6305, 6306, 6307, 6364 | *between 6151 \pm 45 BP (LTL-13784) ^h and 5581 \pm 45 BP (LTL-13783A) ^h | 24 | 2 |
| | Germignac | Gaillard et al., 1984 | GRM1 | 6090 \pm 70 BP (GifA-96770) ⁱ | 2 | 1 |
| | Baume Bourbon | Coste et al., 1987 | SIII-A | not available | 2 | |
| Middle Neolithic | Gurgy | Rottier et al., 2005 | 201, 202, 206, 213, 215A, 215B, 223, 229, 243B, 245B, 248, 252, 253, 257, 264, 277, 289B, 291, 292, 294, 300, 301, 308 | between 6070 \pm 45 BP (Ly-5872) ^j and 4975 \pm 35 BP (Ly-4675) ^j | 23 | 23 |
| | Grotte Mykolas | Chancerel et al., 2007 | LBGM09, 10, 10-5, 12 | *between 5210 \pm 35 BP (Ly-6225) ^k and 4990 \pm 40 BP (Poz-14917) ^k | 4 | 4 |
| | La Lède du Gulp | Roussot-Larroque, 1977 | LdG1 | not available | 1 | 1 |
| | Auneau | Dubois et al., 1986 | AUN-1, 2, 4, 5 | AUN-2: 4865 \pm 100 BP (Ly-4729) ^l | 6 | 2 |
| Total | | | | | 89 | 40 |

^a Gambier et al., 2000; ^b Barshay-Szmidt et al., 2016; ^c Hedges et al., 1997; ^d Duday et al., 1998; ^e Evin and Pachiaudi, 1979; ^f Boulestin, 1999; ^g Binder and Sénépart, 2010; ^h Provost et al., 2014; ⁱ Laporte and Gomez de Soto, 2001; ^j Rivollat et al., 2015; ^k Chancerel et al., 2011; ^l Verjux, 1999.

* Isolated remains or collective burials, not possible to be attributed to one individual.

* Restes isolés ou sépultures collectives, impossibles à attribuer à un individu particulier.

Table 2

| Trait | Scores | Middle Magdalenian | Upper Magdalenian | Azilian/ Laborian | Early Mesolithic | Late Mesolithic | Early Neolithic | Middle Neolithic |
|-------------------|---------------|-------------------------------|------------------------------|------------------------------|-----------------------------|----------------------------|----------------------------|-----------------------------|
| Metacone | 3-5 | 100.00 (4/4) | 100.00 (1/1) | 100.00 (2/2) | 100.00 (4/4) | 100.00 (3/3) | 91.67 (11/12) | 93.10 (27/29) |
| Hypocone | 3-5 | 33.33 (1/3) | - | 100.00 (2/2) | 75.00 (3/4) | 50.00 (1/2) | 91.67 (11/12) | 79.31 (23/29) |
| Metaconule | 1-5 | 33.33 (1/3) | - | 0.00 (0/2) | 0.00 (0/3) | 100.00 (1/1) | 25.00 (2/8) | 57.69 (15/26) |
| Parastyle | 3-5 | 0.00 (0/3) | 0.00 (1/1) | - | 0.00 (0/4) | 0.00 (0/2) | 7.69 (1/13) | 0.00 (0/32) |
| Carabelli's trait | 5-7 | 0.00 (0/4) | - | 0.00 (0/2) | 0.00 (0/4) | 0.00 (0/3) | 0.00 (0/13) | 0.00 (0/28) |

In parentheses: number of specimens for which the traits were present/number of specimens for which the traits were observable.

Entre parenthèses: nombre de spécimens pour lesquels les caractères sont présents/nombre de spécimens pour lesquels les caractères sont observables.

Table 3

| | | Wear stage¹ | AET2D | RET2D | AET3D | RET3D |
|---------------------------|-----------|-------------------------------|--------------|--------------|--------------|--------------|
| Middle Magdalenian | | 1 | 1.54 | 28.78 | 1.61 | 26.75 |
| Upper Magdalenian | | 5* | 1.49 | 21.44 | 0.81* | 12.90* |
| Early Mesolithic | mean ± sd | 2 (mean) | 1.05 ± 0.07 | 17.13 ± 0.93 | 1.04 ± 0.10 | 17.47 ± 1.84 |
| | min-max | 2-3 | 1.01-1.14 | 16.49-18.19 | 0.95-1.14 | 15.35-18.69 |
| Early Neolithic | mean ± sd | 3 (mean) | 1.17 ± 0.14 | 20.25 ± 1.71 | 1.09 ± 0.27 | 18.83 ± 4.10 |
| | min-max | 1-4 | 0.96-1.33 | 18.52-22.98 | 0.75-1.36 | 13.31-22.69 |
| Middle Neolithic | mean ± sd | 2 (mean) | 1.22 ± 0.16 | 20.31 ± 3.56 | 1.25 ± 0.23 | 21.50 ± 4.56 |
| | min-max | 1-4 | 0.90-1.56 | 14.87-29.66 | 0.74-1.68 | 10.41-29.11 |
| | | 5* | 1.10 | 17.82 | 0.62* | 11.57* |

¹ Molnar (1971)

* moderately worn crown, values given for information purposes.

* couronne modérément usée, valeurs données à titre indicatif.

Figure 1

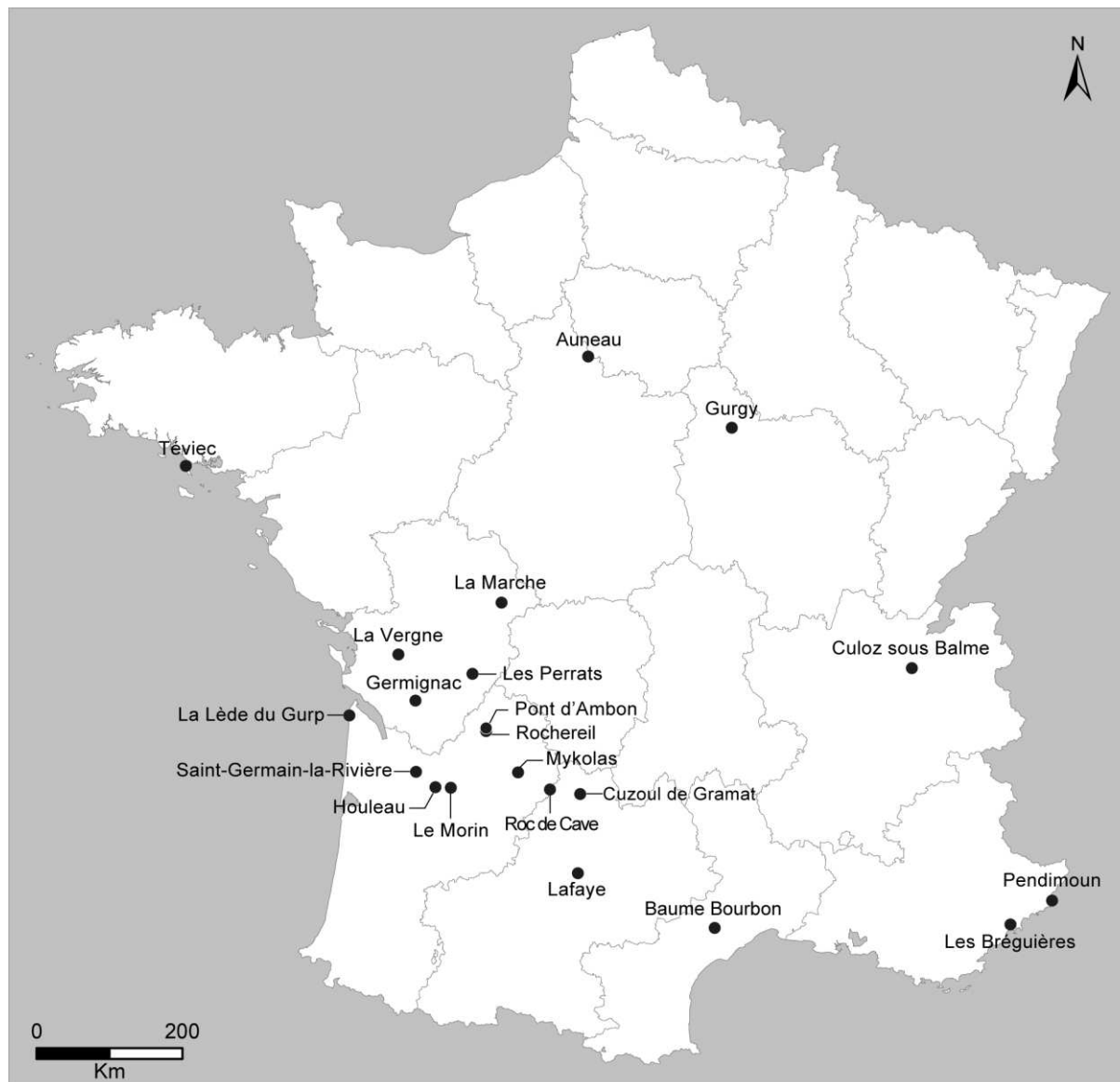


Figure 2

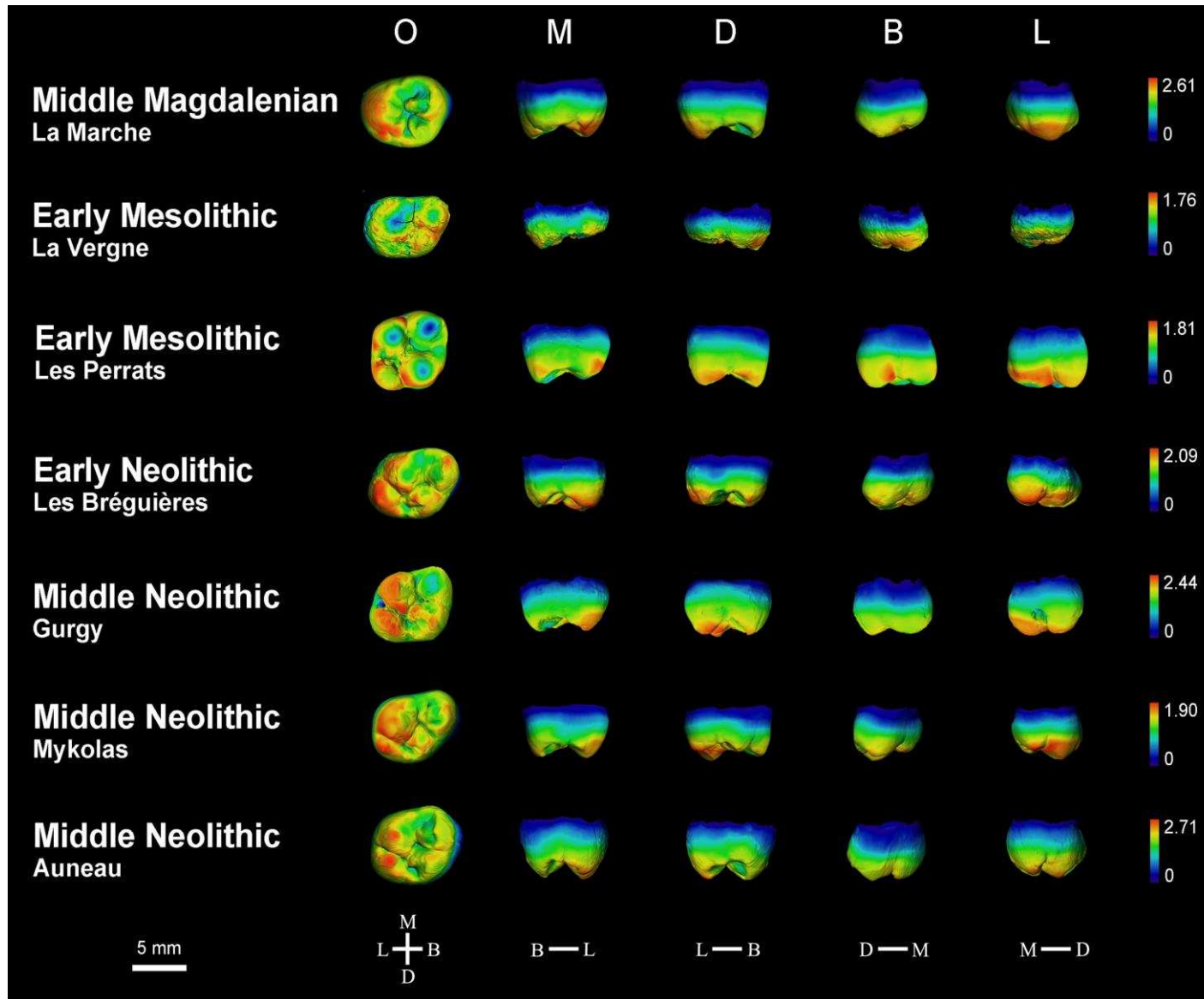


Figure 4

