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Le Luyer, Mona and Bayle, Priscilla (2017) Microevolution of outer and inner structures of upper molars in Late Pleistocene and Early Holocene humans. *Comptes Rendus Palevol*, 16 (5-6). pp. 632-644. ISSN 1631-0683.

DOI

<https://doi.org/10.1016/j.crpv.2016.11.009>

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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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9 6
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22 13 Keywords: Modern humans; Teeth; Non-metric traits; Enamel thickness; enamel-dentine
23 14 junction; Pleistocene; Holocene

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25 15
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27 16 Mots clés: Hommes modernes; Dents; Variations non-métriques; Épaisseur de l'émail;
28 17 Jonction émail-dentine; Pléistocène; 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

16 39 RÉSUMÉ

17 40

18 41 Dans cette étude, nous avons examiné les variations externes et internes des secondes
19 42 molaires supérieures (UM2) d'Hommes de la fin du Pléistocène et du début de l'Holocène,
20 43 période-clé de notre histoire évolutive associée à des changements socioculturels,
21 44 économiques et environnementaux majeurs. Les variations non-métriques ont été enregistrées
22 45 sur 89 UM2 de 66 individus paléolithiques, mésolithiques et néolithiques, et 40 UM2 ont été
23 46 scannées par microtomographie pour évaluer les variations de distribution d'épaisseur de
24 47 l'émail (EE) et de forme de la jonction émail-dentine (JED). Les changements majeurs sont
25 48 trouvés entre le Mésolithique et le Néolithique: diminution de l'expression du métacône
26 49 combinée à un hypocône plus développé; hétérogénéité accrue dans la distribution de l'EE
27 50 entre les cuspides linguales et buccales; et augmentation de taille des cornes de dentine
28 51 correspondant à l'hypocône et, dans une moindre mesure, au métacône. Ces modifications
29 52 morphologiques peuvent être liées aux changements fonctionnels masticatoires associés à la
30 53 transition vers l'agriculture.
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1. Introduction

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

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

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.,
2 259 2012; Marchand and Perrin, 2015; Pinhasi and Stock, 2011). A size reduction and a
3 260 morphological simplification of the teeth have been observed for these periods, and mainly
4 261 linked with cultural and dietary changes associated with the transition to agriculture (Brace,
5 262 1962; Brace et al., 1987; Calcagno, 1986; Frayer, 1977; Greene et al., 1967; Jolly, 1970;
6 263 Macchiarelli and Bondioli, 1986). Based on outer structures only, these dental modifications
7 264 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
15 266 developmental genes and cusp morphogenesis (for a review, see Paul et al., 2016). The
16 267 patterning cascade model (Jernvall, 2000) predicts the future cusp number, size and shape,
17 268 and tooth sizes along the row, and minor changes during the developmental trajectory can
18 269 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
24 271 environmental factors (overview in Hughes and Townsend, 2013; Townsend et al., 2012).
25 272 While the expression of the dental traits shows a high variability in modern humans (e.g.,
26 273 Hanihara et al., 2003; Irish, 1997; Scott and Turner, 1997), they are reliable markers for
27 274 estimate biological relationships between populations and kinship (Coppa et al., 2007;
28 275 Crubézy and Sellier, 1990a, b; Delgado-Burbano, 2007; Desideri, 2003; Irish, 1997, 2006,
29 276 2014; Turner, 1987; Ullinger et al., 2005).

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

54 287 Studies on EDJ have shown that, while differences in dentine horn height, crown height,
55 288 as well as in cervix shape, are more important between adjacent molars of the same taxon than
56 289 for the same molar between taxa (Skinner et al., 2008a), its morphology successfully
57 290 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
1 326 Paleolithic UM2s with a hypocone reduced to the point of a small cusplule. This is consistent
2
3 327 with the results of our study of the Magdalenian specimens at outer and inner levels.
4

5 328 Considering enamel thickness, our Late Pleistocene/Early Holocene specimens show
6
7 329 substantial differences with the mean enamel thicknesses reported for 46 extant humans
8
9 330 (African, Asian, European, and Northern Americans) that range from 1.27 mm to 1.40 mm for
10
11 331 AET2D, and from 20.00 to 21.64 for RET2D (Grine, 2005; Kono, 2004; Smith et al., 2012;
12
13 332 Olejniczak et al., 2008a, b). Notably, the Magdalenian specimens exhibit thicker enamel
14
15 333 while the Mesolithic individuals have particularly thinner enamel compared to the extant
16
17 334 human conditions. The increase of the heterogeneity in its distribution, combined with higher
18
19 335 EDJ horn tips for the thickest cusps, could reveal differences in masticatory biomechanical
20
21 336 constraints. Indeed, significant functional links have been found between enamel thickness,
22
23 337 tooth form and diet (Lucas et al., 2008a, b; Mahoney, 2013; Molnar and Gantt, 1977; Molnar
24
25 338 and Ward, 1977; Schwartz, 2000). Also, thick enamel exhibited on the lingual cusps could be
26
27 339 an adaptation to increase resistance and attritional longevity in response to abrasive diet (Le
28
29 340 Luyer et al., 2014; Lucas et al., 2008b). This suggestion is strengthened by the occlusal wear
30
31 341 differences that have been reported between these populations (Le Luyer, 2016): while Upper
32
33 342 Paleolithic and Mesolithic individuals show a flatter wear associated with a homogenous
34
35 343 distribution of the enamel thickness, the Neolithic molars present an oblique wear direction
36
37 344 combined with a heterogeneous enamel thickness distribution (see also Le Luyer et al., 2014).
38
39 345 This ubiquitous oblique wear direction has been linked to more refined and grinded foodstuffs
40
41 346 with a more abrasive impact (Brace, 1962; Greene et al., 1967; Smith, 1984). Thus, the outer
42
43 347 and inner dental modifications that we observed between these Late Pleistocene and Early
44
45 348 Holocene populations are probably primarily linked with the functional constraints of the
46
47 349 mastication of different dietary items, as major changes in subsistence strategies occurred
48
49 350 between these periods (Bonsall et al., 2004, 2009; Drucker and Henry-Gambier, 2005;
51
52 351 Richards et al., 2003; Schulting and Richards, 2001).

53 352 Even if environmental and/or developmental aspects may have played a role in the
54
55 353 morphological changes observed in these Late Pleistocene and Early Holocene human molars,
56
57 354 we suggest that the development of the hypocone combined with a reinforcement of its
58
59 355 enamel thickness is a functionally-related adaptive modification, linked to dietary changes
60
61 356 associated with the transition to agriculture. Furthermore, considering recent study combining
62
63 357 outer and inner crown assessment on a larger sample of both deciduous and permanent teeth
64
65 358 (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.

367 368 **Acknowledgements**

369
370 We are grateful to the guest editors, Roberto Macchiarelli and Clément Zanolli, for their
371 invitation to contribute to this volume dedicated to the research activity and achievements of
372 our dearly missed friend and colleague, Laurent Puymerau. We thank all the curators for
373 having allowed the microCT acquisitions of the dental remains: Didier Binder, Bruno
374 Boulestin, Patrice Courtaud, Henry Duday, Dominique Henry-Gambier, Michel Lenoir,
375 Stephane Rottier, Julia Roussot-Larroque, Christian Verjux. MicroCT data used in this work
376 were partly produced through the microCT facilities of the MRI platform and the LabEx
377 CeMEB; we acknowledge Renaud Lebrun (Université Montpellier II). Research supported by
378 the Ministère de l'Enseignement Supérieur et de la Recherche (2012-15; to: M. Le Luyer,
379 doctoral grant; Université de Bordeaux); the DHP project (2012-14; to: S. Rottier; Université
380 Bordeaux 1/LaScArBx; ANR-10-LABX-52) and the PEPS 3Dent'in (2013-14; to: P. Bayle;
381 PEPS IdEx Bordeaux/CNRS; ANR-10-IDEX-03-02).

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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
12 813 (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
23 819 dentaires.

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27 821 **Table 3**

29 822 Descriptive statistics for 2D and 3D average (AET) and relative (RET) enamel thickness
30 823 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
36 826 (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
47 832 second molars. All teeth are shown as left, in occlusal (O), mesial (M), distal (D), buccal (B)
48 833 and lingual (L) views. The pseudo-colour scale (in mm), ranging from dark blue (thin enamel)
49 834 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
54 836 secondes molaires supérieures non usées. Toutes les dents sont montrées comme étant des
55 837 gauches, en vues occlusale (O), mésiale (M), distale (D), buccale (B) et linguale (L).
56 838 L'échelle colorimétrique (en mm), allant du bleu foncé (émail fin) au rouge (émail épais), est
57 839 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.

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
12 847 periods and EJD shape variation (in occlusal view, top right) along the first three principal
13 848 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

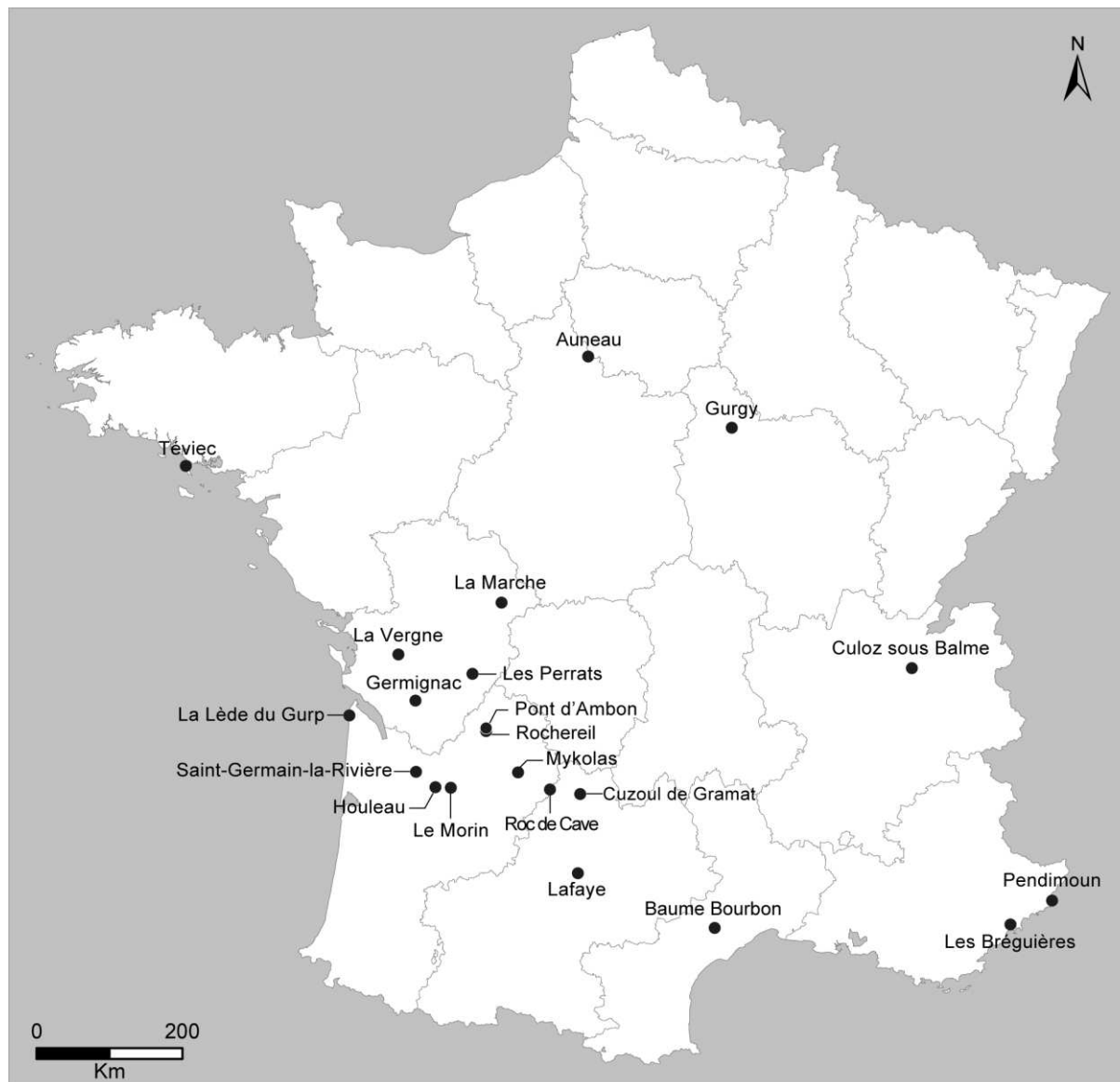


Figure 2

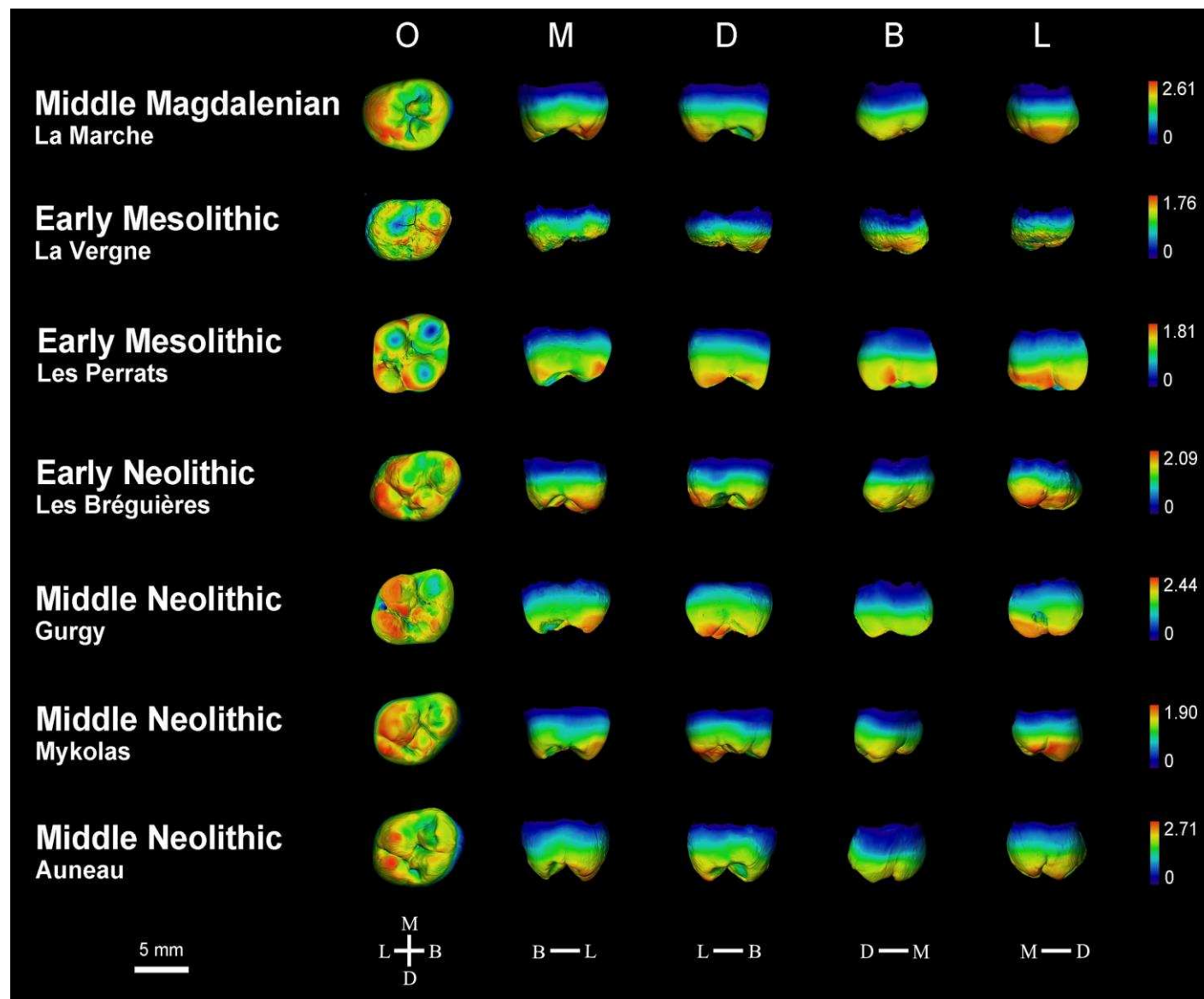


Figure 3

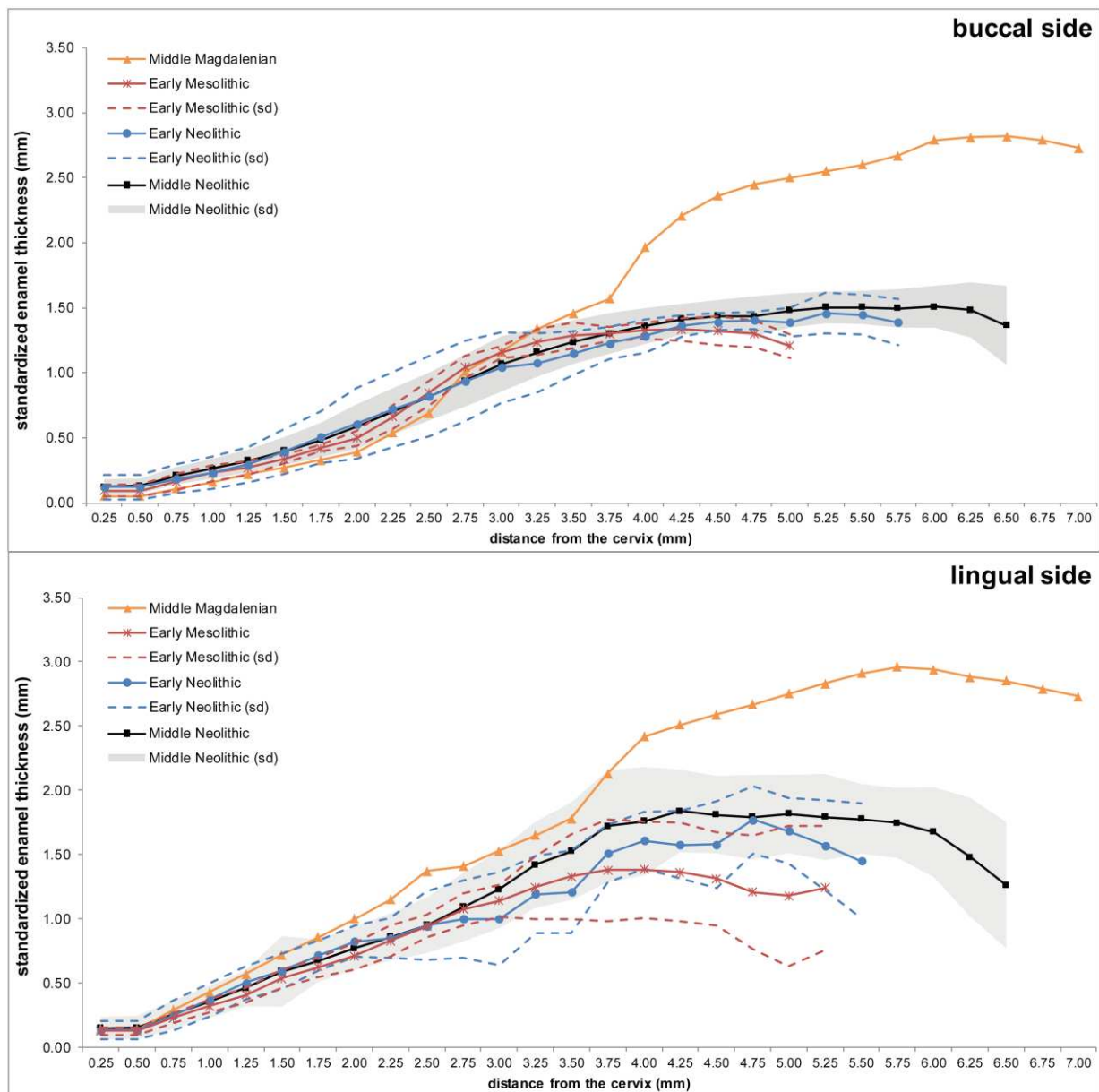


Figure 4

