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

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

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ABSTRACT

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

RÉSUMÉ

Dans cette étude, nous avons examiné les variations externes et internes des secondes molaires supérieures (UM2) d'Hommes de la fin du Pléistocène et du début de l'Holocène, période-clé de notre histoire évolutive associée à des changements socioculturels, économiques et environnementaux majeurs. Les variations non métriques ont été enregistrées sur 89 UM2 de 66 individus paléolithiques, mésolithiques et néolithiques, et 40 UM2 ont été scannées par microtomographie pour évaluer les variations de distribution d'épaisseur de l'émail (EE) et de forme de la jonction émail–dentine (JED). Les changements majeurs sont trouvés entre le Mésolithique et le Néolithique : diminution de l'expression du métacône, combinée à un hypocône plus développé ; hétérogénéité accrue dans la distribution de l'EE entre les cuspides linguales et buccales ; augmentation de taille des

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cornes de dentine correspondant à l'hypocône et, dans une moindre mesure, au métacône. Ces modifications morphologiques peuvent être liées aux changements fonctionnels masticatoires associés à la transition vers l'agriculture.

1. Introduction

Documented since the apparition of the genus *Homo*, a reduction in tooth size together with a morphological simplification has 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 archeological 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 μCT) allow non-invasive quantitative and qualitative characterizations of inner structures. Although major sociocultural and economic changes occurred at the Pleistocene–Holocene boundary (Bonsall et al., 2004; Langlais et al., 2012; Marchand and Perrin, 2015; Pinhasi and Stock, 2011; Richards et al., 2003; Valdeyron, 2014), representatives of the first human societies have been poorly assessed by means of advanced virtual anthropology (but see Le Luyer, 2016; Le Luyer et al., 2014, 2016). This study aims to investigate outer and inner variations of modern humans upper second molars dated from late Pleistocene and early Holocene from a whole crown perspective, by assessing non-metric variation, enamel thickness and EDJ shape.

2. Material and methods

2.1. Samples

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

2.2. Non-metric variations

Crown morphological variations were assessed by recording the number of cusps and their development. Five non-metric traits (metacone, hypocone, metaconule, parastyle, and Carabelli's trait) were scored using the Arizona State University Dental Anthropology System (ASUDAS, Scott and Turner, 1997; Turner et al., 1991). For each individual, observations were made on right and left antimeres if they were present. In case of asymmetry, the antimere exhibiting the greatest degree of trait expression was selected prior to calculated frequencies (Turner and Scott, 1977). The metacone, the hypocone and the parastyle have been considered as present when their expression reached a fully formed cusp (i.e. score 3). According to

Table 1
List of specimens and number of teeth used in this study for outer (UM2) and inner (μCT) aspects.
Tableau 1
Liste des spécimens et nombre de dents utilisées dans cette étude pour les aspects externes (UM2) et internes (μCT).

Chronoculture	Site	Excavation reference	Specimen(s)	Age of specimen(s)	UM2	μCT
Middle Magdalenian	Saint-Germain-la-Rivière	Lepront and Mirande, 1933	STG1	15780 ± 200 BP (GifA-95456) (Gambier et al., 2000)	2	
	Lafaye	Brun, 1867	LF24	15290 ± 150 BP (GifA-95047) (Gambier et al., 2000)	1	
	La Marche	Péricard and Lwoff, 1940	LMR5, LMR6, LMR7	14685 ± 75 BP (OxA-30980) (Barshay-Szmidt et al., 2016)[a]	3	1
Upper Magdalenian	Le Morin	Deffarge, 1956	A4	12275 ± 60 (OxA-28122) (Barshay-Szmidt et al., 2016)	1	1
Azilian/Laborian	Roc de Cave	Blanchard, 1934	1	11210 ± 140 BP (GifA-95047) (Gambier et al., 2000)	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 ± 80 BP (Ly-173/OxA-5683) (Hedges et al., 1997)[a]	1	
	La Vergne	Courtaud and Duday, 1995	LV87-St7	9070 ± 70 BP (Ly-369/OxA-6699) (Duday et al., 1998)	1	1
	Culoz sous Balme	Vilain, 1961	2	8640 ± 380 BP (Ly-1668) (Evin and Pachiaudi, 1979)	2	
	Les Perrats	Gomez de Soto and Boulestin, 1996	PER-C20, PER08-3021	8175 ± 40 BP (Ly-5194/GrA) (Boulestin, 1999) 8100 ± 90 BP (Gif-95476) (Boulestin, 1999)	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 ± 40 BP (GrA-32061) (Binder and Sénépart, 2010) F1: 6445 ± 40 BP (GrA-26893) (Binder and Sénépart, 2010)	4	2
	Les Bréguières	Provost, 2013	BRE7, 3218, 3269, 3354, 3404, 3479, 3428, 6302, 6303, 6305, 6306, 6307, 6364	between 6151 ± 45 BP (LTL-13784) (Provost et al., 2014) and 5581 ± 45 BP (LTL-13783A) (Provost et al., 2014)[a]	24	2
	Germignac	Gaillard et al., 1984	GRM1	6090 ± 70 BP (GifA-96770) (Laporte and Gomez de Soto, 2001)	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 ± 45 BP (Ly-5872) (Rivollat et al., 2015) and 4975 ± 35 BP (Ly-4675) (Rivollat et al., 2015)	23	23
	Grotte Mykolas	Chancerel et al., 2007	LBGM09, 10, 10-5, 12	Between 5210 ± 35 BP (Ly-6225) (Chancerel et al., 2011) and 4990 ± 40 BP (Poz-14917) (Chancerel et al., 2011)[a]	4	4
	La Lède du Gurp	Roussot-Larroque, 1977	LdG1	Not available	1	1
	Auneau	Dubois et al., 1986	AUN-1, 2, 4, 5	AUN-2: 4865 ± 100 BP (Ly-4729) (Verjux, 1999)	6	2
			Total		89	40

[a] Isolated remains or collective burials, not possible to be attributed to one individual.

standard ASUDAS rank-scale trait breakpoint from Scott and Turner (1997), the mecatonule has been recorded present from its first degree while the presence of the Carabelli's trait was determined from the score 5. *Fisher's* exact test was used to compare differences between adult and immature individuals, and between considered periods.

2.3. *Microtomographic record*

To assess the inner structural variation, 40 UM2 have been imaged by using the Skyscan 1076 *in vivo* X-ray equipment set at the MRI platform (University Montpellier 2, France). Scans were realized according to the following parameters: 100 kV voltage, 100 μA

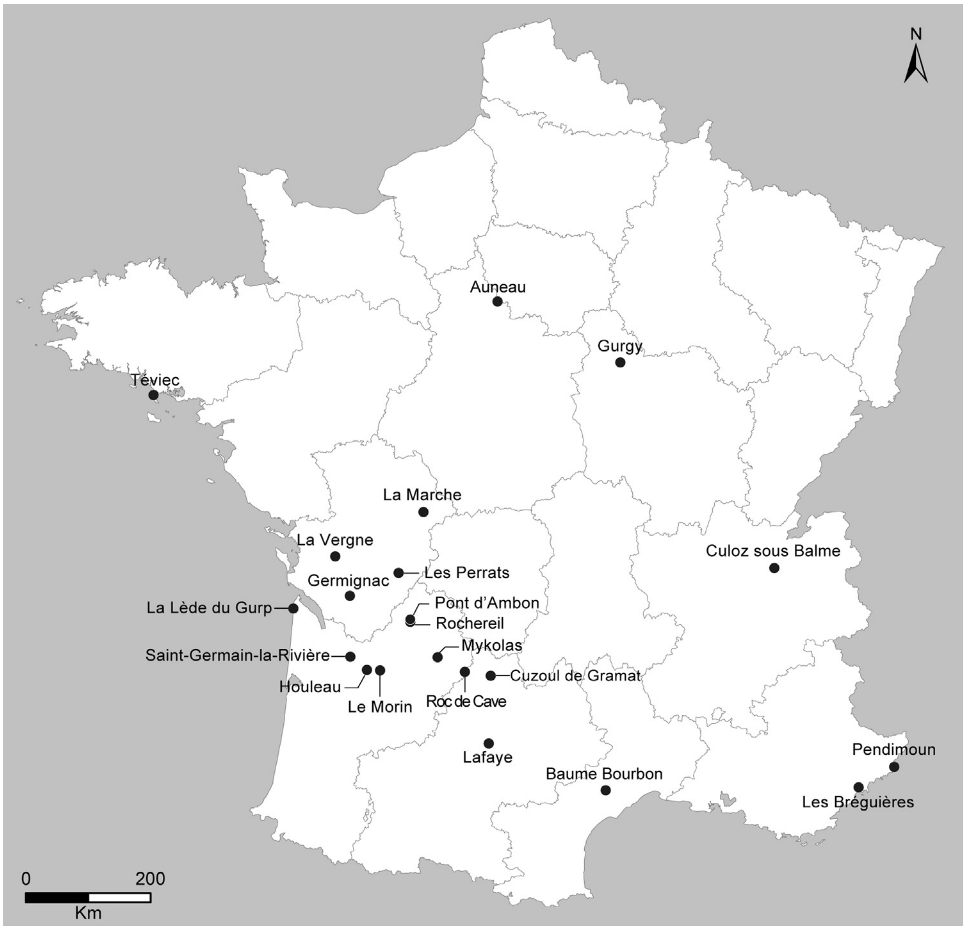

Fig. 1. Map showing the location of the sites studied.

Fig. 1. Carte montrant la localisation des sites étudiés.

Table 2
Results of the study for outer morphology and frequencies of non-metric dental variations.
Tableau 2
Résultats de l'étude morphologique externe et fréquences des variations non métriques dentaires.

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.

current, 1.0 mm aluminum filter and 0.20° rotation step. Using Nrecon 1.6 (Skyscan), the final volumes were reconstructed with an isotropic voxel size ranging from 17.93 μm for isolated teeth to 36.18 μm for jaw fragments. A semi-automatic threshold-based segmentation (HMH, Coleman and Colbert, 2007; Spoor et al., 1993) was conducted using Avizo 9.0 (VSG) with manual corrections (Bayle et al., 2009, 2010; Kono, 2004; Macchiarelli et al., 2006; Olejniczak et al., 2008a,b,c; Smith et al., 2005; Zanolli et al., 2010, 2014). Crowns were digitally isolated from roots (Olejniczak et al., 2008a) and 3D surface models of the OES and the EDJ were generated using a constrained smoothing algorithm (Kupczik and Hublin, 2010).

2.4. Enamel thickness variations

Average enamel thickness (AET) and relative enamel thickness (RET) were calculated in 2D and in 3D (Kono, 2004; Macchiarelli et al., 2006; Martin, 1985; Olejniczak et al., 2008c; Skinner et al., 2015; Smith et al., 2012). For all worn teeth, enamel loss was virtually reconstructed

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

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

		Wear stage (Molnar, 1971)	AET2D	RET2D	AET3D	RET3D
Middle Magdalenian		1	1.54	28.78	1.61	26.75
Upper Magdalenian		5[a]	1.49	21.44	0.81[a]	12.90[a]
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[a]	1.10	17.82	0.62[a]	11.57[a]

[a] Moderately worn crown, values given for information purposes.

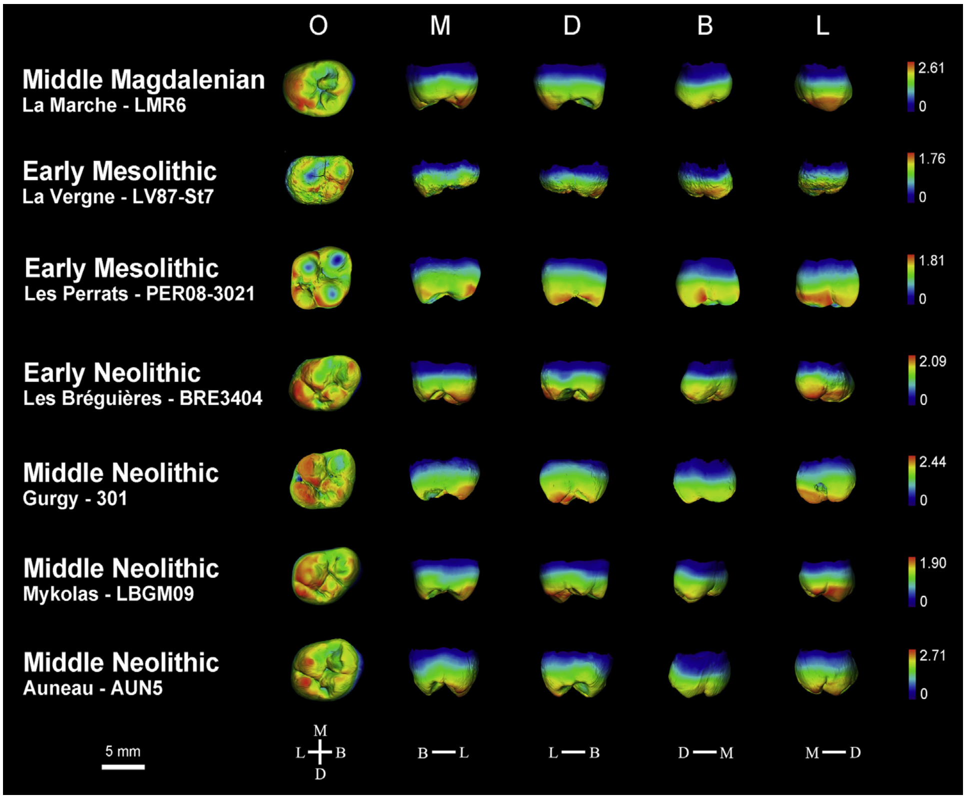

Fig. 2. Comparative cartographies of the distribution of enamel thickness for unworn upper second molars. All teeth are shown as left, in occlusal (O), mesial (M), distal (D), buccal (B) and lingual (L) views. The pseudo-colour scale (in mm), ranging from dark blue (thin enamel) to red (thick enamel),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

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

on the mesial sections prior to measure 2D enamel thicknesses (Smith et al., 2012). Mann-Whitney *U*-tests were performed to detect potential significant differences in enamel thickness between adult and immature individuals, and between periods. Three-dimensional cartographies of the distribution of enamel thickness were created by measuring the distance between the OES and EDJ (Macchiarelli et al., 2008). Also, using MPSAK v2.9 (developed by L. Bondioli, available in Dean and Wood, 2003), the topographical variation of the standardized enamel thickness was measured from the cervix to the apex of the cusps, on both lingual and buccal sides of the mesial sections (Le Luyer et al., 2014; Macchiarelli et al., 2007). For the enamel thickness analyses, only unworn to slightly worn teeth (wear stage inferior or equal to 4, Molnar, 1971) have been included. Two teeth (the upper Magdalenian of Le

Morin and a middle Neolithic one from Gurgy) exhibiting a wear stage of 5 (Molnar, 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).

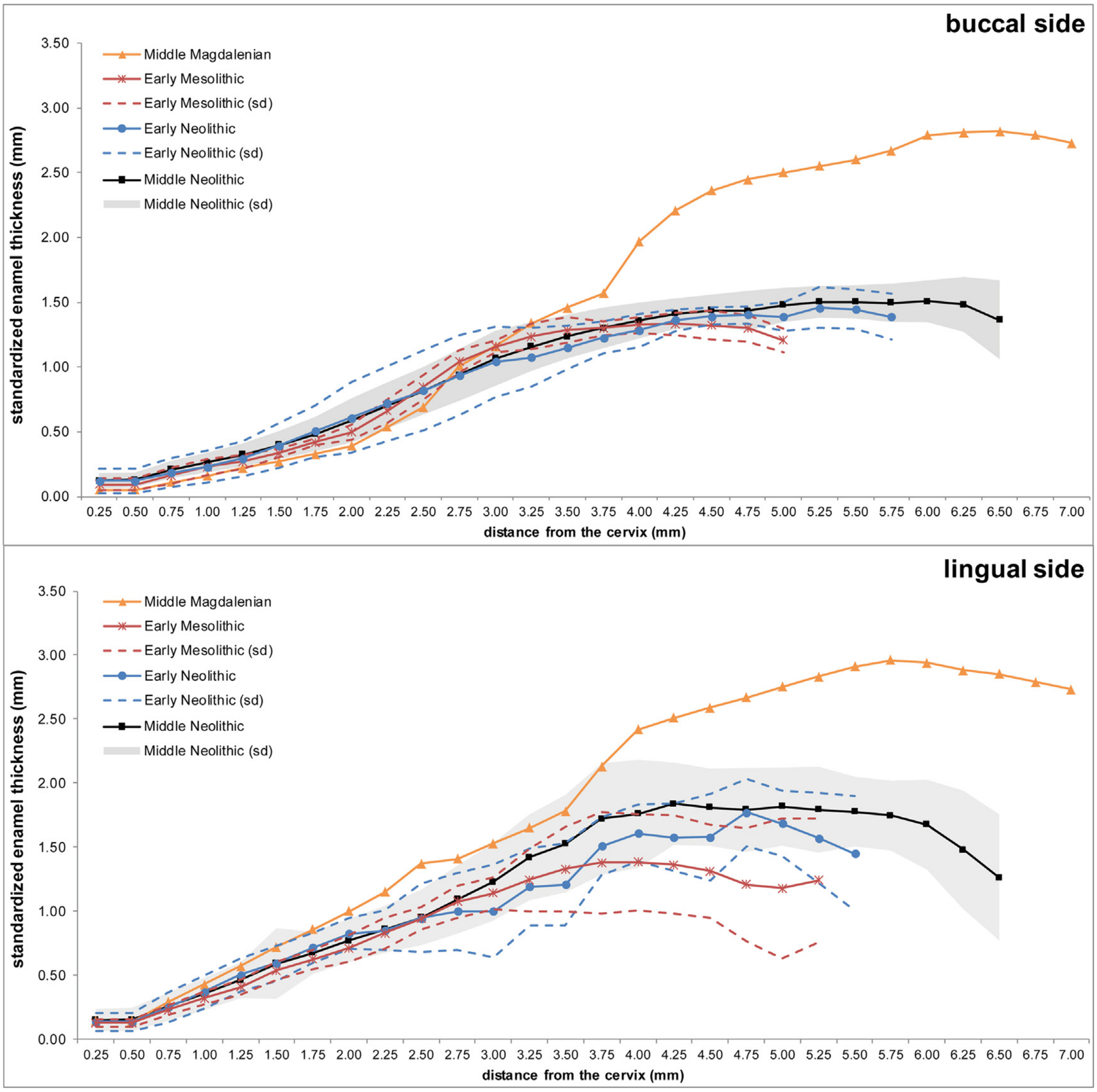

Fig. 3. Topographical variation of standardized enamel thickness measured on the buccal (top) and lingual (bottom) sides of the mesial sections. sd = standard deviation.

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

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

3.2. Inner morphology

3.2.1. 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 ($\chi^2 = 2.447$; $dl = 2$; $P = 0.294$). No significant differences were found between the considered periods, except for the RET2D which is

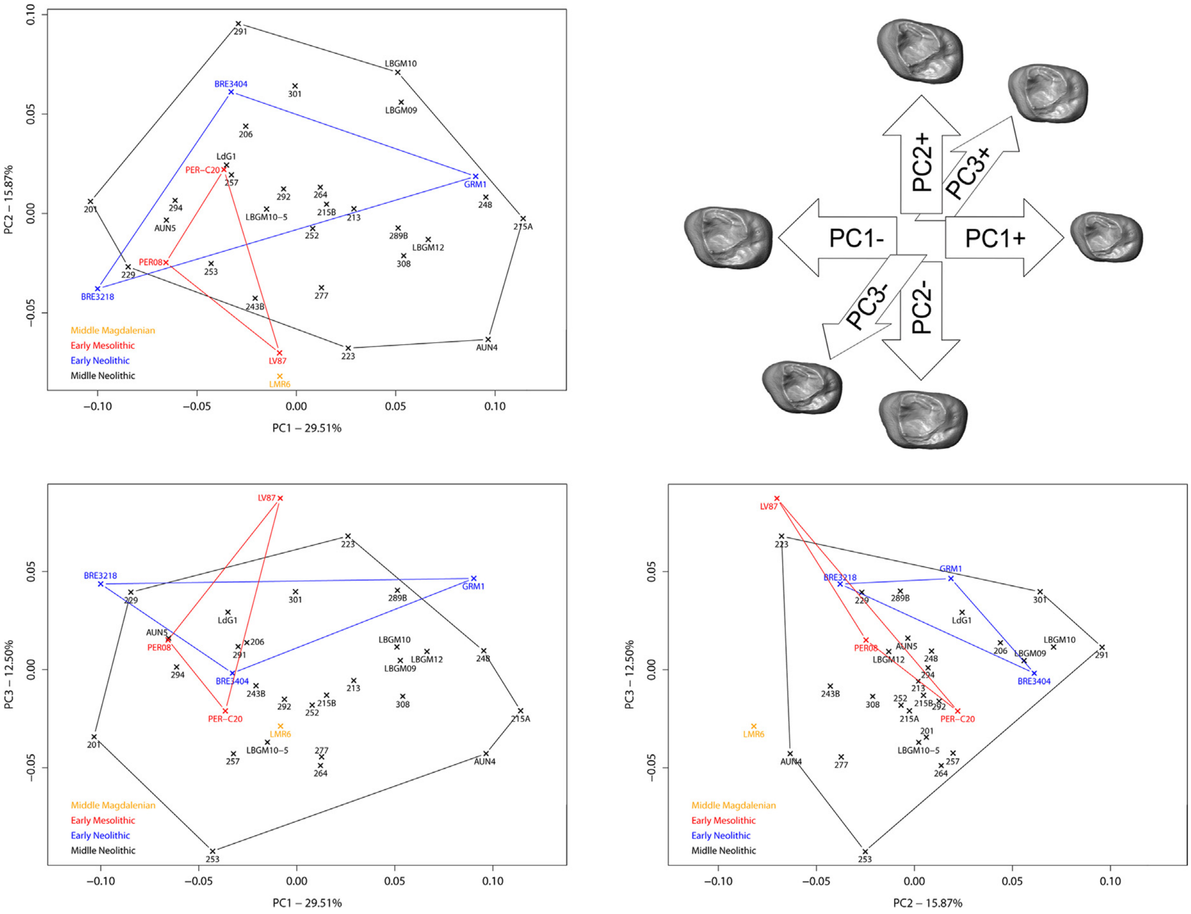

Fig. 4. Results of PCA on the EDJ shape on form space according to the chronocultural periods and EJD shape variation (in occlusal view, top right) along the first three principal components (PC).

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

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 thicker on the hypocone. Indeed, the heterogeneity of enamel thickness between buccal and lingual cusps is accentuated for both early and middle Neolithic unworn UM2s.

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

3.2.2. Enamel–dentine junction shape

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

4. Discussion and conclusions

The late Pleistocene and early Holocene periods were marked by major environmental, cultural and biological changes (e.g., Brace, 1962, 1967; Greene et al., 1967; Langlais et al., 2012; Marchand and Perrin, 2015; Pinhasi and Stock, 2011). A size reduction and a morphological simplification of the teeth have been observed for these periods, and mainly linked with cultural and dietary changes associated with the transition to agriculture (Brace, 1962; Brace et al., 1987; Calcagno, 1986; Frayer, 1977; Greene et al., 1967; Jolly, 1970; Macchiarelli and Bondioli, 1986). Based on outer structures only, these dental modifications have not been assessed for the inner structures neither from a whole crown perspective.

The crown morphology is determined by a morphodynamic interaction between developmental genes and cusp morphogenesis (for a review, see Paul et al., 2017). The patterning cascade model (Jernvall, 2000) predicts the future cusp number, size and shape, and tooth sizes along the row, and minor changes during the developmental trajectory can alter these features (Evans et al., 2016; Jernvall, 2000; Salazar-Ciudad and Jernvall, 2002).

Non-metric dental traits are under multiple controls, influenced by genetic, epigenetic and environmental factors (overview in Hughes and Townsend, 2013; Townsend et al., 2012). While the expression of the dental traits shows a high variability in modern humans (e.g., Hanihara et al., 2003; Irish, 1997; Scott and Turner, 1997), they are reliable markers for estimate biological relationships between populations and kinship (Coppa et al., 2007; Crubézy and Sellier, 1990a,b; Delgado-Burbano, 2007; Desideri, 2003; Irish, 1997, 2006, 2014; Turner, 1987; Ullinger et al., 2005).

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

Studies on EDJ have shown that, while differences in dentine horn height, crown height, as well as in cervix shape, are more important between adjacent molars of the same taxon than for the same molar between taxa (Skinner et al., 2008a), its morphology successfully discriminates taxonomic and phylogenetic relationships (e.g., Bailey et al., 2011; Olejniczak et al., 2007; Skinner et al., 2008a,b, 2009a,b). Recently explored at a microevolutionary scale in a middle Neolithic sample (Le Luyer et al., 2016), the EDJ shape has been suggesting as a reliable proxy to track individuals sharing similar cultural and burial practices.

In this study, even though it should be noted that our results could be affected by a bias due to a small sample, particularly for the inner structure, and the heterogeneity of the sample size between the periods, the upper molars from late Pleistocene to early Holocene human individuals tend to show a reduction of the metacone combined with a more developed hypocone, and even if no statistically significant difference has been found, this tendency is particularly marked since the beginning of the Neolithic. Even if an overlap is shown for the samples from all the periods, the EDJ morphology shows an increase of the height of the dentine horn tips from Magdalenian to middle Neolithic, and particularly for those corresponding to the hypocone cusp. Thus, this EDJ signal is consistent with the data we obtained from the study of non-metric variations on a larger sample, and allow us to quantify these morphological changes. Average and relative enamel thicknesses have been found to be higher in upper Paleolithic teeth and smaller in early Mesolithic teeth, then increasing from Mesolithic to middle Neolithic individuals. Whatever period is considered, systematically, enamel thickness distribution is asymmetric between the functional and the non-functional cusps of the UM2s, with thicker enamel on the lingual cusps. While the distribution of enamel is more homogeneous for the upper Paleolithic and the Mesolithic teeth in our sample, it is noteworthy that the Neolithic individuals show an increase of the heterogeneity of enamel thickness distribution.

Major changes in outer and inner structural morphology from late Pleistocene to early Holocene human individuals are found for the functional cusps (e.g., Kay and Hiiemae, 1974; Macho and Berner, 1994), and particularly the hypocone. These results are consistent with previous studies showing that mesial cusps of upper molars are more stable in modern human populations (Macho and Moggi-Cecchi, 1992) while distal cusps are more plastic to environmental stress (e.g., Riga et al., 2014; Scott and Turner, 1997). According to the patterning cascade model of development (Salazar-Ciudad and Jernvall, 2002), initial differences (even small) during development will have cumulative effects on the later-forming cusps, reducing or deleted them (Jernvall and Jung, 2000; Paul et al., 2017; Skinner and Gunz, 2010). However, the complete or near-complete loss of the hypocone (three-cusped UM2s) occurs in relatively low frequencies (0–33.7%) in all recent human populations (Irish, 2016; Scott and Turner, 1997). The study of Bailey (2000) reported the lowest hypocone frequency for upper Paleolithic Central European specimens. While no complete loss of the hypocone was found in later fossil *Homo*, Bailey and Hublin (2013) observed four upper Paleolithic UM2s with a hypocone reduced to the point of a small cuspule. This is consistent with the results of our study of the Magdalenian specimens at outer and inner levels.

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

Even if environmental and/or developmental aspects may have played a role in the morphological changes observed in these late Pleistocene and early Holocene human molars, we suggest that the development of the hypocone combined with a reinforcement of its enamel thickness is a functionally-related adaptive modification, linked to dietary changes associated with the transition to agriculture. Furthermore, considering recent study combining outer and inner crown assessment on a larger sample of both deciduous and permanent teeth (Le Luyer, 2016), discontinuities found between late Pleistocene and early Holocene human groups suggest that environmentally-driven modifications beginning at the Holocene had a major impact on dental size reduction, while Neolithic cultural changes had mostly affected enamel distribution (Le Luyer, 2016). Explanatory models proposed and discussed so far do not explain all the inner modifications, but some models can help to interpret some differences. Thus, a reappraisal in a whole crown perspective is needed for the interpretation of the time-related trend of dental structural reduction. Further studies on a larger sample will track the underlying factors and the microevolutionary mechanisms having affected dental evolution, notably across the key-period of the Pleistocene–Holocene transition.

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