Neanderthal Teeth from Moula-Guercy, Ardèche, France

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ABSTRACT   Here we describe dental remains from a Neanderthal fossil assemblage from Moula-Guercy, France. Our report demonstrates that the Moula-Guercy hominid remains contribute important morphological, developmental, and behavioral data to understanding Neanderthal evolutionary history. We include gross comparative morphological descriptions and enamel surface microstructure and microwear data. These teeth reveal numerous characteristics that are diagnostic of Neanderthals and provide no evidence for the presence of any other hominid taxa. Enamel growth increment data from the Moula-Guercy specimens yield evidence of a Neanderthal pattern of development, although at the lower end of the range of variation. The presence of a significant number of linear enamel hypoplasias indicates that these individuals were stressed during childhood. Molar microwear data suggest that these Neanderthals did not differ significantly from modern humans in terms of the fracture properties of the food they were consuming. The incisor microwear and macro striations provide evidence that these individuals may have been using their anterior teeth as tools, similar to the practices of several modern human populations such as the Inuit, Ipiutak, and Australian Aboriginals, and reminiscent of evidence from other Neanderthals from Krapina, Croatia, as well as the 600,000 year old hominids from Sima de los Huesos, Spain. Am J Phys Anthropol 151:477–491, 2013.   © 2013 Wiley Periodicals, Inc.

Ever since the first extensive study of Neanderthal skeletal variation (Gorjanović-Kramberger, 1906), the dentition has proven to be highly informative of Neanderthal origins, adaptation, and evolution (e.g., Kallay, 1951; Carbonell, 1965; Dean et al., 1986; Brace et al., 1987; Stringer et al., 1997; Irish, 1998; Bailey, 2006aa,b). New discoveries continue to be made in the field, laboratory, and also in museum collections (e.g., Walker et al., 2008; Crevecoeur et al., 2010; Smith et al., 2010; Benazzi et al., 2011; Walker et al., 2011), making Neanderthals one of the most important extinct hominids for studying species paleobiology. Here, we describe for the first time the Neanderthal fossil dental assemblage from Moula-Guercy, France. Our analysis includes three approaches to understanding these remains: (1) comparative descriptions of the fossil material, (2) enamel surface microstructure, and (3) microwear. Other anatomical components of the skeleton are forthcoming.

STRATIGRAPHIC, CHRONOLOGICAL, ECOLOGICAL, AND ARCHEOLOGICAL CONTEXTS

Discovered in 1972, Moula-Guercy cave overlooks the Rhone River 10 km south of the city of Valence in the parish of Soyons, Ardèche, France. Initial work at the site between 1975 and 1982 uncovered 5 m of infill characterized by a Mousterian assemblage associated with fauna indicating a cold climate (Defleur et al., 1993aa). Subsequent excavations spanning from 1991–1999 extended the sequence to a total of 7 m and revealed the first Neanderthal remains (Defleur et al., 1998). Stratigraphic analysis led to the division of the sequence into 20 layers grouped into three climatic phases corresponding to marine isotope stages 4–6 (Desclaux and Defleur, 1997; Defleur et al., 1998; Defleur et al., 2001). The upper unit, Phase I, comprises Layers VI–XI. A date of 72 ± 12 ka has been assigned to a volcanic ash (Layer VI) above the hominid level (Sanzelle et al., 2000). Fauna from this Phase includes *Mammuthus primigenius* and *Rangifer tardanus*. Together with associated micromammals, these taxa indicate a cold climate consistent with MIS 4. The underlying unit, Phase II, consists of Layers XII–XVI and includes the majority of the archeological material, all of

the Neanderthal remains, and fauna and charcoal consistent with a more temperate climate. Biostratigraphy of micromammals indicates a date of 100–120 ka for Phase II, consistent with MIS 5. The base of the sequence, Phase III, includes Layers XVII–XX. These contain micromammal remains indicating a cold, steppe environment consistent with MIS 6.

When excavations were halted in 1999, 108 hominid remains (45 craniodental and 63 postcranial specimens) had been recovered from Layer XV. The best preserved of the elements are two partial crania, a partial femur, teeth, and many complete hand and foot bones. As reported previously (Defleur et al., 1993b; Defleur et al., 1999), the remains conform to typical Neanderthal morphology and diagnostic characters include Neanderthal apomorphies. These remains also show significant perimortem damage consistent with the nutritional exploitation of a minimum of six individuals: four juveniles/children, two adults (Defleur et al., 1999). Shortly after the publication of these remains (Defleur et al., 1999), excavations were halted by local officials. As only 30% of the primary layer (Layer XV) had been excavated prior to this, full taphonomic assessment and determination of the minimum number of individuals is being withheld pending resumption and completion of the excavation work. However, we do note that our reassessment does not counter the original interpretation of six individuals: two were 15–16 years of age at death, two were 6–7 years of age at death, and there are two adult specimens representing one large and one small individual (Defleur et al., 1999).

THE STUDY OF NEANDERTHAL DENTAL REMAINS

The gross morphological structure of teeth provides enormous information about an organism's adaptive regime and evolutionary history. Given their largely inorganic content, teeth are often the only remaining body part we have for many extinct animals. Neanderthals are no exception, as numerous studies of their phylogeny and paleobiology have relied on tooth crown shape (e.g., Boule, 1921; Bailey, 2006a,b). Trinkaus' summary of primitive versus derived traits in Neanderthals compared to Early and Late Modern humans found that Neanderthals have at least three autapomorphic dental traits and lack the seven or eight derived dental traits seen in early and late modern humans, respectively (2006). These traits and others provide the basis for the morphological descriptions presented here, as we investigate whether or not the hominid dental remains from Moula-Guercy align more closely with the Neanderthals, as determined previously (Defleur et al., 1999), or have a closer affinity with Early Modern Humans.

Enamel surface microstructures also provide insight into an organism's growth rates and patterns, and disruptions to growth (e.g., Hillson and Bond, 1997). We investigated two components of enamel microstructure of the Moula-Guercy remains: perikymata and linear enamel hypoplasia.

Perikymata are enamel surface manifestations of internal growth increments known as striae of Retzius (Hillson, 1996) representing 7 or 8 days' worth of enamel growth in Neanderthals (Macchiarelli et al., 2006; Smith et al., 2009; Smith et al., 2010). Perikymata cover the surface of lateral enamel, forming shallow grooves or waves approximately 100 μm apart (Hillson and Bond, 1997). In the cuspal region of the tooth, striae of Retzius do not emerge onto the enamel surface, such that this portion of enamel growth is hidden from a surface view. However, the time lateral enamel takes to form represents approximately 85% or more of the overall enamel formation time of anterior teeth, at least in modern humans (Reid and Dean, 2006). Thus, the number of perikymata on anterior teeth reflects a large percentage of the time it took for the crown to form. Perikymata counts on Neanderthal teeth tend to fall within the range of modern human variation, but are at the low end of that range for particular teeth (the upper incisors and lower canines, Guatelli-Steinberg and Reid, 2008; anterior teeth, Ramirez-Rozzi and Bermudez de Castro, 2004). In addition, in Neanderthals perikymata are more evenly distributed across the enamel surface than they are in modern humans (Guatelli-Steinberg et al., 2007; Guatelli-Steinberg and Reid, 2008).

Linear enamel hypoplasia (LEH) appears as a line, groove or furrow in the enamel surface, reflecting periods of disrupted growth caused by systemic physiological stress, such as malnutrition and disease (Goodman and Rose, 1990; Ten Cate, 1994). Systemic physiological stress is likely to affect all of the teeth of an individual developing at the time of the stress episode (Hillson and Bond, 1997). Growth increments on the surface of the root known as periradicular bands also may become accentuated, presumably as a result of growth disruption (Smith et al., 2007).
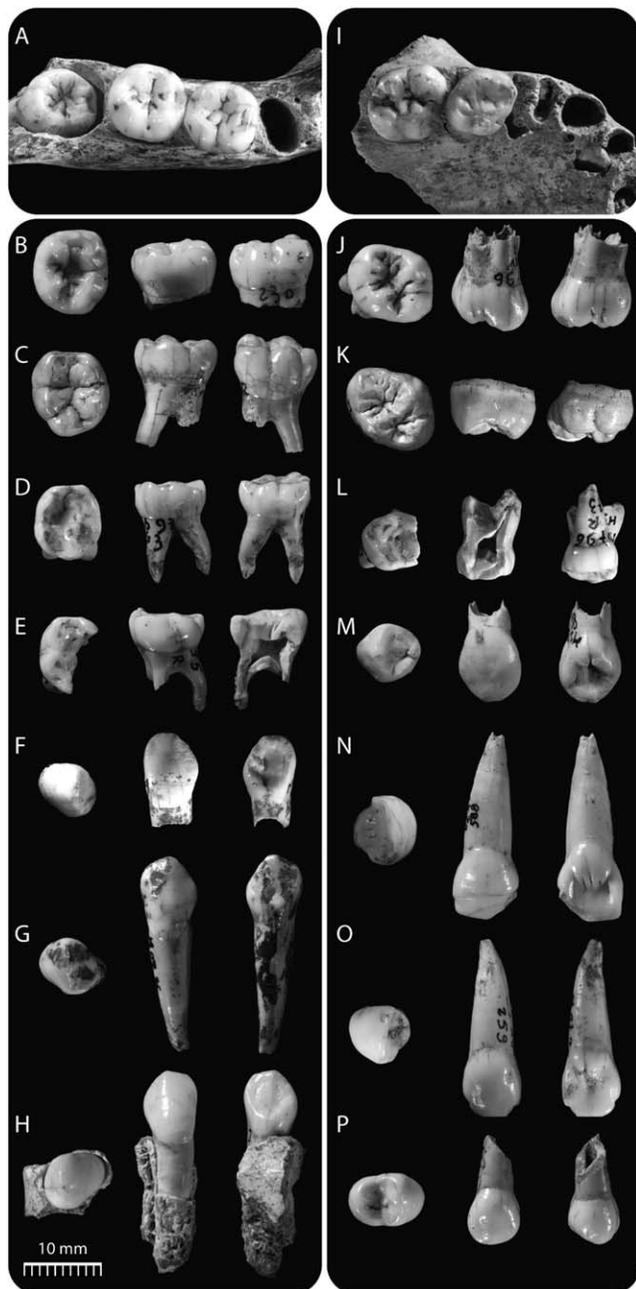
While the enamel microstructure of a tooth is informative of the development and health of an individual, we can add to our reconstruction of an organism's life history by investigating the damage to the crown surface during life. We have also undertaken an investigation of dental wear—the study of microscopic scratches and pits that form on a tooth's surface as the result of its use. Such analyses of nonhuman primates and recent human foragers indicate that microwear patterns on incisors vary with front tooth behaviors and those on molars vary with the fracture properties of foods eaten (see Ungar et al., 2007 for review). Dental microwear patterns have also been shown to distinguish fossil hominids, suggesting their value for inferring diet and tooth use in these taxa (e.g., Grine, 1987; Ungar, 2011). Here we include a description of the dental microwear of the Neanderthal specimens from Moula-Guercy.

A summary and brief contextualization of the results is provided in the discussion section.

MATERIALS

Original hominid fossil material from Moula-Guercy Cave, France, was used for the morphological descriptions. Replicas (described in detail below) were used for the enamel microstructure and dental microwear analyses. The original specimens are shown in Figure 1 and basic linear measurements are presented in Table 1. Comparative metrics for mandibular canines and first molars are presented in Figure 2.

Isolated teeth are described individually and have unique specimen numbers. Teeth still rooted in jaws were given the same specimen number, and are described in the same paragraph. Appendix 1 (Supporting Information) lists all cast material used for comparison, all

Fig. 1. Moula-Guercy Neanderthal mandibular (left panel) and maxillary (right panel) dental material. From left to right: occlusal [mesial is up, except (A) and (I)], buccal/labial, and lingual views, with the exception of (J), where the distal view is pictured. Mandible: (A) M-G2-419, (B) M-D1-230, (C) M-L4-TNN5, (D) M-G3-251, (E) M-J5-TNN4, (F) M-*-TNN2, (G) M-G4-144, (H) M-S-TNN1; Maxilla: (I) M-I4-55, (J) M-G2-117, (K) M-F3-215, (L) M-H3-73, (M) M-I4-TNN3, (N) M-D2-588, (O) M-D1-259, (P) M-S-27.

available at the Human Evolution Research Center at the University of California, Berkeley.

ABBREVIATIONS

Specimen numbers were assigned as follows: "M" designates Moula-Guercy cave, followed by a two-character alphanumeric code corresponding to the excavation grid square from which the specimen came, then a sequential specimen number or arbitrary identifier. For specimens that could not be located to a specific square, a longer code was given to indicate the range of possible source grid squares. An "S" in this position indicates a specimen recovered from a pit dug outside the standard grid (S = "sondage," or test pit in French). The sequential specimen number stems from the count of all specimens (hominid and non-hominid) within the indicated grid square. Where a sequential number could not be assigned, an arbitrary code was given. For example, M-G2-419, a mandible fragment, is the 419th specimen recovered from grid square G2, whereas M-L4-TNN5 was recovered from square L4, but not assigned a specimen number until this study began (and so received an arbitrary "new number" designation). An exception to this is M-*-TNN2, which was recovered from the backfill from layer XV, and cannot be allocated to a grid square.

Tooth identification abbreviations follow the convention in which numerical subscripts indicate mandibular and superscripts indicate maxillary (thus, a maxillary right second molar is abbreviated RM^2, and a left mandibular third premolar is LP_3). Deciduous teeth are denoted with a lowercase "d" after the designation of right or left and the tooth type in lowercase, e.g., mandibular right deciduous second molar is Rdm_2.

METHODS

Morphological descriptions

Descriptions of hominid material are most useful and relevant when comparative (White et al., 2000). The descriptions included here were done through comparison with a large cast collection in the Human Evolution Research Center at the University of California, Berkeley and against published descriptions (in addition to the publications cited within the descriptions that follow, these monographs and chapters were studied: Martin, 1923, 1926; Patte, 1957; Sakura, 1970; Tillier and Genet-Varcin, 1980; Heim, 1982; Radovčić et al., 1988; Madre-Dupouy, 1992; Condemi, 2001; Maureille et al., 2001; Bilsborough and Thompson, 2005; Garralda et al., 2008). See the Supporting Information for list of comparative specimens (all casts) that were used (this table does not include material for which only published data were employed, only the list of casts studied). Best-matches were identified and are included in the descriptions, along with the ways in which the Moula specimen differs from the best-match.

As part of the morphological descriptions, we employed five descriptive standards that facilitate comparisons between specimens. For describing non-linear shape variation, we refer to Crummett's (1994: 93) stages for incisor shoveling, the Arizona State University Dental Anthropology System (ASUDAS; Turner et al., 1991) for describing traits such as the distal accessory ridge, and Bailey's (2002) scoring system for postcanine traits not encompassed by the ASUDAS range of variation, which is based on modern humans. Liversidge and Molleson (2004) provide useful crown and root formation stages for deciduous teeth, and Demirjian et al. (1973) outlined the same for the permanent dentition. We employ these when relevant.

Enamel surface microstructure

To count perikymata in the Moula-Guercy sample, replicas of 11 of the crowns with the best preservation were
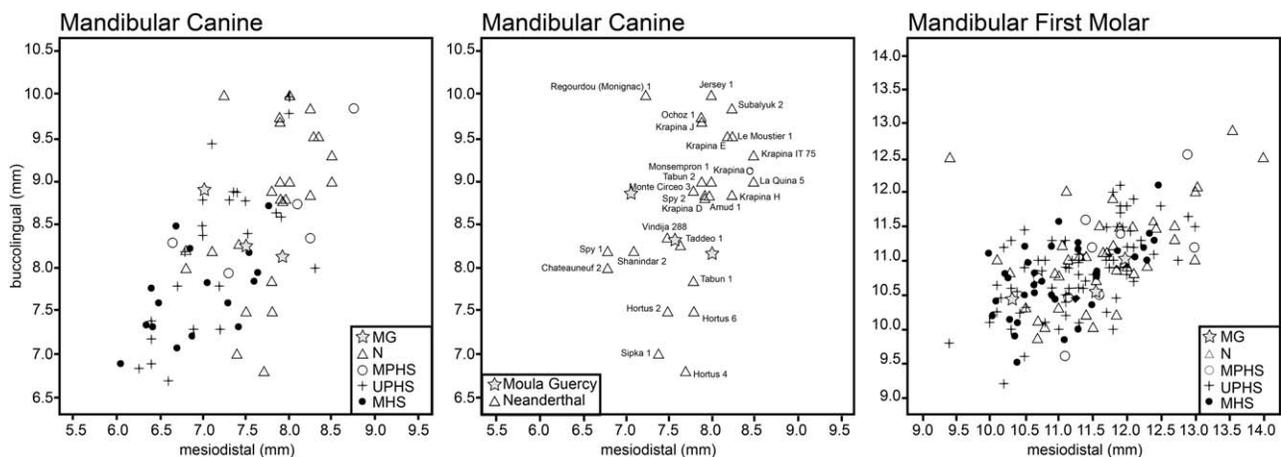
TABLE 1. *Measurements for all Moula-Guercy Neanderthal Teeth*[a]

Specimen number	Tooth identification	Buccolingual	Mesiodistal	Cervicoincisal
M-G2-419	RM_1	10.45	(10.3)	
M-G2-419	RM_2	11.1	(11.6)	
M-G2-419	RM_3	10.5	(11.3)	
M-D1-230	RM_1	10.6	(11.6)	
M-L4-TNN5	LM_1	10.9	(11.9)	
M-G3-251	Rdm_2	9.0	(9.8)	
M-J5-TNN4	Ldm_2	00	(10.4)	
M-*-TNN2	LC_1	8.2	7.6	10.9
M-G4-144	LC_1	8.1	7.9	11.6
M-S-TNN1	RC_1	8.9	7.1	11.4
M-I4-55	Rdm^2	10.1	9.2	
M-I4-55	RM^1	11.1	11.4	
M-F3-215	RM^2	11.6	10.6	
M-G2-117	RM^2	12.0	10.4	
M-H3-73	Rdm^1	00	7.4	
M-I4-TNN3	RC^1	9.5	8.6	(11.6)
M-D2-588	LI^1	8.4	00	00
M-D1-259	RI^2	8.5	8.0	10.8
M-S-27	LP^3	10.7	7.5	

[a] measurements presented in mm; estimates in parentheses.
00 indicates that the tooth is broken or too worn to accurately assess this measurement.
Tooth identifications follow the same convention as the text. Measurement protocols followed Suwa et al. (2009, see their SOM).

Fig. 2. Mesiodistal and buccolingual lengths for mandibular canines and first molars of Neanderthals (N), Middle Paleolithic *Homo sapiens* (MHPS), European Upper Paleolithic *Homo sapiens* (UPHS), Modern *Homo sapiens* (MHS), and Moula-Guercy (MG). Figure is modified from Benazzi et al.'s (2011) Figure 4, using data presented and cited therein. Note that Moula-Guercy specimens are in the center of the cluster in each panel.

placed on the stage of a measuring microscope (Spectra Services). Under a magnification of 50x, along the midline of the tooth's labial surface, the positions of perikymata were recorded using the Vision Gauge software associated with the microscope. In some instances, perikymata counts were double-checked using counts made from SEM images. In this dental sample, the anterior teeth were minimally worn, with the exception of M-D2-588, a LI^1 with an oblique incisal edge created by wear. Because the teeth were minimally worn, perikymata were counted within deciles of measured crown height, numbered from 1 to 10 from the cusp tip to the cement-enamel junction (CEJ). This protocol differs slightly from that established by Dean and Reid (2001) which also included decile lengths based on crown height reconstructions from worn teeth. For the worn upper LI^1, the crown height was assumed to be the height of the crown along the mesial edge, the least worn. When perikymata could not be clearly seen, due, for example to abrasion, they were not counted. All perikymata counts were done by one person who reported an average percentage difference between first and second counts as 5.55% on a set of various non-human primate teeth on which perikymata were counted using the same microscope used here (Guatelli-Steinberg et al., 2009). Linear enamel hypoplasias (LEHs) were identified using oblique lighting with the aid of a 10x hand lens. The locations of LEH defects were marked on the tooth replica surface. Using the measuring microscope, distances of LEH defects were measured from the CEJ to the midpoint of each defect. Widths of defects were also measured from the cervical to occlusal border of an LEH groove. Where possible, perikymata were also counted within a defect, to gain insight into the duration of growth disruption.

TABLE 2. Dental microwear texture data for Neanderthal specimens from Moula-Guercy

Specimen	Tooth	Asfc	eplsar	Smc	Tfv	$HAsfc_9$	$HAsfc_{81}$
M-I4-55	Rdm^2	2.95	0.0030	0.15	10239.19	0.45	0.89
M-I4-55	RM^1	4.31	0.0012	0.15	14202.11	0.54	0.88
M-D1-230	RM_1	1.01	0.0025	0.27	4632.41	0.37	0.56
M-G2-419	RM_1	1.35	0.0016	0.27	10875.93	0.51	0.64
M-L4-TNN5	LM_1	2.51	0.0042	0.27	10815.40	0.66	1.16
M-S-27	LP^3	3.87	0.0022	0.21	11812.66	0.48	0.63
M-G4-144	LC_1	1.39	0.0025	0.27	19102.02	0.43	0.67
M-S-TNN1	RC_1	0.88	0.0043	0.42	10806.62	0.46	0.55
M-D1-259	RI^2	1.90	0.0022	0.21	11600.83	0.56	1.17
M-D2-588	LI^1	4.33	0.0013	0.15	15069.99	0.70	1.56

Dental microwear analysis

Specimens were prepared and analyzed using standard dental microwear texture analysis protocols. Molds were made using President's Jet polyvinylsiloxane dental impression material (Coltène-Whaledent), and high-resolution casts were prepared using Epotek 301 epoxy and hardener (Epoxy Technologies). Data were collected for all available specimens that had sufficient areas of unobscured antemortem microwear (Table 2). Microwear surface preservation for the Moula-Guercy individuals was typically good when compared with many other fossil hominids; most teeth excluded from this study were either unworn, or were overwhelmed by postmortem cracks.

Nine individuals preserved unobscured antemortem microwear (Table 2). Data are reported for a dm^2 and a M^1 (M-I4-55), three M_1s (M-D1-230, M-G2-419, and M-L4-TNN5), two C_1s (M-G4-144 and M-S-TNN1), a P^3 (M-S-27), an I^2 (M-D1-259), and an I^1 (M-D2-588). We report data here for both specimens of M-I4-55 because both of these teeth preserved antemortem microwear.

Specimens were analyzed using a Sensofar Plμ white-light confocal profiler with an integrated vertical scanning interferometer and a 100x long-working-distance objective (Solarius). Elevation data were collected from four adjacent fields of view, each measuring 138 μm × 102 μm, for a total work area of 276 μm × 204 μm for each tooth. Point clouds were generated using a lateral sampling interval of 0.18 μm, and a vertical resolution of 0.05 μm. The cheek teeth were sampled for microwear on "Phase II" facets 9 or 10n, and the incisors and canines were sampled on the labial surface just above the incisal edge. These locations were chosen following convention (see Krueger et al., 2008; Krueger and Ungar, 2010). Points representing artifacts, such as dust, were deleted prior to analysis.

Point clouds were analyzed using Toothfrax and SFrax scale-sensitive fractal analysis software packages (Surfract Corp), and data were generated for the five texture attributes that have proven to be particularly useful for characterizing microwear surfaces: area-scale fractal complexity (*Asfc*), scale of maximum complexity (*Smc*), heterogeneity of complexity (*HAsfc*), textural fill volume (*Tfv*), and length-scale anisotropy of relief (*epLsar*). *HAsfc* was calculated by dividing each field of view using both 3 × 3 and 9 × 9 grids ($HAsfc_9$ and $HAsfc_{81}$, respectively). Median values for the four fields of view sampled in each tooth are presented here.

Detailed descriptions of each of these variables can be found in Scott et al. (2006) and Ungar et al. (2007).

Complexity is a measure of how surface roughness, the ratio of surface area to planimetric area, changes with scale of observation. Complex surfaces are those that show increasing roughness at progressively finer scales of observation; a heavily pitted surface with overlapping features of many sizes has a high *Asfc* value. The scale of maximum complexity reflects the point at which a surface no longer gets rougher with progressively finer scales of observation; a surface dominated by large features but lacking smaller ones would have a high *Smc* value. Heterogeneity is measured by dividing each field into a number of equal size subfields, and calculating variation in *Asfc* among them; heterogeneous surfaces have higher *HAsfc* values than do homogeneous ones. Textural fill volume is a measure of the summed volume of small squared cuboids (in this case 2 μm on a side) that would fill a surface divided by that of large squared cuboids (10μm on a side); an area with many deep moderate-size microwear features (between 2 μm and 10 μm in diameter) would have a high *Tfv* value. Finally, anisotropy is a measure of directionality of surface roughness. Average relative lengths of transects (ratios of summed 1.8 μm segments to straight-line distances between endpoints) are sampled at different orientations (5° intervals) across each surface. Greater variation in those lengths indicates greater anisotropy; a surface dominated by parallel striations has a higher *epLsar* value than one with randomly oriented scratches or pits.

RESULTS

Morphological descriptions

Mandibular. M-G2-419 is a right mandibular fragment with M_{1-2} erupted and M_3 in the crypt (Fig. 1A). The mandibular body is described in detail elsewhere (Defleur et al., in preparation). The first molar has an X5 cusp pattern that is only slightly worn with no dentine exposed. The M_2 and M_3 are unworn, although M_2 is fully erupted. The M_2 is relatively unusual for a Neanderthal in having four cusps in the cruciform cusp configuration (Scott and Turner, 1997, p. 50; Bailey, 2002). The M_3 has a Y5 cusp pattern and root formation to 6.9 mm (incomplete). An anterior fovea and mid-trigonid crest is present on all three molars (score of 2 for all three molars), a common Neanderthal trait infrequently seen on modern human M_1s, and rare on modern human M_2s and M_3s (Bailey, 2002). The M_1 and M_2 are most similar in size and shape to those preserved on the Regourdou mandible, though less worn. The Moula-Guercy M_3 is more rounded and slightly smaller, more similar in overall size and shape to Hortus VI and Vindija 206, and a little smaller than the RM_3 of Krapina mandible G.

M-D1-230 is a right M_1 with a Y5 cusp pattern, slight wear on the lingual cusps but no dentine exposed (Fig. 1B). It has a clear anterior fovea and mid-trigonid crest with a score of 1 (Bailey, 2002). The root is incompletely developed to 2 mm below cervix and fractured on the lingual side (Stage E; Demirjian et al., 1973). Its morphology is very similar to Vindija 206 (RM_1) but less worn.

M-L4-TNN5 (Fig. 1C) is a left M_1 with X5 cusp pattern, anterior fovea and slight mid-trigonid crest (score of 1; Bailey, 2002), and Stage G root development (Demirjian et al., 1973). The buccal cusps are slightly worn, but no dentine is exposed. There is a mesial contact facet but no distal interstitial facet. This crown is less worn than the M-G2-419 M_1 and larger, with a much

more pronounced cusp 5, suggesting that they are not antimeres. This LM_1 is most similar to Vindija 206 but less worn, with the hypoconulid more prominent (likely due to the reduced amount of wear on the Moula-Guercy crown). This tooth also has similarities to the LM_1 of Le Moustier.

Mesiodistal and buccolingual measurements for these three M1s are shown in Figure 2 relative to populations of other Neanderthals, modern *Homo sapiens*, European Upper Paleolithic *Homo sapiens*, and Middle Paleolithic *Homo sapiens*. This figure is modified from Benazzi et al. (2011) and relies on data presented and cited therein. Note that the three Moula-Guercy specimens fall in the middle of the distribution for the three *Homo sapiens* populations and the smaller half of the Neanderthal distribution.

M-G3-251 and M-J5-TNN4 (Fig. 1D,E) are right and left dm_2s, respectively. M-J5-TNN4 is fractured and as such is missing the lingual cusps. However, both crowns (M-G3-251 and M-J5-TNN4) have a similar estimated mesiodistal length, and are similar in morphology and wear stage. Both teeth have anterior fovea and a mid-trigonid crest that, although worn, is a score of 1. Given the similar morphology, these teeth are interpreted to be antimeres. Roots are completely formed on M-G3-251 (averaging 9 mm in length from the cervix; root development stage H2, Liversidge and Molleson, 2004). These two crowns are bigger than the dm_2 from the Kebara infant and a little smaller than K66.

M-*-TNN2 (Fig. 1F) is a left mandibular canine with the root incompletely developed (2.9 mm in length, Stage E; Demirjian et al., 1973). The crown has a strongly developed distal accessory ridge (approximately a score of 5 on the ASUDAS; Turner et al., 1991) and is shoveled, very similar in size and morphology to Hortus VIII.

M-G4-144 is a left mandibular canine (LC_1) with morphology and pattern of LEH defects that indicates it is the antimere of M-S-TNN1 (RC_1) (Fig. 1G and H, respectively). Both canines have fully developed roots (16.7 mm and 17.4 mm from cervix, left and right respectively; Stage H, Demirjian et al., 1973), but only the right crown has slight apical wear, the left is unworn. These two canines are most similar to, though less worn than Hortus VIII.

The Moula-Guercy mandibular canines fall within the middle of the size distribution of other Neanderthals and European Upper Paleolithic *Homo sapiens*, and toward the larger end of the range of variation reported for modern *Homo sapiens* (see Figs. 2 and 4, Benazzi et al., 2011).

Maxillary. M-I4-55 (Fig. 1I) is a maxillary jaw with right deciduous second molar (dm^2) and a permanent first molar (M^1). As the crowns are still in the jaw, root length could not be measured. The M^1 is relatively skewed, with internally compressed cusps. This combination of features differentiates Neanderthal maxillary molars from modern humans (Bailey, 2004). There is no Carabelli's cusp on the M^1, although the dm^2 is worn in this area, making it difficult to discern the full extent of the original morphology. The M^1 does have a small pit on the lingual surface of the protocone. The dm^2 is very similar in size and shape to the Ldm^2 from the Kebara infant (though more worn) and Gibraltar 2. The M^1 is most similar to Hortus III, although the distal aspect is more rounded on the Moula-Guercy specimen.

M-G2-117 is a RM^2 with three roots (Fig. 1J). Root formation is more extensive than is seen for M-F3-215 (described below), with a maximum length of 8.6 mm (Stage F, Demirjian et al., 1973). This crown is not as skewed as is M-F3-215, although the hypocone is very small. There is no Carabelli's cusp, but the crown does have a crease and pit between the protocone and hypocone on the lingual surface. This tooth is very similar in size and shape to Krapina 98 and 96.

M-F3-215 (Fig. 1K) is a right maxillary second molar (RM^2). The root formation is slight with a maximum length of 1.3 mm (Stage D, Demirjian et al., 1973). As is common in Neanderthals (Bailey, 2004), the crown is very skewed, with the metacone centered buccolingually between the protocone and paracone. The hypocone is present but diminished and set lingually. The crown is unworn with no Carabelli's cusp and a crease on the lingual surface between the protocone and hypocone. Like M-G2-117, this crown bears a striking resemblance to Krapina 98 and 96.

M-H3-73 is a right deciduous maxillary first molar (dm^1) with perimortem damage resulting in root and crown fracture (Fig. 1L). The buccal cusp is broken off and the crown is worn, with significant dentine exposure. The roots are fully formed (stage H2; Liversidge and Molleson, 2004); although the buccal roots are broken the lingual root extends 7.8 mm from cervix. This crown is most similar to the Kebara infant, although the Moula-Guercy crown is more worn.

M-I4-TNN3 is a right maxillary canine with a fully developed crown and an incomplete root that measures only 3.8 mm in length (Fig. 1M). The lingual side of the crown has a strongly expressed mesial lingual ridge and tuberculum dentale, giving it a somewhat shoveled appearance. This RC^1 is most similar in morphology to the canine preserved on Krapina Maxilla E (though less worn).

M-D2-588 (Fig. 1N) is a maxillary left central incisor (LI^1). The incisal edge is rounded, as is typical of Neanderthals (Crummett, 1994; Bailey, 2006bb), and lightly worn exposing a thin line of dentine. The distal corner is broken and the lingual surface has a marked triple tuberculum extension (score of 2 following Crummett's 1994 system, page 93). Shoveling on the lingual surface also approximates a score of 2 following Crummett (1994: 93). Because this crown is only lightly worn, its overall shape is most similar to Krapina Maxilla B, particularly when compared with other Neanderthal incisors that are often more worn. The root is developed to Stage G (Demirjian et al., 1973).

There are superficial but macroscopic scratch marks on the labial surface of M-D2-588. These marks are similar to the vestibular striations on the more incisal and lateral edge of the crown reported for the younger (in terms of ontogenetic age) hominid specimens from Sima de los Huesos, the 600,000-year-old *Homo heidelbergensis* population (Lozano et al., 2008). Lozano et al. (2008) conducted a detailed investigation of this wear across the large Sima de los Huesos fossil assemblage. Their analysis supports the hypothesis that these scratches are evidence of the use of the incisors as tools, similar to how Australian Aborigines use their incisors in the preparation of different types of materials, including the removal of bark from branches, and holding and stretching materials (Lozano et al., 2008, and references therein). Similar scratches have also been reported from Neanderthal specimens from Krapina (Lalueza Fox and Frayer, 1997).

TABLE 3. Perikymata counts for anterior (top) and posterior teeth (bottom)

Specimen	Tooth	CH (mm)	Deciles of crown height numbered from cusp to cervix										Sum	% pk in cervical region
			1	2	3	4	5	6	7	8	9	10		
M-G4-144	LC_1	11.6			11	13	12	12	12	12	16	15		
M-S-TNN1	RC_1	11.3	11	11	10	10	10	11	11	13	13	15	115	54.8%
M-*-TNN2	LC_1	10.9	9	8	10	9	10	10	12	11	18	21	118	61.0%
M-I4-TNN3	RC^1	10.9	11	11	11	12	11	13	10	12	16	15	122	54.0%
M-D2-588	LI^1	11.6	15	11	14	12	16	13	13	13	13	13	133	48.9%
M-D1-259	RI^2	10.3						15	15	13	17	15		

Specimen	Tooth	CH (mm)	Deciles of crown height numbered from cusp to cervix										Sum over 9 deciles
			1	2	3	4	5	6	7	8	9	10	
M-S-27	LP^3	8.5		7	8	8	8	8	7	11	11	11	79
M-D1-230	RM_1	6.7			12	14	12	11	10	11	10	10	
M-L4-TNN5	LM_1	7.5		7	6	8	13	15	17	18	16	12	112
M-F3-215	RM^2	6.9				7	6	7	6	9	10	12	
M-G2-117	RM^2	7.2								11	11	22	

CH, measured crown height; pk, perikymata.

M-D1-259 (Fig. 1O) is a maxillary right lateral incisor (RI^2) with a labial convex incisal edge, as is typical of Neanderthals. Lingual shoveling is present but not extreme; the dominant lingual feature is a strong lingual tubercle with a score between 4 and 5 (Crummett, 1994: 93), another feature common to Neanderthals (Crummett, 1994; Bailey, 2006bb). This crown is relatively unworn, similar to M-D2-588 with a fully developed root (Stage H, Demirjian et al., 1973). Like M-D2-588, it resembles the RI^2 of Krapina Maxilla B, although it is a bit larger and the lingual tubercle less developed compared to the Krapina specimen.

M-S-27 (Fig. 1P) is an unworn LP^3. The root is broken 7.5 mm beyond the cervix. This crown is most similar in morphology to the RP^3 of Hortus IX, although the Moula-Guercy crown is slightly larger and taller.

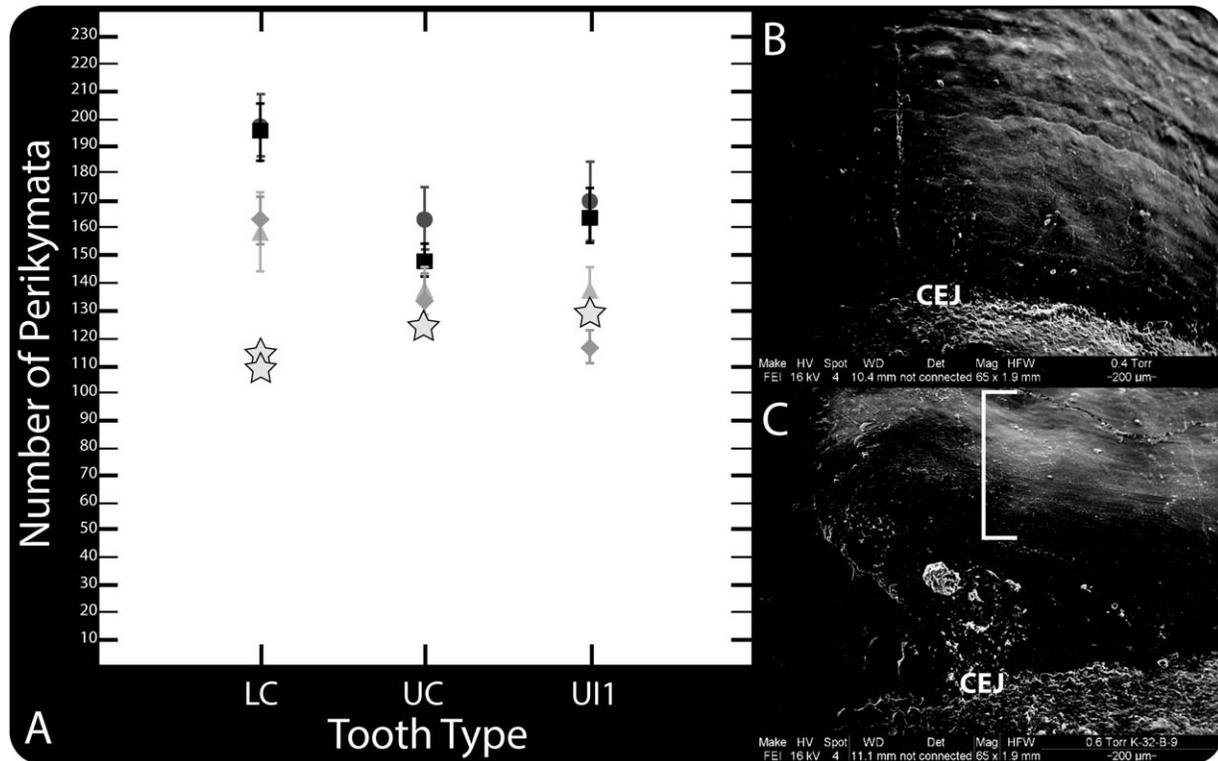## RESULTS

Enamel surface microstructure

Perikymata counts and distribution. Both lower canines, with counts of 115 and 118 (see Table 3), fall below the range given by Guatelli-Steinberg and Reid (2008) for Neanderthal lower canines (135–198 for ten lower canines). The upper canine perikymata total falls toward the low end of the range for Neanderthal upper canines given in Guatelli-Steinberg and Reid (2008) (114–157, for 14 upper canines). The I^1 also falls closer to the low than to the high end of the Neanderthal range given in Guatelli-Steinberg and Reid (2008) (121–161, for ten I^1s). In Figure 3, the Moula-Guercy counts (represented by asterisks) are superimposed over the summary statistics given in Guatelli-Steinberg and Reid (2008). These counts suggest that lateral enamel formation times for these specimens, depending on their perikymata periodicities, may have been on the shorter end of the spectrum for Neanderthals. However, all of the teeth in this sample exhibited some minimal wear, such that these perikymata count totals are less than those that would have been obtained from newly erupted teeth. These teeth also appear to exhibit a Neanderthal perikymata distribution pattern, in which perikymata are less concentrated in the cervical half of the tooth crown than they are in modern humans (Ramirez-Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2007; Guatelli-Steinberg and Reid, 2008).

For posterior teeth, the percentage of overall enamel formation time represented by lateral enamel is smaller than it is in anterior teeth—approximately 80% in premolars (Reid et al., 2008) and 65–70% in molars (Reid and Dean, 2006). Perikymata counts on the posterior teeth are given in Table 3. Premolars counts are for the buccal cusp. For the molars, perikymata were counted on the mesiobuccal cusps.

For none of the posterior teeth was it possible to obtain complete perikymata counts, owing primarily to surface abrasion but also to some attrition. Totals are given for the last 9 deciles of growth for two specimens in Table 3. It is notable that the M-L4-TNN5 LM_1 has a count of 112 perikymata in just these 9 deciles. Under an SEM, used to double-check this number, 113 perikymata were counted on this tooth. The Neanderthal range of perikymata given in Guatelli-Steinberg and Reid (2008) extends from 75 to 129 perikymata for the lower molar mesiobuccal cusp, placing M-L4-TNN5 toward the higher end of the Neanderthal range. Counts of perikymata per decile in this tooth are higher than they are in the RM_1, M-D1-230. As can be determined by dividing the number of perikymata in each decile by the length of the decile, the spacing of perikymata on M-D1-230 is generally wider than it is on the M-L4-TNN5 LM_1. Under an SEM, the perikymata subjectively appear to be very closely spaced on the M-L4-TNN5 LM_1 (Fig. 2). Such close spacing might reflect a lower periodicity for this tooth than that of M-D1-230 (Reid and Ferrell, 2006). These facts, as well as others (see morphological description above and of hypoplasia below) suggest that these right and left molars do not belong to the same individual, as periodicities are constant for all the teeth of an individual (Fitzgerald, 1998).

Linear enamel hypoplasia and accentuated periradicular bands. Table 4 summarizes the number of LEH defects in the Moula-Guercy sample and their approximate locations, given as the midpoint of a line or

Fig. 3. (A) Moula-Guercy perikymata numbers (stars) plotted among means and 95% confidence intervals for other Neanderthals and for various modern human groups given in Guatelli-Steinberg and Reid (2008). SEM images in comparable regions of Moula-Guercy first molars: M-D1-230 shown as (B), M-L4-TNN5 shown as (C). Note the more closely spaced perikymata in M-L4-TNN5, especially in bracketed region.

TABLE 4. Location of linear enamel hypoplasia

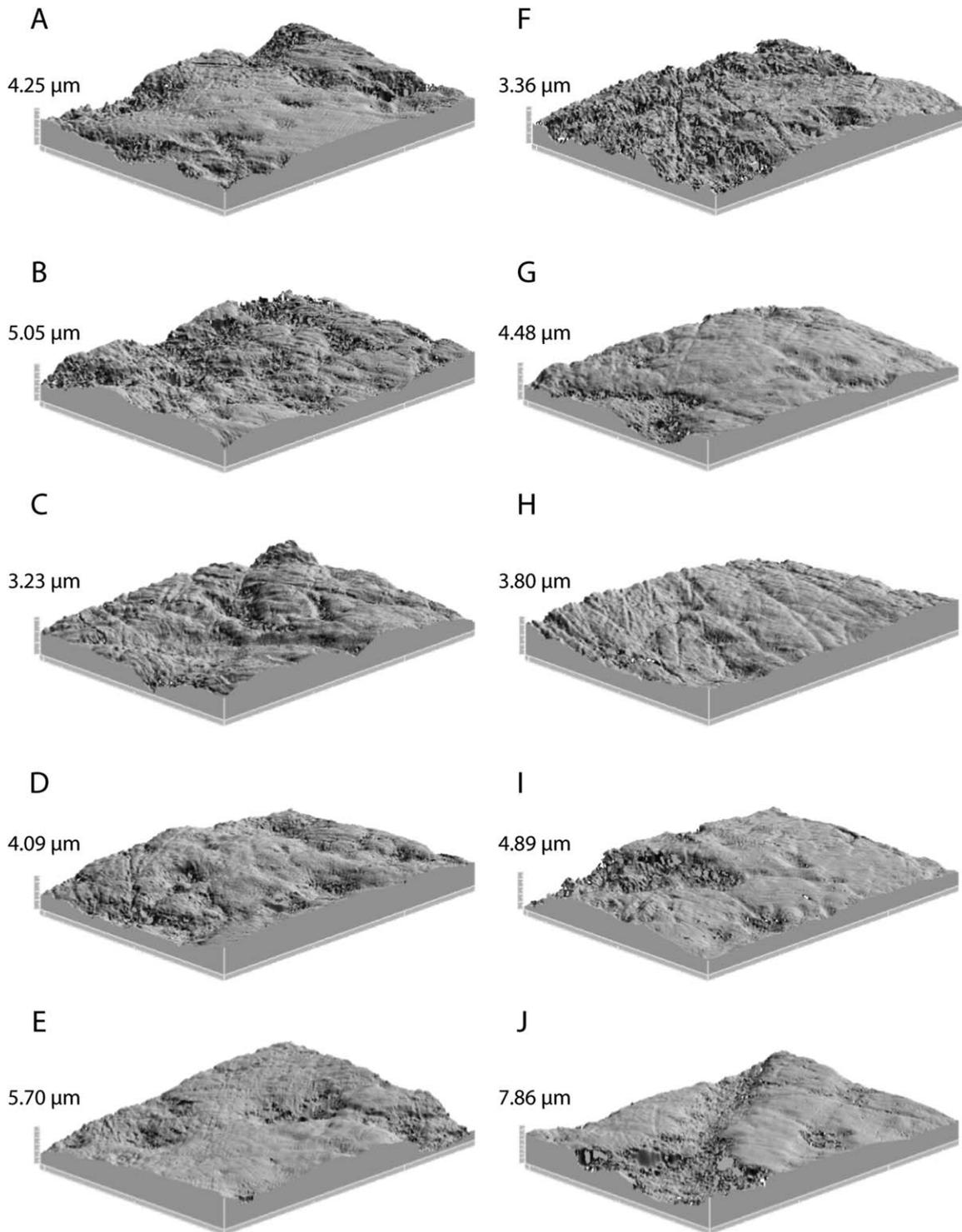|		Distance from midpoint of LEH or accentuated periradicular band to CEJ (mm)					
Specimen	Tooth	LEH1	LEH2	LEH3	LEH4	Accentuated band 1	Accentuated band 2
M-G4-144	LC_1	2.8	5.3	6.9	8.8	3.6	
M-S-TNN1	RC_1	3.0	5.0	7.1	9.0	3.6	
M-*-TNN2	LC_1	2.3					
M-14-TNN3	RC^1	3.0					
M-D2-588	LI^1	5.7	8.0			4.9	
M-D1-259	RI^2	7.7					
M-S-27	LP^3	0.8	3.0				
M-D1-230	RM_1	0.5	2.2				
M-L4-TNN5	LM_1	1.3	2.7			3.1[a]	5.2[a]
M-F3-215	RM^2						
M-G2-117	RM^2						

[a] Observed on distal surface of distal root. LEH, linear enamel hypoplasia; CEJ, cementoenamel junction.

groove from the CEJ. For some teeth, we were also able to observe periradicular bands on portions of preserved roots. For these teeth, we give the location of these accentuated bands as a distance from the CEJ.

As can be seen in Table 4, only the two M2s were lacking in LEH. M-G4-144 (LC_1) and M-S-TNN1 (RC_1), have the same number of LEH defects (4) and accentuated periradicular bands (1) on their partially preserved roots, which also occur in similar locations. These matching defects strongly support the designation of these teeth as antimeres (and see morphological description above). Similarly, the different location of LEH defects on the right and LM_1s (M-D1-230 and M-L4-TNN5, respectively) supports their attribution to different individuals, as does the difference in perikymata spacing on these teeth noted above.
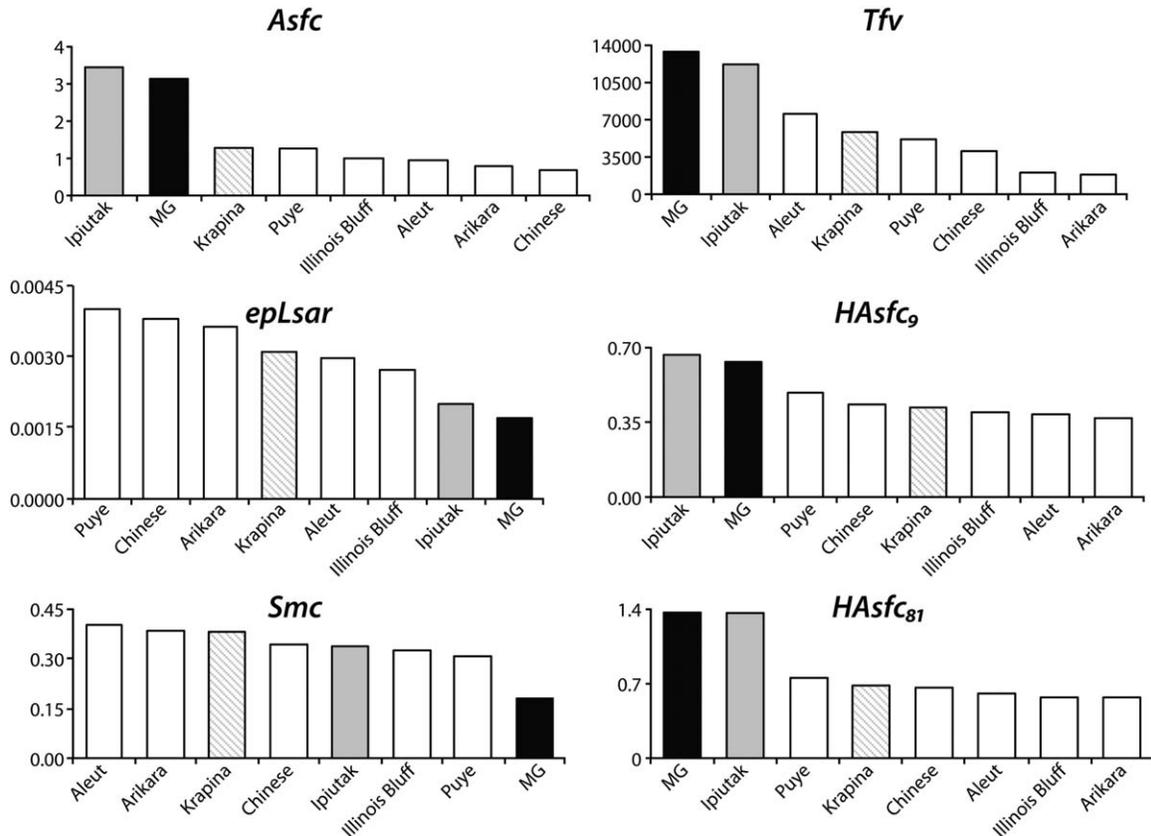
The second defect (2.7 mm from the CEJ) on the M-L4-TNN5 LM_1 is particularly interesting in that it encompasses approximately 15–20 perikymata (the exact number is unclear, given difficulty in precisely identifying the borders of this defect). Linear enamel hypoplasias can consist of one or many perikymata, depending upon the length of the growth disruption (Hillson and Bond, 1997). In furrow-form defects, the number of

A

4.25 μm

F

3.36 μm

B

5.05 μm

G

4.48 μm

C

3.23 μm

H

3.80 μm

D

4.09 μm

I

4.89 μm

E

5.70 μm

J

7.86 μm

Fig. 4. Three-dimensional axiomatic representations of microwear surfaces of specimens described in this study. Each image represents 138 μm × 102 μm for: (A) M-I4-55, dm^2; (B) M-I4-55, M^1; (C) M-D1-230, RM_1; (D) M-G2-419, RM_1; (E) M-L4-TNN5, LM_1; (F) M-S-27, P^3; (G) M-G4-144, LC_1; (H) M-S-TNN1, RC_1; (I) M-D1-259, RI^2; (J) M-D2-588, LI^1.

perikymata in the occlusal wall of the furrow represents the period of disrupted growth, while the number of perikymata in the cervical wall appear to represent a return to normal growth (Hillson and Bond, 1997). It was not possible to differentiate the occlusal and cervical walls of the M-L4-TNN5 LM_1 defect. Nevertheless, a defect encompassing 15–20 perikymata represents a significant period of growth disruption.

Fig. 5. Microwear texture attribute averages for the Moula-Guercy incisors (black) compared with averages for various bioarcheological groups from Krueger and Ungar (2010) (white). Average values for an Ipiutak sample from Point Hope, Alaska and the Krapina Neanderthals (Krueger, 2011; Krueger and Ungar, 2012) are also presented for comparison (grey and stripe, respectively).
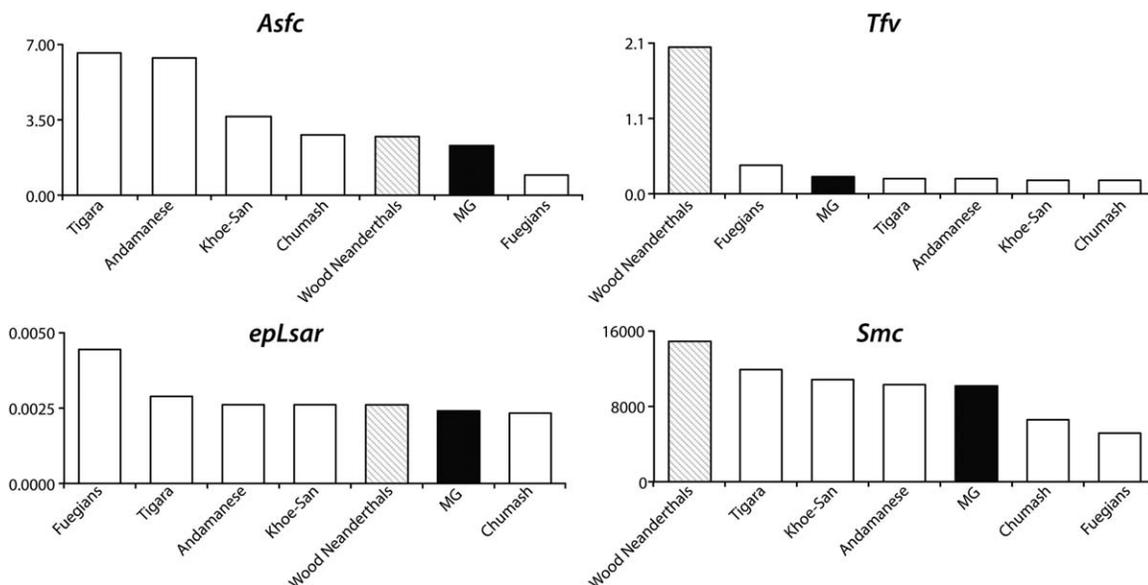
RESULTS
Dental microwear analysis

Microwear surface descriptions and texture data. The microwear texture data for the Moula-Guercy specimens are presented in Table 2 and illustrated in Figures 4–6. While there are no comparative baseline datasets available for premolars or deciduous teeth, it is possible to compare the permanent anterior and molar teeth with published and recently completed Neanderthal studies, including the large sample from Krapina (El Zaatari et al., 2011; Krueger, 2011; Krueger and Ungar, 2012). Moreover, dental microwear texture analyses of incisors and permanent molars have been published for several bioarcheological groups (El Zaatari, 2010; Krueger and Ungar, 2010; Krueger, 2011), and together, these data can help put the Moula-Guercy anterior teeth and molars into some context. Figures 5 and 6 compare average values for the Moula-Guercy incisors and molars (each represented by one tooth per individual) with those reported by several completed Neanderthal and bioarcheological studies (for the incisors: Krueger, 2011; Krueger and Ungar, 2010, 2012; for the molars: El Zaatari, 2010; El Zaatari et al., 2011). Texture attribute averages are presented for Point Hope Ipiutak incisors specifically because Ryan (1980) suggested anterior dental microwear similarities between this sample and Neanderthals. Indeed, researchers have proposed that Neanderthal front tooth use closely resembled that

of recent Alaskan Eskimos and Canadian and Greenland Inuit for many decades (e.g., Brace, 1975).

Incisors. Both incisors have large, deep microwear pits and gouges on their labial surfaces, though there are pits of varying sizes and depths on M-D1-259. Both also have striations, but these do not dominate either surface, and they show little directionality. Microwear texture data for these individuals not only stand apart from the penecontemporaneous Krapina Neanderthals, but also from all bioarcheological groups presented here except the Point Hope Ipiutak. The Moula-Guercy incisors share with this Point Hope sample extremely high Asfc, Tfv, and HAsfc values and low epLsar values (Fig. 5; note that this shows the average of the Moula-Guercy incisor data presented in Table 2, which includes a range of variation that, while seemingly large at first glance, is not remarkable relative to other samples). They separate from all other groups by their low Smc values.

Canines. The maxillary canines are more striated, with most scratches running apicocervically, especially for M-S-TNN1. M-G4-144 has more pits and gouges, mostly small to moderate in size, and shows less homogeneity of feature orientation. The overall pattern is consistent with lower complexity and higher anisotropy

Fig. 6. Microwear texture attribute averages for the Moula-Guercy permanent molars (black) compared with averages for various bioarcheological groups from El Zaatari (2010) (white) and wooded-environment Neanderthals (El Zaatari et al., 2011).

values compared with the incisors. The Smc values are also relatively high.

Premolar. The M-S-27 surface is deeply pitted with microwear features of varying sizes. There are also a few deep striations. Its Asfc value is high, and epLsar and Smc values are comparable to those of the M-D1-259 RI2, and its HAsfc values are in the range of those for the canines and permanent molars.

Permanent molars. The permanent molar "phase II" facets are dominated by small to moderate sized and fairly shallow pits. These surfaces also have a few larger striations, but these tend not to show tightly constrained orientations. Microwear texture values for the four specimens vary, but averages for all of the attributes are most comparable to those reported for Neanderthals from wooded environments (El Zaatari et al., 2011). The Moula-Guercy microwear texture attributes are unremarkable compared with those for nonhuman primate molars (Scott et al., 2006; Ungar et al., 2007). The Tfv, epLsar, and Smc averages are also well within the ranges of those reported by El Zaatari (2010) for bioarcheological samples, though the Moula-Guercy molar Asfc average is near the low end (Fig. 6). El Zaatari did not report HAsfc$_9$ or HAsfc$_{81}$ values.

Deciduous molars. The deciduous molar of M-14-55 has microwear features similar to those on facet 9 of its M^1. These include large, deep microwear pits and a few striations. The Asfc, epLsar, Tfv, and HAsfc values are in line with those for the permanent molars, and the Smc value is the same as that of the M^1 of this specimen.

DISCUSSION

Although Neanderthal teeth have been recognized to differ from modern human teeth for well over a century

(e.g., Gorjanović-Kramberger, 1906, Keith, 1913) and from those of *Homo erectus* for almost as long (e.g., Weidenreich, 1937), recent work by Bailey (2002, 2004, 2006aa, b), Bailey and Lynch (2005), Crummett (1994), Irish (1998), Kupczik and Hublin (2010), Martinón-Torres et al. (2006) and others have refined and increased our understanding of the diagnostic elements. Their work has established that maxillary and mandibular incisors, M^1, P$_4$, and M$_{1-3}$ of Neanderthals have such unique combinations of traits that these teeth are often identifiable even if found in isolation (Bailey, 2006c: S43).

The Moula-Guercy dental assemblage has representatives for all of these more diagnostic elements save for the P$_4$, and all of these specimens demonstrate traits characteristic of Neanderthals. For example, the M^1 from M-I4-55 has the typically Neanderthal skewed and internally compressed cusp configuration; the M$_{1-3}$ of M-G2-419 have the Neanderthal configuration of strongly expressed mid-trigonid crests and large anterior fovea; and the two incisors are characteristically Neanderthal in their labial convexity, shoveling and tuberculum dentale. None of the dental material recovered from Moula-Guercy provide evidence of a hominid taxon other than Neanderthals.

The dental remains from Moula-Guercy add to the continually growing sample of Neanderthals from Europe and Eurasia (e.g., Bailey and Hublin, 2006; Arsuaga et al., 2007; Trinkaus et al., 2007). While all of these specimens increase our understanding of the geographic and temporal variation of this hominid taxon, considerable controversy about the evolutionary history of Neanderthals remains (as succinctly summarized in Endicott et al., 2010).

Turning to a different data set from the fossilized morphology, recent reassessment of the ancient mtDNA data from Neanderthals (Endicott et al., 2010) finds that Neanderthals and *H. sapiens* shared a last mtDNA common ancestor 410–440 kya. Endicott et al. (2010) interpret these genetic data to support only the paleontological hypothesis that Neanderthals and the lineage

leading to *H. sapiens* diverged in the Middle Pleistocene from *Homo heidelbergensis*. Interestingly, they also find that Neanderthals and *H. sapiens* have *within* species/population coalescent dates of about 115 kya and 137 kya respectively—a relatively recent date that may indicate substantial genetic drift during the MIS 6 glaciation (∼130–191 kya) (Endicott et al., 2010:93). With this purported demographic history, it is perhaps not surprising that the specimens from Moula-Guercy have some similarities in size and morphology to the relatively penecontemporaneous site of Krapina, Croatia, at approximately 100 kya, although more work needs to be done (and in conjunction with the rest of the skeletal material) to test this hypothesis. Denoting further affinities based on these incomplete and isolated dental remains would be imprudent at this time.

In terms of the paleobiology of the Neanderthals, the Moula-Guercy dental remains yield an interesting combination of expected and unexpected results. For example, we find from the enamel surface microstructure results that the Moula-Guercy specimens are fairly characteristic of Neanderthals. Perikymata in Neanderthal teeth tend to be distributed more evenly along the enamel surface than they are in the teeth of modern humans, such that the percentage of total perikymata in the cervical halves of Neanderthal teeth is smaller than that of modern humans (Guatelli-Steinberg et al., 2007). In Neanderthals, average percentages of total perikymata present in the cervical halves of teeth range from 58.4% (I^1) to 62.4% (I_2), whereas in various modern human samples, averages range from 64.1% (southern African I^1 and Northern European C^1) to 68.5% (Inupiaq I^2) (Guatelli-Steinberg et al., 2007). The Moula-Guercy enamel surface microstructure data yield evidence of a Neanderthal pattern of development, although at the lower end of the range of variation.

However, in the Moula-Guercy sample the presence of LEH defects in the lower first molars of, presumably, two different individuals suggests an early occurrence of physiological stress that is not seen in the Krapina sample or other studied Neanderthals. LEH is less prevalent on molars than it is on other permanent teeth in both modern humans and Neanderthals (Molnar and Molnar, 1985; Goodman and Rose, 1990; Hutchinson et al., 1997), presumably because of the way molars grow (Hillson and Bond, 1997). In contrast to the presence of LEH on the first molars reported here for Moula-Guercy, no LEH defects were reported on any of the M_1s of the Krapina Neanderthals (Molnar and Molnar, 1985; Hutchinson et al., 1997). Ogilvie et al. (1989), whose data included enamel hypoplasia of all types (not only LEH but also enamel pits) did, however, find some enamel hypoplasia on first molars in an expanded sample of Neanderthals from the Near East and Europe.

The ontogenetic timing of this stress is somewhat complicated to pinpoint. The first molar initiates before birth in modern humans and completes formation early in the third year of life (Reid and Dean, 2006). First molar enamel formation may have even been completed slightly earlier in Neanderthals (Smith et al., 2007; 2009; 2010). Using modern human standards to age LEH defects, Skinner (1996) found that LEH in his Middle Paleolithic samples clustered between 3.5 and 5.5 years of age, while in his upper Paleolithic sample, LEH defects were more evenly distributed between 2 and 5 years of age. In their study of the ∼40 kya Le Moustier 1 Neanderthal, Bilsborough and Thompson (2005)

estimated that the majority of hypoplastic insults occurred between 3 and 4 years of age. They suggest that this could be the result of weaning (Thompson, 1998; Bilsborough and Thompson, 2005), although given the developmental timing of tooth mineralization and the nature of the weaning process, the ability to link LEHs directly with weaning is dubious (Humphrey, 2008). While the early stress indicated by the Moula-Guercy first molar LEHs is atypical of Middle Paleolithic individuals, the implications of what the perikymata data imply in terms of life history differences between humans and Neanderthals remain unclear (as discussed in detail in Guatelli-Steinberg and Reid, 2008).

Antemortem molar microwear data suggest that the Neanderthals from Moula-Guercy did not differ significantly from some modern humans in terms of the fracture properties of the food they were consuming (see Ungar et al., 2007, for non-human primate comparative molar data). Moreover, the texture attributes of these individuals are most congruent with other Neanderthals from wooded environments, consistent with the reconstructed environmental context of the Moula-Guercy hominins (El Zaatari et al., 2011). These data suggest that the Moula-Guercy individuals most likely relied on meat for subsistence, but ate other foods, perhaps including a richer plant resource base (El Zaatari et al., 2011).

The anterior dental microwear data indicate that these Neanderthals may have used their teeth as tools, similar to the practices of some modern human populations from the arctic (e.g., Brace, 1975). Indeed, the incisor and canine microwear texture signatures of the Moula-Guercy specimens examined here are most similar to those of the Ipiutak from Point Hope, Alaska. This bioarcheological sample is inferred to have participated in intense clamping and grasping activities in relation to the production of clothing (Krueger, 2011). This suggests that these Neanderthal individuals may have been participating in similar behavioral strategies, or at least behaviors that also required substantial anterior tooth loading.

On the other hand, the Moula-Guercy Neanderthals are different in their anterior dental microwear textures compared to those from the penecontemporaneous site of Krapina. While the incisor textures of Moula-Guercy are on the extreme ends of the spectrum overall, the Krapina sample is moderate in its values (Fig. 4). The Krapina sample shows moderate complexity, textural fill volume, and heterogeneity, and moderately low anisotropy (Krueger, 2011; Krueger and Ungar, 2012). While these values fall within the range of using the teeth as tools, they are not congruent with intense clamping or grasping activities. The Krapina Neanderthals are most similar in their values to the Coast Tsimshian from Prince Rupert Harbour, a sample inferred to have used their anterior dentition in vegetation softening for weaving tasks (Cybulski, 1974; Krueger, 2011; Krueger and Ungar, 2012). This not only indicates a lower anterior loading regime in these Neanderthals, but is also consistent with the inferred importance of plant resources (Henry et al., 2011). Consequently, the data from Moula-Guercy, coupled with those from Krapina, suggest varying Neanderthal behavioral strategies.

The larger-scale macro-striations noted on the labial surface of one of the maxillary incisors from Moula-Guercy also suggest that these Neanderthals participated in several behavioral practices affecting their

anterior teeth. These macro-striations, distinct from smaller microwear textures presented above, are similar to those reported for Neanderthals from Krapina (Lalueza Fox and Frayer, 1997) and the much older (perhaps as old as 600,000 years ago) hominids from Sima de los Huesos (Lozano et al., 2008).

In conclusion, in the morphological descriptions presented here we firmly establish that the Moula-Guercy hominids were Neanderthals with no evidence of there being another hominid taxon represented. Until excavations are completed at the site we will not know the full extent of this population, i.e., the number of individuals or the demographic composition. However, from the remains recovered to date, it is evident that Moula-Guercy already provides important sets of morphological, developmental, and behavioral data bearing on our understanding of the evolutionary history of this hominid.

ACKNOWLEDGMENTS

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