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Erik Trinkaus, Sarah A Lacy, Adrien Thibeault, Sébastien Villotte. Disentangling Cro-Magnon: The dental and alveolar remains. *Journal of Archaeological Science: Reports*, 2021, 37, 10.1016/j.jasrep.2021.102911 . hal-03441696

HAL Id: hal-03441696

<https://hal.science/hal-03441696>

Submitted on 22 Nov 2021

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Disentangling Cro-Magnon: The Dental and Alveolar Remains

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The authors declare no conflicts of interest.

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Highlights

- The Cro-Magnon human remains include the dentoalveolar remains of four individuals
- Cro-Magnon 1 (4253) exhibits advanced periodontal resorption and 3 granulomata
- Cro-Magnon 4257/58 has exceptionally large molars, for an Upper Paleolithic human
- Cro-Magnon 4253, 4256 and 4257 exhibit rotated premolars
- Cro-Magnon teeth and alveoli are otherwise unexceptional for the Upper Paleolithic

Abstract

The dental and alveolar remains of the Upper Paleolithic early modern humans from the Abri de Cro-Magnon (Dordogne, France) are described and reassessed, building on descriptions since their discovery in 1868. There are four individuals represented; two (Cro-Magnon (CM) 4253 and 4254) are portions of numbered skulls (Cro-Magnon 1 and 2) and two (Cro-Magnon 4256 and 4257/58) are unassociated but likely deriving from Cro-Magnon 3 and 4. CM 4253 exhibits advanced periodontal lesions, likely secondary to tooth wear, CM 4256 has moderate alveolar resorption, but the others show little alveolar pathology. CM 4253, 4256 and 4257 have premolar rotation, and CM 4257/58 had impacted M3s. The CM 4254 molars are average in size for the Late Pleistocene, but those of CM 4257/58 are at or beyond the upper limits of known ranges of Upper Paleolithic variation. Only the dental dimensions of the CM 4257/58 molars are exceptional for earlier Upper Paleolithic humans.

Key Words: Paleoanthropology, Upper Paleolithic, Gravettian, Dentition, Paleopathology, Granulomata, Caries

1. Introduction

The Cro-Magnon rock shelter (Les Eyzies-de-Tayac-Sireuil, Dordogne, France) is one of the premier Upper Paleolithic sites, best known for establishing the contemporaneity of early modern humans with Upper Paleolithic assemblages and Pleistocene fauna (Broca, 1868; Lartet, 1868). Although described in relative detail by Broca (1868) and Pruner-Bey (1865-75) shortly after their discovery, and reassessed 100 years later by Vallois and Billy (1965), the human skeletal assemblage from Cro-Magnon has remained poorly known despite the incorporation of various elements into Late Pleistocene comparative analyses. In this context, and in the

framework of a broader refocus on western Eurasian Upper Paleolithic human paleobiology, we have undertaken the reassessment of the Cro-Magnon human remains (Thibeault and Villotte, 2018; Villotte and Balzeau, 2018; Partiot et al., 2020; Villotte et al., 2020); in this contribution, we provide a description and reassessment of the dental and alveolar remains of the adults.

The human remains from Cro-Magnon were formerly attributed generally to the “Aurignacian,” but they are currently dated to the Mid Upper Paleolithic (MUP), to an early phase of the Gravettian technocomplex (33–31,000 cal BP) based on radiocarbon dating of associated archeological remains (Henry-Gambier, 2002; Henry-Gambier et al., 2013). The relatively abundant human remains represent all portions of the skeleton. However, they became commingled, whether in situ or subsequently, resulting in various attempts to reassociate them by individual (e.g., Broca, 1868; Pruner-Bey, 1865-75; Vallois and Billy, 1965; Henry-Gambier et al., 2013; Thibeault and Villotte, 2018; Villotte and Balzeau, 2018; Villotte et al., 2020). Based on the cranial remains, four adults are present (Broca, 1868; Lartet, 1868; Pruner-Bey, 1865-75; Vallois and Billy, 1965). Gambier et al. (2006) also identified four adults from pelvic remains, but reassessment indicates that only three are pelvically represented (Thibeault and Villotte, 2018; see also Pruner-Bey, 1865-75). Most recently, Villotte et al. (2020) determined that there is a fourth adult represented by the ulnae.

In this contribution to the reassessment of the Cro-Magnon assemblage, we focus on the adult dental and alveolar remains. These remains were a primary focus of the original Cro-Magnon description by Broca (1868), in that he used the dental remains to assess the ages-at-death of three individuals. He assessed the associated maxillae and mandible of Cro-Magnon 1 and the maxillae of Cro-Magnon 2, plus the isolated maxilla (Cro-Magnon (CM) 4257) which he assigned to Cro-Magnon 3 (Table 1). He did not consider the two separate mandibles, CM 4256 and 4258. These remains were described in more detail with respect to age-at-death, morphology, pathology and dental attrition by Pruner-Bey (1865-75), who assigned them to the four cranially identified individuals. A century later, Vallois and Billy (1965) reassessed the sample with a more inclusive discussion of the full dental and alveolar sample; they attributed the isolated CM 4256 mandible to Cro-Magnon 3, but did not assign the isolated CM 4257 and 4258 elements.

None of these papers provided detailed descriptions of the dental and especially alveolar remains, although Broca (1868) commented in particular on patterns of dental wear and both

Pruner-Bey (1865-75) and Vallois and Billy (1965) provided broader assessments of morphological and paleopathological aspects. The considerations here are intended to both reassess previously noted aspects of these alveolar and dental remains and fill out the descriptions of them.

Table 1. Previous assignments of the Cro-Magnon craniomandibular remains with dentoalveolar portions by individual.

	Broca 1868	Pruner-Bey 1865-75	Vallois & Billy 1965
CM 4253 cranium	Cro-Magnon 1	Cro-Magnon 1	Cro-Magnon 1
CM 4253 mandible	Cro-Magnon 1	Cro-Magnon 1	Cro-Magnon 1
CM 4254 cranium	Cro-Magnon 2	Cro-Magnon 2 (“3”) ¹	Cro-Magnon 2
CM 4256 mandible	no mention	Cro-Magnon 3 (“2”) ¹	Cro-Magnon 3
CM 4257 maxilla	Cro-Magnon 3	Cro-Magnon 4	unassigned
CM 4258 mandible	no mention	Cro-Magnon 4	unassigned

¹ Pruner-Bey (1865-75) referred to Cro-Magnon 2 (CM 4254) as number 3, and Cro-Magnon 3 (CM 4255) as number 2.

2. Materials

2.1 The Cro-Magnon Dentoalveolar Remains

The human remains from the Abri de Cro-Magnon are curated in the Musée de l’Homme, Muséum national d’Histoire naturelle (MNHN), Paris. The specimens of consideration here consist of the maxillae of two crania (CM 4253 [Cro-Magnon 1]) and (CM 4254 (Cro-Magnon 2)), the mandible with the first cranium (CM 4253), an isolated partial maxilla (CM 4257), and two isolated partial mandibles (CM 4256 and 4258).

The Cro-Magnon 4253 maxillae and mandible (Fig. 1) retain their full dental arcades (each M3 to M3), although both have sustained extensive postmortem abrasion and the maxillae in particular retain a coating of irregular carbonate. The carbonate cannot be removed from the fragile bone, and attempts to “clean” the cranium virtually have failed given the thinness of the layer and similar radiodensity to the underlying bone (Fig. S1). Only one partial tooth, the right M², and partial roots of two others, the right M₁ and M₃, remain in situ (Fig. 1).

The Cro-Magnon 4254 maxillary alveoli are largely present from the mesial right M³ alveolus to the mesiodistal middle of the left M¹ alveolus (Fig. 2). There is erosion especially to

the labial anterior alveoli and the buccal postcanine alveoli. The right M¹ and M² are in situ, and a root fragment of the left M¹ is present.

Cro-Magnon 4256 (Fig. 3) is a complete mandibular corpus, from incomplete M₃ alveolus to incomplete M₃ alveolus. It is largely without teeth, but the alveolar processes sustained only minor damage, primarily to those of the buccal M₁s. Although all dental crowns are absent, root portions remains for the left I₁ and both P₃s.

The Cro-Magnon 4257 left maxilla (Fig. 4) retains the lingual alveoli from the I¹ to distal of the M². There are three teeth remaining, a P⁴ and the left M¹ and M². The two molars are securely in situ. However, the P⁴ does not fit the left maxilla (see SI S5). It would be appropriate as a right P⁴ for the same individual, and it is so considered here.

The Cro-Magnon 4258 right posterior mandibular corpus and ramus (Fig. 4) retains the damaged M₁ and M₂ and the complete M₃, the last impacted in its crypt. The buccal alveoli from the mid-M₁ to the ramus are intact, but there is damage to the lingual M₁ alveolus and the lingual M₂ alveolus was lost. Most of the alveolar margins of the M₃ crypt are intact.

2.2 Comparative Samples

The principal comparative sample, and the primary context for the Cro-Magnon sample, is the human remains from the earlier Upper Paleolithic of Europe, the Early (EUP) and Mid (MUP) Upper Paleolithic combined and referred to as E/MUP. The majority of these remains derive from the MUP. Additional data for dental crown diameters are provided for European Late Upper Paleolithic (LUP) humans, and reference as appropriate is made to Middle Paleolithic late archaic (Neandertal) and early modern human remains.

3. Methods

The reassessment of these oral remains is based on visual observation of the original remains in the Musée de l'Homme in 2012 (SAL) and 2018 (ET and SV), combined with images taken in 1978 and 1985. Microtomodensitometric (μCT) data for these bones were acquired at the AST-RX platform in the MNHN. They were obtained with the microfocus tube of the μCT scanner “v|tome|xL 240” (GE Sensing and Inspection Technologies Phoenix X ray). Each final volume was then reconstructed with isotropic voxels ranging from 30 to 115 μm (Table S4) and

using NRecon v2.0 (Bruker microCT) in 16-bit format. Surface rendering (STL format) of these 3D models was obtained with Avizo v.9 (Visualization Sciences Group Inc.).

Osteometrics are limited to standard dental crown diameters (Bräuer, 1988), discrete occlusal traits follow the ASUDAS system (Turner et al., 1991; Scott and Turner, 1997), and occlusal wear is scored following Smith (1984). Comparative dental crown diameters are provided [as mean $\pm$ standard deviation (N)]. Mesiodistal diameters of the crowns with interproximal wear were estimated by continuing the rounded crown contour in occlusal view, following Wood and Abbott (1983). Data are from the published literature and personal measurement, and available on request. Right and left diameters, if available for an individual, were averaged prior to graphing and statistical calculations.

4. Results and Comparisons

4.1 Morphology and Dental Dimensions

The postmortem loss of most of the Cro-Magnon 4253, 4254 and 4256 teeth for which alveoli are preserved, crown breakage to their few remaining teeth, and extensive occlusal wear to the Cro-Magnon 4257 and 4258 molars have resulted in little available morphological data on their dentitions.

As noted by Pruner-Bey (1865-75) and Vallois and Billy (1965), both CM 4254 and 4257 have two rooted P³s, bilaterally where preserved in the former (Figs. 2 and 4). CM 4253 appears to have had single rooted P³s (Fig. S1). With the possible exception of the CM 4256 M₂s (Fig. 3), all of the molars or the molar alveoli exhibit clearly separated molar roots, indicating a general absence of taurodontism. Among the maxillary molars, the CM 4254 and 4257 M¹s appear to have been 4-cusped, or have had well developed hypocones (ASUDAS stage $\approx$ 4) (Figs. 2 and 4). The CM 4257 M² appears to have had some hypocone reduction (Fig. 4), probably ASUDAS stage 3. None of these molars retain sufficient occlusal morphology for further scoring given wear.

The one tooth providing a complete, if partially observable, occlusal surface is the CM 4258 impacted M₃. The tooth has a simple Y-5 cusp pattern without a mid-trigonid crest or other distinct features (Fig. 4). As such, it is relatively simple, especially compared to other Upper Paleolithic M₃s (see Bailey (2006) and Martín-Torres et al. (2012) for mixed early modern human comparative data).

The only reliable crown morphometrics, given wear and damage, are mesiodistal and buccolingual diameters for the CM 4254 and 4257 M¹s and M²s, the same diameters for the CM 4257 P⁴ and the CM 4258 M₂, and the mesiodistal diameter of the CM 4258 M₃ (Table S2). Even so, several of those dimensions have required estimation given interproximal wear and postmortem breakage (Table S2). The dimensions of the CM 4254 molars are unexceptional for an E/MUP (or Upper Paleolithic) human, even if the dimensions of its M² may be modestly underestimated given postmortem damage (Fig. 5).

At the same time, the dimensions of CM 4257 are unusually large for the Upper Paleolithic. The “area” (length x breadth) of the P⁴ is exceeded only by that of the E/MUP Baoussou da Torre 2. The M¹ “area” is above the known Upper Paleolithic range, and the M² “area” is exceeded only by that of the E/MUP Oase 2 (Fig. 5). The same pattern holds if the comparative sample is Late Pleistocene, thereby including Middle Paleolithic archaic and modern humans. Only the Oase 2 M² and the Baoussou da Torre 2 and Neandertal Obi-Rakhmat 1 P⁴s are larger than the Cro-Magnon 4257 teeth.

The dimensions of the CM 4258 molar crowns are more difficult to assess, given wear and postmortem damage (Fig. 4). The more complete crown, the M₂, as preserved, has mesiodistal and buccolingual diameters of 12.5 and ≈12.0 mm. Correcting for interproximal and occlusal wear, they were likely ≈13.0 and ≈12.5 mm respectively. When the respective “areas” (≈150 mm² and ≈162.5 mm²) are placed in an Upper Paleolithic context (Fig. 5), the latter one is beyond the comparative ranges and may well be modestly too high. But the preserved (minimum) values are exceeded only by the E/MUP Předmostí 9 and Oase 1.

Therefore, both CM 4257 and CM 4258 have unusually large teeth. Contra Vallois and Billy (1965), these dimensions are exceptional. They fall in the size range especially of the Oase 1 and 2 molars, dentitions which have been highlighted for having very large molars for early modern humans (Trinkaus et al., 2013; Trinkaus, 2018). The only Late Pleistocene M¹ and M₂ teeth with larger crowns are archaic human ones from the Middle/Late Pleistocene site of Krapina (Wolpoff, 1979) and the Aterian sites of Dar-es-Soltane, El Haroura and Témara (Hublin et al., 2012).

4.2 Variations in Number and Position

None of the Cro-Magnon alveoli or dental remains indicate dental agenesis or supernumerary teeth. In particular, both sides of CM 4253 and 4256 and one side each of CM 4254, 4257 and 4258 indicate the presence of third molars, the most common tooth to exhibit agenesis and the only one documented among E/MUP humans (Lacy, 2021). Among E/MUP humans, M_3 agenesis is documented for Dolní Věstonice 16 and may have been present in Předmosti 3 (Matiegka, 1934; Hillson, 2006), and supernumerary teeth occurred in Dolní Věstonice 15, Pataud 1 and Sunghir 2 (Hillson, 2006; Trinkaus et al., 2014; Villotte et al., 2018).

At the same time, the CM 4253, 4256 and 4257 alveoli indicate several orthodontic alterations. The right P_3 of CM 4253 is rotated, such that the buccal side is displaced distally, and the right C_1 may have been as well (Figs. 1 and S4). Both P_3 s of CM 4256 exhibit the same rotation. In addition, the I_2 s of CM 4256 were slightly rotated with the labial portion mesially displaced (Figs. 3 and S7), and its right M_2 was mesially sloping, with its mesial occlusal surface against the M_1 . These mandibular dental rotations (Table S3) are accompanied by a possible rotation of the CM 4253 left P^3 and the rotated left P^3 of CM 4257. The two root sockets of the latter tooth are aligned along the mesiodistal axis of the dental arcade (Figs. 4 and S8), indicating a crown rotated $\approx 90^\circ$.

Rotated mandibular premolars in particular are evident in other E/MUP humans, being present in Dolní Věstonice 13, 14 and 15, Muierii 1 and Pataud 1 (Hillson, 2006; Doboş et al., 2010; Villotte et al., 2018). The first four are unilateral, the last is bilateral, and all involve P_4 s. All of them except Muierii 1 have the buccal side displaced mesially. Rotated P_3 s are also well known in both archaic and modern Middle Paleolithic humans (Rougier et al., 2006; Hillson, 2006; Willman et al., 2012). The etiology of rotated premolars is poorly known (Stefan, 2006), but it appears to have a genetic basis (Rougier et al., 2006; McMullan and Kvam, 1990). The presence of premolar rotations in three Cro-Magnon specimens, all from separate individuals (see below), therefore reinforces the population coherence of the sample.

The CM 4258 mandible exhibits a completely impacted M_3 , such that its mesial occlusal margin is in contact with the vertical middle of the distal M_2 root below the alveolar plane (Fig. 4). There is a bony opening into the gingival area above the M_3 occlusal surface, but even the raised distal occlusal margin did not rise above the alveolar plane. As the M_3 roots are completely closed, the tooth was mature and hence fully impacted. The M^3 of the CM 4257 maxilla is not preserved. However, the distal M^2 lacks an interproximal facet, there is a section

of retromolar alveolar bone distal of the M², and there is a crypt above the M² roots of an appropriate size for an M³ crown (Figs. 4, S8 and S10). As noted by Vallois and Billy (1965), this cavity represents the position of an impacted M³ in this maxilla. Among E/MUP humans, impacted M₃s are known for Dolní Věstonice 3, 15 and 16 (Hillson, 2006; Lacy, 2014), and Pataud 1 presents an impacted M³ (Villotte et al., 2018).

4.3 Occlusal Wear

The extent of dental occlusal wear was first noted by Broca (1868) with reference to ages-at-death. In particular, he emphasized the marked wear (to or below the cervix) of CM 4253 and started the reference to the individual as a “veillard” (or old man). Indeed, the preserved mesial root of the right M₁ appears to have been occlusally worn, suggesting tooth wear below the root bifurcation, root separation, and continued functioning of the mesial root. Yet, the right M² retained at least some of its crown enamel (see SI S1 and Fig. S2), indicating that a number of the CM 4253 teeth retained crowns (see antemortem tooth loss below). It remains unclear to what extent the periodontal changes of CM 4253 (see below) may have affected his rates of dental wear (or vice versa).

The two preserved CM 4254 molars exhibit moderately pronounced wear, but unexceptional for a late third or fourth decade E/MUP individual. The CM 4257 and 4258 teeth, however, are markedly more worn, to similar degrees. In particular the M₁s retain little of their occlusal enamel, with the CM 4258 M₁ having worn away the crown enamel on a portion of its circumference. Modestly more crown is present on the M₂s.

There is nothing unusual in the patterns of occlusal (or interproximal) wear on these Cro-Magnon teeth. Nonetheless, they permit a general seriation of these individuals by degrees of wear, and assuming similar rates of wear, by ages-at-death. CM 4254 would be the youngest, followed by CM 4257 and probably CM 4258, and then CM 4253 the oldest. In comparison with other E/MUP individuals with dentitions and age-at-death assessments based on skeletal (non-dental) aspects (e.g., Hillson et al., 2006; Trinkaus et al., 2014; de Lumley, 2016), these degrees of occlusal wear suggest a range of ages-at-death for these Cro-Magnon individuals spanning the fourth to the sixth decades. This implied age range is recognized to be approximate, given expected variation within and between samples in rates of occlusal wear. Yet, it is sufficient to provide a contrast with previous age assessments based on the auricular metamorphosis of two

Cro-Magnon pelvis (Gambier et al., 2006) and considerations of the degenerations of a third individual (Thibeault and Villotte, 2018). Those age assessments suggest that all of the Cro-Magnon individuals were at the older end of this range, in agreement with CM 4253, 4257 and 4258, but definitely older than CM 4254.

4.4 Dental and Alveolar Pathology

Discussions of the Cro-Magnon dentoalveolar paleopathology have focused primarily on the possible antemortem loss of teeth by CM 4253 and on the alveolar lesions of that individual. There have been additional comments on dental carious lesions.

4.4.1 Antemortem Tooth Loss

None of the alveolar remains other than CM 4253 indicate possible antemortem tooth loss (AMTL). Their preserved portions either contain teeth or portions of teeth, or they present root sockets with portions of the lamina dura indicating postmortem loss of the teeth. CM 4253, however, retains extensively remodeled alveoli with only portions of a premolar and three molars in situ.

Vallois and Billy (1965) stated that an unspecified number of CM 4253's teeth were lost antemortem due to his alveolar lesions, although Broca (1868) and Pruner-Bey (1865-75) concluded that CM 4253 retained all 32 teeth until death. The same conclusion was reached by one of us (Lacy, 2014), although she inferred that some of the teeth may have been lost shortly prior to death. Reassessment of the alveoli (Table S1; SI S1 and S2; see Figs. 1, S1, S3 and S4) agrees with these conclusions. Four of the teeth (the M², P₃, M₁ and M₃ right) are represented by roots in situ and the M² retained a small portion of the crown (Fig. S2). Twenty-five of the empty alveoli retain sufficient portions of their sockets, mostly with intact lamina dura, to indicate postmortem loss of the teeth. The last two teeth, the left M², the right I₂ and the left M₁, are less clear. All three have alterations of their alveoli from granulomata, although each retains some portion of its root socket. Either they were lost shortly prior to death, with little time for alveolar remodeling, or they were still present but reduced in function given tenuous attachments to the alveolar bone. CM 4253 therefore had no AMTL or minor loss close to death.

As a result, the Cro-Magnon dentoalveolar remains indicate little or no AMTL, despite pronounced occlusal wear on the teeth of at least CM 4253, 4257 and 4258. In this aspect, they follow the general pattern of E/MUP dentitions. The three other complete E/MUP dental arches

with advanced wear – Caviglione 1, Dolní Věstonice 16 and Sunghir 1 – retained all of their teeth (Hillson, 2006; Trinkaus et al., 2014; Pinilla et al., 2016). Clear evidence of E/MUP AMTL is present on Barma Grande 4, Mladeč 1 and 8, and two isolated mandibles from Isturitz, and Brno 2 and Willendorf 2 may have each lost one tooth antemortem (Lacy, 2014).

4.4.2. *Dental Carious Lesion*

There is only one apparent lesion on the teeth, a dental carious lesion. It is a small occlusal pit into the dentin slightly to the lingual of the middle of the M₂ of CM 4258 (Figs. 4 and S12), as noted by Brennan (1991) and Lacy (2014). Dental carious lesions are relatively uncommon among E/MUP individuals, having been documented on the molars of Abeilles 1898-5-2, Barma Grande 2, Dolní Věstonice 13 and 15, and Pavlov 1, plus three isolated teeth from Les Rois (Lacy, 2014). [Note that Pruner-Bey (1865-75) referred to alveolar osteophytic lesions as “caries”; he did not document dental carious lesions.] There is no evidence of dental enamel hypoplasia, although the extent of occlusal wear may have removed evidence of these developmental lesions.

4.4.3 *Periodontal Alterations*

In addition, as noted and variously described by Broca (1868), Pruner-Bey (1865-75), Vallois and Billy (1965) and Lacy (2014), the CM 4253 cranium and mandible exhibit a suite of alveolar lesions. There is general periodontal alteration through the alveoli (SI S1 and S2), and it is accompanied by three granulomata. In the maxilla, there is an area of extensive resorption on the lingual sides of the left M¹ and M² alveoli, which manifests itself as a granuloma primarily associated with the M² (Figs. 1 and S1). In the mandible, there is a fenestration below the left I₁ and I₂ (Fig. S4). It is the labial opening of a granuloma centered below the I₁/I₂ septum with its largest portion below the I₁. There is new bone in the I₁ socket and rounded trabeculae in the inferior portion of the cavity.

The primary alveolar lesion, as previously noted, is below the left P₃ to M₁ (SI S2; Figs. 1, S3 to S5). It consists of a large void in the middle and lateral corpus between the inferior alveolar nerve canal and the remaining lingual alveoli for the P₃ to M₁. The bone was resorbed around the roots of the M₁, especially near their apices. The resorbed area continues buccally/laterally, such that the lateral portion of the corpus is absent from the alveolar margin (or where it would have been) inferiorly to the vertical middle of the corpus. The resorptive area rounds onto the lateral corpus below the M₁, and the exposed trabeculae within the exposed area

are rounded (see especially Fig. S5C). This area is best interpreted as a large granuloma from the M₁. As noted above, it is unclear whether the M₁ was in situ at death, given the presence of lingual root sockets, albeit with altered and resorbed bone.

The void from the left M₁ granuloma continues mesially below the P₄ and P₃, with resorption of the buccal/lateral corpus along their roots. The void rounds onto the lateral corpus by the P₄, slightly superior and distal of the mental foramen, and the bone within the void is rounded and hence resorbed. It is unclear whether the resorptive area for the P₄ is an extension of the M₁ granuloma or an additional one through the P₄. The void around the P₃ is less clear, as the margins of the void consist of both rounded resorptive surfaces, small bony growths, and broken edges. Therefore, the large left lateral mandibular void consists of either a granuloma of the M₁, which spread mesially under the P₄ and P₃, or granulomata from the M₁ and P₄ (plus possibly the P₃) that combined into a single void along the lateral corpus. A number of other E/MUP individuals exhibit granulomata, both with and without extensive occlusal wear (e.g., Barma Grande 4, Brno 2, Dolní Věstonice 16, Isturitz 4, 11 and 111, Mladeč 2 and 5457, Oreille d'Enfer 1, Pataud 1, Pavlov 1, Předmostí 21 and 26, and Sunghir 1 (Teschler-Nicola et al., 2006; Lacy, 2014; Trinkaus et al., 2006, 2014).

Cro-Magnon 4253 therefore has extensive periodontal disease, reflected in general alveolar resorption and multiple granulomata. Given the absence of all of the tooth crowns except for a small piece of the right M², it is not possible to determine to what extent the granulomata were secondary to advanced dental wear. The alveoli of the other Cro-Magnon individuals exhibit some resorption of the preserved alveolar crests, as reflected in cervix-to-alveolar crest (CAC) heights, but the advanced wear of especially CM 4257 and 4258 suggests that it may be due more to supraeruption than periodontal inflammation (see Craddock and Youngson, 2004).

Cro-Magnon 4254, 4257 and 4258 exhibit only modest amounts of alveolar remodeling from periodontal disease, to the extent that the alveolar bone is preserved. The first has little alteration around the anterior teeth, but there was some resorption around the M¹ (Figs. 2 and S6). A similar situation is present for the CM 4257 maxilla, although the root exposure is primarily from postmortem bone loss (Figs. 4 and S8). The CM 4258 mandible, despite its extensive tooth wear and hence expected supraeruption, has little change in the molar alveolar margins where preserved around the M₂ and the impacted M₃ (Figs. 4 and S11). On the other

hand, the CM 4256 mandible exhibits general resorption and rounding of the alveolar crests (Fig. 3 and S7).

4.5 Associations by Individual

The cranial remains from Cro-Magnon have traditionally (Broca, 1868; Pruner-Bey 1865-75; Vallois and Billy, 1965, Villotte and Balzeau, 2018) been used to indicate the presence of four adult partial skeletons (Cro-Magnon 1 to 4) in the fossil assemblage. Based on cranial morphology, Cro-Magnon 1, 3 and 4 have been considered to be male, whereas Cro-Magnon 2 was viewed as female (i.e., Vallois and Billy, 1965). However, a reassessment of the sexes of the Cro-Magnon crania (Guyomarc'h et al., 2017) was unable to confirm these sex determinations for Cro-Magnon 2 and 3. Cro-Magnon 4 has been considered male based only on the moderately large external occipital protuberance of CM 4259 (Vallois and Billy, 1965); similarly large ones are not unusual among recent human females (Walker, 2008), making its sex ambiguous.

The recent resorting of the lower limb remains (Thibeault and Villotte, 2018) was only able to identify three pelvically sexed adults (referred to as Alpha (male), Beta (female) and Gamma (male)), although the subsequent reassessment of the upper limb remains (Villotte et al., 2020) was able to identify a fourth large adult (Delta). Their ages-at-death are elderly for Alpha and Beta and modestly younger for Gamma, but it is unknown but probably younger adult for Delta (Thibeault and Villotte, 2018; Villotte et al., 2020). In the appendicular assessments, Alpha has been linked to Cro-Magnon 1 based on sex, advanced age, carbonate coating, and systemic pathological lesions (Gambier et al., 2006; Thibeault and Villotte, 2018), but the connections between Beta to Delta and Cro-Magnon 2 to 4 have been left unresolved.

As has been accepted since the Cro-Magnon remains were first recovered, the CM 4253 cranium and mandible fit together (as Cro-Magnon 1) and show a similar degree of age-related dental and alveolar alterations. The pathological alterations of the alveoli, however, are merely advanced conditions of normal periodontal resorption combined with several granulomata, the latter most likely related to advanced tooth wear and pulpal exposure (Clarke, 1990; Alt et al., 1998).

Similarly, as noted by Pruner-Bey (1865-75), the CM 4257 and 4258 maxilla and mandible make a logical pair in several respects. They exhibit very similar degrees of occlusal and interproximal wear. Each exhibits an impacted M3. They have little evidence of periodontal

disease despite their advanced dental wear. And they both have teeth that are among the largest in the E/MUP and in the Late Pleistocene generally.

The CM 4254 maxillae and teeth are part of the Cro-Magnon 2 cranium, which lacks a directly associated mandible. The CM 4258 mandible does not fit with CM 4254 given the marked contrasts in molar occlusal wear and dental dimensions. The CM 4256 mandible could be associated with CM 4254; however, the periodontal resorption throughout the CM 4256 dental arcade contrast with the minimal alveolar changes of CM 4254, making a pairing of them unlikely. As a result, the dentoalveolar remains from Cro-Magnon indicate four individuals: CM 4253 (Cro-Magnon 1), CM 4254 (Cro-Magnon 2), CM 4256, and CM 4257/58.

The first two of these dentoalveolar individuals are portions of the Cro-Magnon 1 and 2 craniomandibular remains. The other two represent older individuals, based on periodontal alterations and dental wear. Each one could be associated with either Cro-Magnon 3 or 4, both of which have been considered as an older but not aged individual, albeit on the basis of suture closure (e.g., Vallois and Billy, 1965). Contra Broca (1868), Pruner-Bey (1865-75) and Vallois and Billy (1965) (Table 1), it is not possible to resolve which maxilla/mandible belongs with which of these crania.

The associations with the appendicular Alpha to Delta individuals include Cro-Magnon 1 with Alpha, but the others are less clear. The unsexed CM 4254 cranium (Cro-Magnon 2), as a probable fourth decade adult based on dental wear, cannot be associated with the female Beta given that the latter's age-at-death was ≥ 60 years based on auricular metamorphosis (Gambier et al., 2006). It could be linked to the male Gamma, although it is unlikely given that Gamma's age-at-death was similarly assessed to be >40 years. Assuming that there are four adults represented in the Cro-Magnon sample, CM 4254 was therefore either the same individual as Delta or, unlikely, Gamma. If CM 4254 and Delta were the same individual, then CM 4256 and 4257/58 would then be the same individuals as Beta and Gamma. It is nonetheless not possible to assess which of the CM 4256 and 4257/58 dentoalveolar remains would go with Beta versus Gamma.

The most likely combinations, therefore (Fig. 6; Table S5), are CM 4253/Cro-Magnon 1 with Alpha and CM 4254/Cro-Magnon 2 with Delta. CM 4256 and CM 4257/58 appear equally likely to associate with either Cro-Magnon 3 or 4 and with either Beta or Gamma.

5. Discussion and Conclusion

This reassessment of the adult Cro-Magnon dental and alveolar remains provides additional data on their associations by individual, ages-at-death, oral health, and dental dimensions and morphology. In most respects, they fall comfortably within the patterns evident in other Early and Mid Upper Paleolithic remains.

These dentoalveolar remains (three mandibles, a maxilla, and two maxillae within crania) indicate the presence of four adults in the sample, in agreement with the cranial and upper limb remains. The CM 4253 (Cro-Magnon 1) maxilla and mandible, given their advanced dental wear and periodontal changes, fit well together and with the older male postcranial remains designated Alpha. The modest degree of dental wear on the CM 4254 (Cro-Magnon 2) maxilla indicates a younger adult, which makes it unlikely to be associated with the older Beta and Gamma postcrania and therefore, by default, associates it with the Delta upper limb remains. The CM 4257 maxilla and 4258 mandible go together by several criteria as from an older adult. The CM 4256 mandible does not fit with the CM 4254 maxilla given its alveolar alterations and thus remains as a separate adult. It remains unclear which of the other crania (Cro-Magnon 3 and 4) or postcranial sets (Beta and Gamma) go with CM 4257/58 versus with CM 4256.

The Cro-Magnon dental and alveolar remains, in combination with the Alpha to Gamma postcrania, therefore indicate three older adults and one younger adult in the sample. In the broader European E/MUP sample of older versus younger adults (approximately <40 and >40 years) (Trinkaus, 2011), the addition of these four Cro-Magnon adults provides a sample with 32.6% (n = 43) older adults (31.4% (n = 51) if African and Asian E/MUP remains are included). Although this percentage of older adults is higher than the previous value (26.5%), it remains well below the average percentage (65.0%) for six ethnohistorical samples (52.0% – 80.4%), below the average (39.3%) for nine recent archeological samples, and at the bottom of the range for the archeological ones (30.5% – 48.5%) (Trinkaus, 2011); the lowest of these recent human values has been critiqued as providing a demographic, social and subsistence-related challenges to the population in question (Howell, 1982; Paine and Harpending, 1998). The addition of the older age profile for the Cro-Magnon adults therefore shifts the E/MUP age distribution, but the E/MUP sample still exhibits the modest number of older adults present throughout the Pleistocene fossil record (Trinkaus, 2011; Streeter et al., 2001).

Although there has been emphasis on the condition of the alveoli of Cro-Magnon 1 since the early discussions of Broca (1868) and Pruner-Bey (1865-75), the indications of oral health among the Cro-Magnon adults are unexceptional for the E/MUP. Granulomata, some associated with advanced dental wear, are relatively common in the E/MUP, and periodontal disease in general was widespread in the Upper Paleolithic (Lacy, 2014). All of the Cro-Magnon adults exhibit dental calculus, as do most Pleistocene human remains. The impacted M3s of CM 4257/58 do not appear to have generated any periodontal disease. These remains indicate little or no antemortem tooth loss, a condition evident in many E/MUP specimens. And the small occlusal carious lesion of CM 4258 adds to the modest number of such lesions among E/MUP humans but does not indicate serious dental decay.

The only dental features of note are the premolar rotations of CM 4253, 4256 and 4257 and the crown dimensions of the CM 4257/58 molars. Premolar rotations are moderately common among E/MUP humans, and Late Pleistocene remains in general. To the extent that they are genetically determined, they provide some unity to the Cro-Magnon sample but do not imply broader relationships among E/MUP humans. The dimensions of the CM 4254 M¹ and M² are average for an Upper Paleolithic human, but those of CM 4257/58 are exceptional. The CM 4257/58 P³ is matched by only one E/MUP specimen (Baoussou da Torre 2), its M² is exceeded only by that of Oase 2, and its probable M¹ and M₂ dimensions are beyond even the very large teeth of the Oase 1 and 2. The only Late Pleistocene M¹ and M₂ teeth with larger crowns are earlier Middle Paleolithic archaic human ones from Krapina and northwest African Aterian sites.

The dental and alveolar remains from the Abri de Cro-Magnon therefore contribute to the disentangling of this paleontologically and historically important sample, and they provide further evidence on the oral health and dental configurations of Early/Mid Upper Paleolithic Europeans. With the exception of the very large molars of Cro-Magnon 4257/58, these Mid Upper Paleolithic remains enter comfortably into the variation of these earlier Upper Paleolithic humans.

Acknowledgments

The authors thank Veronique Laborde, Aurélie Fort (curators at the Musée de l'Homme) and Dominique Grimaud-Hervé (in charge of the collection) for granting access to the Cro-Magnon remains. Funding: This research was supported by ANR Gravett'Os (ANR-15-CE33-

0004) and the Leakey Foundation. Neither funding agency had a role in research design or publication.

References

- Alt, K.W., Türp, J.C., Wächter, R., 1998. Periapical lesions—clinical and anthropological aspects. in: Alt, K.W., Rösing F.W., Teschler-Nicola M. (Eds.), *Dental Anthropology*. Springer, Vienna. pp. 247-276. https://doi.org/10.1007/978-3-7091-7496-8_14.
- Bailey, S., 2006. Beyond shovel-shaped incisors: Neandertal dental morphology in a comparative context. *Periodicum Biologorum* 108, 253-267.
- Bräuer, G., 1988. Osteometrie. in: Knussman, R. (Ed.) *Anthropologie I*. Fischer, Stuttgart. pp. 160-232.
- Brennan, M.U., 1991. Health and disease in the Middle and Upper Paleolithic of southwestern France: a bioarcheological study. Ph.D. Thesis. New York University.
- Broca, P., 1868. Sur les crânes et ossements des Eyzies. *Bull. Soc. Anthropol. Paris* 3, 350–392. <https://doi.org/10.3406/bmsap.1868.9548>
- Clarke, N.G., 1990. Periodontal defects of pulpal origin: evidence in early man. *Am. J. Phys. Anthropol.* 82(3), 371-376.
- Craddock, H.L., Youngson, C.C., 2004. Eruptive tooth movement – the current state of knowledge. *Br. Dent. J.* 197, 385-391. <https://doi.org/10.1038/sj.bdj.4811712>.
- de Lumley, M.A., 2016. Estimation de l'âge au décès de “La Dame de Cavillon.” in: de Lumley, H. (Ed.), *La Grotte du Cavillon sous la Falaise des Baousse Rousse, Grimaldi, Vintimille, Italie III: Étude Anatomique du Squelette de “la Dame du Cavillon.”* CNRS, Paris. pp. 939-940.
- Doboş, A., Sofîcaru, A., Trinkaus, E., 2010. The Prehistory and Paleontology of the Peştera Muierii, Romania. *Étud. Rech. Archéol. Univ. Liège* 124, 1-122.
- Gambier, D., Brůžek, J., Schmitt, A., Houët, F., Murail, P. 2006. Révision du sexe et de l'âge au décès des fossiles de Cro-Magnon (Dordogne, France) à partir de l'os coxal. *C. R. Palevol* 5, 735-741. <https://doi.org/10.1016/j.crpv.2005.12.011>.
- Guyomarc'h, P., Samsel, M., Courtaud, P., Mora, P., Dutailly, B., Villotte, S., 2017. New data on the paleobiology of the Gravettian individual L2A from Cussac cave (Dordogne, France)

through a virtual approach. *J. Archaeol. Sci. Rep.* 14, 365–373.
<https://doi.org/10.1016/j.jasrep.2017.06.005>.

Henry-Gambier, D., 2002. Les fossiles de Cro-Magnon (Les Eyzies-de-Tayac, Dordogne) : nouvelles données sur leur position chronologique et leur attribution culturelle. *Bull. Soc. Anthropol. Paris* n.s., 14, 89–112. <http://bmsap.revues.org/459>.

Henry-Gambier, D., Nespoulet, R., Chiotti, L., 2013. An Early Gravettian cultural attribution for the human fossils from the Cro-Magnon rock shelter (Les Eyzies-de-Tayac, Dordogne). *Paleo* 24, 121–138.

Hillson, S.W., 2006. Dental morphology, proportions and attrition. in: Trinkaus, E., Svoboda, J.A. (Eds.), *Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov*. Oxford University Press, New York, pp. 179-223.

Hillson, S.W., Franciscus, R.G., Holliday, T.W., Trinkaus, E., 2006. The ages-at-death. in: Trinkaus, E., Svoboda, J.A. (Eds.), *Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov*. Oxford University Press, New York, pp. 31-45.

Howell, N., 1982. Village composition implied by paleodemographic life table: the Libben site. *Am. J. Phys. Anthropol.* 59, 263-269.

Hublin, J.J., Verna, C., Bailey, S., Smith, T., Olejnczak, A., Sbihi-Alaoui, F.Z., Zouak, M., 2012. Dental evidence from the Aterian human populations of Morocco. in: Hublin, J.J., McPherron, S.P. (Eds.), *Modern Origins: A North African Perspective*, Springer, Dordrecht, pp 189-204. https://doi.org/10.1007/978-94-007-2929-2_13.

Lacy, S.A., 2014. Oral Health and its Implications in Late Pleistocene Western Eurasian Humans. Ph.D.Thesis, Washington University in Saint Louis.

Lacy, S.A., (2021). Evidence of dental agenesis in Late Pleistocene *Homo*. *Intl. J. Paleopathol.* in 32, 103-110. <https://doi.org/10.1016/j.ijpp.2021.01.001>.

Lartet, L., 1868. Une sépulture des troglodytes du Périgord (crânes des Eyzies). *Bull. Soc. Anthropol. Paris* 3, 335–349. <https://doi.org/10.3406/bmsap.1868.9547>

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L., Arsuaga, J.L., 2012. Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *J. Hum. Evol.* 62, 7-58.
<https://doi.org/10.1016/j.jhevol.2011.08.007>.

Matiegka J., 1934. *Homo předměstensis*. Fossilní člověk z Předmostí na Moravě I. Lebký. Česká Akademie Věd a Umění, Prague.

McMullan, R.E., Kvam, E., 1990. Investigation of premolar rotation in a group of 15-year-old Norwegian children. *Eur. J. Orthodont.* 12, 311-315.

Paine, R.R., Harpending, H.C., 1998. Effect of sample bias on paleodemographic fertility estimates. *Am. J. Phys. Anthropol.* 105, 231-240. [https://doi.org/10.1002/\(sici\)1096-8644](https://doi.org/10.1002/(sici)1096-8644).

Partiot, C., Trinkaus, E., Knüsel, C.J., Villotte, S., 2020. The Cro-Magnon babies: Morphology and mortuary implications of the Cro-Magnon immature remains. *J. Archaeol. Sci. Rep.* 30, 102257. <https://doi.org/10.1016/j.jasrep.2020.102257>.

Pinilla, B., Pérez-Pérez, A., Puech, B., Puech, P.F., Garrigue, N., 2016. Usure dentaire et mode masticatoire de “La Dame du Cavillon.” Variabilité de la nourriture des hommes modernes lors du dernier maximum glaciaire. in: de Lumley, H. (Ed.), *La Grotte du Cavillon sous la Falaise des Baousses Rousse, Grimaldi, Vintimille, Italie III: Étude Anatomique du Squelette de “La Dame du Cavillon.”* CNRS, Paris, pp. 1213-1234.

Pruner-Bey, F., 1865-75. An account of the human bones found in the cave of Cro-Magnon, in Dordogne, in: Lartet, E., Christy, H. (Eds.), *Reliquiae Aquitanicae: Being Contributions to Archaeology and Palaeontology of Périgord and the Adjoining Provinces of Southern France*. Williams and Norgate, London, pp. 73–92.

Rougier, H., Crevecoeur, I., Wolpoff, M.H., 2006. Lower third premolar rotation in the Krapina dental sample. *Periodicum Biologorum* 108, 269-278.

Scott, G.R., Turner, C.G. II, 1997. *The Anthropology of Modern Human Teeth. Dental Morphology and its Variation in Recent Human Populations*. Cambridge University Press, Cambridge UK.

Smith, B.H., 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J. Phys. Anthropol.* 63, 39-56.

Stefan, V.H., 2006. Rotation of the maxillary premolars: Evidence in support of premolar morphogenetic field. *Dent. Anthropol.* 19, 70-73.

Streeter, M., Stout, S.D., Trinkaus, E., Stringer, C.B., Roberts, M.B. & Parfitt, S.A., 2001. Histomorphometric age assessment of the Boxgrove 1 tibial diaphysis. *J. Hum. Evol.* 40, 331-338. <https://doi.org/10.1006/jhev.2001.0460>.

- Teschler-Nicola, M., Czerny, C., Oliva, M., Schamall, D., & Schultz, M., 2006. Pathological alterations and traumas in the human skeletal remains from Mladeč. in: Teschler-Nicola, M. (Ed.), *Early Modern Humans at the Moravian Gate*. Springer, Vienna. pp. 473-489.
- Thibeault, A., Villotte, S., 2018. Disentangling Cro-Magnon: A multiproxy approach to reassociate lower limb skeletal remains and to determine the biological profiles of the adult individuals. *J. Archaeol. Sci. Rep.* 21, 76-86.
<https://doi.10.1016/j.jasrep.2018.06.038>.
- Trinkaus, E. (2011) Late Pleistocene adult mortality patterns and modern human establishment. *Proc. Natl. Acad. Sci USA* 108, 1267-1271. <https://doi.10.1073/pnas.1018700108>.
- Trinkaus, E., 2018. An abundance of developmental anomalies and abnormalities in Pleistocene people. *Proc. Natl. Acad. Sci. USA* 115(47), 11941-11946.
<https://doi.10.1073/pnas.1814989115>.
- Trinkaus, E., Hillson, S.W., Franciscus, R.G., Holliday, T.W., 2006. Skeletal and dental paleopathology. in: Trinkaus, E., Svoboda, J.A. (Eds.), *Early Modern Human Evolution in Central Europe: The People of Dolní Věstonice and Pavlov*. Oxford University Press, New York, pp. 419-458.
- Trinkaus, E., Bailey, S.E., Rougier, H., 2013. The dental and alveolar remains of Oase 1 and 2. in: Trinkaus, E., Constantin, S., Zilhão, J. (Eds.), *Life and Death at the Peștera cu Oase. A Setting for Modern Human Emergence in Europe*. Oxford University Press, New York, pp. 348-374.
- Trinkaus, E., Buzhilova, A.P., Mednikova, M.B., Dobrovolskaya, M.V., 2014. *The People of Sunghir: Burials, Bodies and Behavior in the Earlier Upper Paleolithic*. Oxford University Press, New York.
- Turner, C.G II, 1991. Scoring produces for key morphological traits of the permanent dentition: The Arizona State University dental anthropology system. in: Kelley, M.S., Larsen, C.S. (Eds.), *Advances in Dental Anthropology*, Wiley-Liss, New York, pp. 13-31.
- Vallois, H.V., Billy, G., 1965. Nouvelles recherches sur les hommes fossiles de l'abri de Cro-Magnon. *L'Anthropol.* 69, 47-74.
- Villotte, S., Balzeau, A., 2018. Que reste-t-il des hommes de Cro-Magnon 150 ans après leur découverte? *Bull. Soc. Anthropol. Paris* 30, 146-152. <https://doi.org/10.3166/bmsap-2018-0026>.

- Villotte, S., Ogden, A.R., Trinkaus, E., 2018. Dental abnormalities and oral pathology of the Pataud 1 Upper Paleolithic human. *Bull. Soc. Anthropol. Paris* 30, 153–161. <https://doi.10.3166/bmsap-2018-0020>.
- Villotte, S., Samsel, M., Sparacello, V., 2017. The paleobiology of two adult skeletons from Baoussou da Torre (Bausu da Ture) (Liguria, Italy): Implications for Gravettian lifestyle. *C. R. Palevol* 16, 462–473. <https://doi.org/10.1016/j.crpv.2016.09.004>.
- Villotte, S., Thibeault, A., Sparacello, V., Trinkaus, E., 2020. Disentangling Cro-Magnon: The adult upper limb skeleton. *J. Archaeol. Sci. Rep.* 33, 102475. <https://doi.org/10.1016/j.jasrep.2020.102475>.
- Walker, P.L., 2008. Sexing skulls using discriminant function analysis of visually assessed traits. *Am. J. Phys. Anthropol.* 136, 39–50. <https://doi.10.1002/ajpa.20776>.
- Willman, J.C., Maki, J., Bayle, P., Trinkaus, E., Zilhão, J., 2012. Middle Paleolithic human remains from the Gruta da Oliveira (Torres Nova), Portugal. *Am. J. Phys. Anthropol.* 149, 39–51. <https://doi.10.1002/ajpa.22091>.
- Wolpoff MH. 1979. The Krapina dental remains. *Am. J. Phys. Anthropol.* 50, 67–114.
- Wood, B., Abbott, S., 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. *J. Anat.* 136, 197–219.

Captions to the Figures

Figure 1. Occlusal views of the Cro-Magnon 4253 (Cro-Magnon 1) maxillae (above) and mandible (below). The maxillary alveoli are encrusted with thin carbonate. The mandibular alveoli have sustained some erosion, especially lingually by the molars, and the left buccal alveolus is extensively resorbed from an M₁-centered granuloma. Portions of teeth are present for the right M² and the right P₃ and M₁.

Figure 2. Occlusal view of the Cro-Magnon 4254 (Cro-Magnon 2) maxillae.

Figure 3. Occlusal view of the Cro-Magnon 4256 mandibular corpus. Portions of the roots are preserved for the left I₁ and both P₃s.

Figure 4. The Cro-Magnon 4257 left maxilla in occlusal and buccal views (above) and the Cro-Magnon 4258 right mandible in medial and occlusal views (below). Note that the CM 4257 P³ does not fit into the left maxilla, and it probably represents the right P³ of the same individual (see Fig. S8).

Figure 5. The maxillary P⁴, M¹ and M² and mandibular M₂ crown “areas” (length x breadth) for Cro-Magnon 4254, 4257 and 4258 compared to boxplot distributions of European Upper Paleolithic samples: E/MUP: Early and Mid Upper Paleolithic; LUP: Late Upper Paleolithic. Samples sizes are: E/MUP: 26, 49, 42 and 43; LUP: 5, 13, 11 and 12 for the P⁴, M¹, M² and M₂ respectively. The E/MUP high outlier in the M¹ and especially the M² plots is Oase 2 (Trinkaus et al., 2013); the high E/MUP P⁴ value is Baouso da Torre (Bausu da Ture) 2 (Villotte et al., 2017). The two values for CM 4258 M₂ are the minimum “area” (4258a) and the estimated “area” (4258b); the high E/MUP M₂ values are Předmostí 9 and Oase 1 (Matiegka, 1934; Trinkaus et al., 2013).

Figure 6. Probable and possible associations of the Cro-Magnon dentoalveolar remains (middle) with the numbered crania (left) and the appendicular sets (right).

Figure

Figure

Figure

5 cm

Cro-Magnon 1 CM 4253 Alpha

Cro-Magnon 2 CM 4254

Delta

Author contributions:

Erik Trinkaus: Conceptualization, Data curation, Investigation, Methodology, Visualization, Writing - original draft. **Sarah A. Lacy:** Funding acquisition, Data curation, Investigation, Methodology, Writing-review & editing. **Adrien Thibeault:** Methodology, Visualization, Writing-review & editing. **Sébastien Villotte:** Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Writing-review & editing.

Disentangling Cro-Magnon: The Dental and Alveolar Remains Supporting Information

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S1: Cro-Magnon 4253 (Cro-Magnon 1) Maxillary Dentoalveolar Remains

All of the Cro-Magnon 1 maxillary alveoli are encrusted with a thin layer of carbonate, which contains “pearls” of concretions, especially in the postcanine areas. The observations are based on visual assessment of the original specimen combined with a CT slice of the maxilla (Figs. S1 and S3).

Except as noted otherwise for molars, all of the sockets appear normal without the resorption associated with antemortem tooth loss, despite damage to the alveolar margins. The incisors, canines and premolars are therefore inferred to have been lost postmortem. Three of the teeth, the left P³ and the right C₁ and P₃, were rotated and/or appear to have been rotated (Table S3).

Figure S1. Occlusal view of the Cro-Magnon 4253 maxillae (left) and horizontal CT slice through the alveoli of the maxillae (right). There are also palatine ridges along the intermaxillary suture, whose developmental basis remains unclear (Léonard et al., 2014)

I¹ Right

There is a largely complete alveolus lacking the labial margin.

I¹ Left

The alveolus is essentially complete.

31
32 *I² Right*

33 The lingual half of the alveolus remains with a portion of the mesial side. Carbonate
34 partially filling the mesial side of the socket.

35
36 *I² Left*

37 The lingual and mesial sides of the alveolus are present.

38
39 *C¹ Right*

40 The alveolus is open mesially and labially. The root is tilted such that its apex points
41 distally. based on the lingual side of the socket.

42
43 *C¹ Left*

44 Primarily the lingual side of the tooth socket is preserved. The lingual socket, and hence
45 the root, is angled superior-distally to occlusal-mesially more than the right one.

46
47 *P³ Right*

48 A normal and largely preserved socket is vertically set in maxilla. It appears
49 radiographically to have been single rooted.

50
51 *P³ Left*

52 It appears as a normal, mesiodistally compressed socket, open buccally but intact,
53 especially lingually and distally. The socket slants superior-distally to occlusal-mesially, along
54 with the left C¹. It appears radiographically to have been single rooted. The lingual root is also
55 displaced slightly mesially, suggesting some mesiolingual to distobuccal rotation of the tooth.

56
57 *P⁴ Right*

58 The alveolus is visually obscured, but radiographically the socket appears normal and
59 single rooted.

60
61 *P⁴ Left*

62 The tooth socket is broken open buccally and partially distally. The socket, and hence the
63 root, slants superior-distally to occlusal-mesially, along with the left C¹ and P³.

64
65 *M¹ Right*

66 The alveolus of the right M¹ is damaged lingually and buccally, but it exhibits the apex
67 area and most of the mesial side of the lingual root socket, and an open area for the distobuccal
68 root. The area of the mesiobuccal root is less apparent, but it is likely represented by a buccal
69 depression evident especially radiographically.

70
71 *M¹ Left*

72 There is buccal exposure of both buccal root sockets and lingual exposure of the lingual
73 root socket. All three sockets (hence roots) appear to have been complete, although the distal
74 side of the lingual root socket appears to have been partially resorbed (see M² left). All of the
75 root sockets slant mesially, such that the whole tooth would have been markedly tilted mesially.

For the mesiobuccal root, its angle to the approximate alveolar plane is 40°-55°. The condition of the sockets indicates postmortem loss despite the lingual alveolar resorption.

Figure S2. The Cro-Magnon 4253 right maxillary alveolus and dentition, with the originally remaining portion of the M² exhibiting crown enamel preservation.

M² Right

The right M² was in situ at death. The normal three roots are evident in the radiographic slice, and there is a portion of the mesiolingual cervix exposed currently. However, at least in 1985 (when photographed by ET), the mesiolingual corner of the crown extended to the occlusal surface, retaining at least 2 mm of the crown height (Fig. S2). It is therefore inferred that most, if not all of the crown, was present and functioning at the time of death.

M² Left

The M² socket is an open, irregularly circular cavity about ≈9 mm in diameter. There is nonetheless a buccal groove for the distobuccal root at its distobuccal corner, but otherwise the void is irregularly smooth or at least without root indications. The lingual side is open, continuing distally the resorption on the lingual side of the M¹ lingual root alveolus. The M² buccal alveolus side retains its bony wall.

The tooth therefore appears to have had a large lingual granuloma, especially around the lingual and mesiobuccal roots. The tooth may have been lost antemortem, but if so, shortly prior to death. Alternatively, the tooth was retained by the distobuccal root but reduced in function.

M³ Right

The tooth is absent, but in occlusal view the alveolus is evident with the clear apical sockets for the three roots with short septa between the depressions. The M³ was therefore three-rooted and apparently lost postmortem..

M³ Left

The area of the left M³ retains (in matrix) buccal bone for its alveolus and what appear to be small sockets for three roots. The two buccal sockets are separate but very close together, and the lingual one is very separate and displaced distally of the distobuccal root. It appears that the tooth was present at death, but that it was altered in position.

Figure S3. The premolar and molar alveoli of Cro-Magnon 4253 in bucco-occlusal views. The maxillary arcades are above and the right sides are to the left. Note the large resorptive area of the left mandibular M₁ area, and the remains of the right P₃, mesial M₁ and distal M₃ roots.

S2: Cro-Magnon 4253 (Cro-Magnon 1) Mandibular Dentoalveolar Remains

The mandibular alveoli lack the carbonate encrustation of the maxillary alveoli. However, most of them sustained postmortem erosion, especially labially by the anterior teeth and lingually along the postcanine teeth (Figs. S3 and S4). The preserved dental remains consist of portions of the right P₃ root, the right M₁ mesial root, and the right M₃ distal root.

There was extensive antemortem resorption buccally by the left P₄ and M₁ with possible antemortem tooth loss, and the right I₂ socket apex contains a bony growth suggesting antemortem tooth loss (see below). All of the other alveoli indicate postmortem loss of the teeth.

I₁ Right

The root socket has the lingual and mesial alveolar margins intact. The other alveolar margins are largely eroded.

I₁ Left

The left I₁ preserves a complete socket with eroded alveolar margins. The apex of the socket opens into a granuloma that has its largest portion and opening below the left I₁ (Fig. S4). The anterior/labial opening of the granuloma has been broken superiorly and distally, but the core of the fenestration and its mesial and inferior margins are the original bone. The fenestration is 4.8 mm wide, currently 9.1 mm high, but originally 4.5-5.0 mm high. The interior

of the granuloma has new bone laid down up into I₁ left socket, but mostly rounded trabeculae are exposed in lower portion of it.

Figure S4. The Cro-Magnon 4253 Mandible in occlusal view (left), detail of the anterior alveoli (middle) with the granuloma fenestration below the left incisors, and radiograph of the incisor granuloma (right). Scale for the superior view only.

I₂ Right

The socket consists of a lingual margin and the lower portion of the I_{1/2} septum, with loss of the labial and distal margins of the socket. There is an expansion of the apical region of the socket partly filled with matrix distally, but the middle portion has a bony growth within it. Therefore, the tooth was probably lost shortly before death, with only partial remodeling of the socket and a bony growth around the apex of the socket.

I₂ Left

The tooth socket is complete with the labial midline and mesial septum lower than the distal I₂ septum. The apex opens in a moderately large granuloma that is below the I_{1/2} septum and enlarged primarily below the I₁ socket (see left I₁).

C₁ Right

The lingual socket remains with intact lamina dura. It has lost of all but a small superior the lingual edge of the mesial (I₂/C₁) septum, but most of the lingual margin and two-thirds of the distal septum with lamina dura are preserved. All of the labial socket is gone except for the lower few millimeters to the apex. The labial edge is rounded with tiny knobs of bone, and therefore the labial alveolus was resorbed with the tooth in place. The preserved deeper portion of the tooth socket suggests some mesiolingual to distobuccal rotation of the root, similar to the right P₃, but its extent is unclear given the labial alveolar damage.

C₁ Left

The largely complete socket is preserved with the mesial, lingual and distal walls presenting with clean lamina dura. Almost all of the labial wall is absent; the edges appear broken, but they are rounded and there are small growths of bone on them especially around the inferior half of the socket. Therefore, the tooth was in situ, but there was resorption of the labial

175 wall. The maximum height of the socket is 15.3 mm, but only ≈ 1.5 mm remained on the labial
176 side.

177
178 *P₃ – M₁ Left*

179 There is a large void below the left P₃ and P₄, back to the M₁ (Figs. S3 to S5). The bone is
180 clearly resorbed where the M₁ should be, especially at the bottoms of the root sockets and the
181 buccal side, with a rounding out onto the lateral corpus. The buccal/lateral bone is broken below
182 the P₃ and partially broken below the P₄, and it is unclear to what extent the large void below the
183 P₃ and P₄ is resorption versus breakage.

185
186
187 **Figure S5.** Above: anterolateral virtual reconstruction of the Cro-Magnon 4253 left mandibular
188 corpus with the positions (A to E) of the CT slices through the P₃ to M₁ resorptive area.
189 Below: the CT slices (lateral to the right) through the damaged and pathologically
190 resorbed area of the mandible.

191
192 *P₃ Right*

193 The socket is present and contains the broken root. The alveolar margin is intact lingually, but it
194 slopes down buccally such that it is ≈ 10 mm lower buccally. The same small
195 buccal growths are present as with the C₁. The root is rotated such that it is oriented mesiolingual
196 to distobuccal.

197
198 *P₃ Left*

199 The superior 10.4 mm of the lamina dura is present mesially and 6.7 mm of it distally
200 with the appropriate septa for the root sides, along with 8.2 mm of the lingual socket with its
201 lamina dura. The adjacent lateral wall is absent, but its lateral edges have rows of small bony
202 growths, and hence there was resorption of the buccal wall antemortem. The remainder of the
203 root socket would have been within the lateral corporeal void, which has broken edges. The P₃

therefore sustained buccal socket resorption, possibly extending interiorly to its apex, but the tooth remained in situ.

P₄ Right

The single rooted socket is mostly preserved with the buccal margin lower by 7.8 than the lingual one; the adjacent septa slope down from the largely normal lingual alveolar margin. There is the same rounding of the edges as with the P₃. The socket is broken within the mesial side, but the lamina dura appears mostly normal.

P₄ Left

The socket and its lamina dura are preserved only on the mesial septum with P₃ and on the mesial half of the lingual side. The distal and buccal sides are absent. There is a large void under the preserved portion. Approximately where the root apex should be ends in irregular rounded bone that rounds out onto the lateral corpus. This portion of the reworked bone is just superior and just distal of the mental foramen. The preservation of mesial and lingual lamina dura suggests that the tooth was at least tenuously in situ at death, even through most of its socket was resorbed.

M₁ Right

The lingual alveolar margin is eroded, but the root sockets and the buccal side are intact, with resorption of the buccal alveolus. The mesial root socket retains the broken mesial and lingual portions of the mesial root in place. It is unclear whether the mesial root was merely broken postmortem and eroded (as is most of the mandible), or whether it was worn down to the root, with the consequent separation of the two roots. The distal root socket is empty and had expanded around the superior alveolar margin, with a tiny raised lip of bone buccally. It is unclear whether the distal root was lost antemortem, after separation from the mesial root and resorption around the socket, or if it was lost postmortem.

M₁ Left

The only remaining portion of the left M₁ socket is a distolingual and lingual section for the mesial root. For the distolingual corner, there is a small area 5.7 mm obliquely wide and 7.6 mm high at the alveolar margin. The lateral margin of it distally is a rounded small bony growth. The small portion of the original lingual alveolar margin is rounded and reduced in height. The margin is 4.6 mm thick, and 5.6 mm high. It lacks the lamina dura and exhibits soft and porous bone.

Below these portions of mesial root socket is a void, which ends inferiorly in a large area of irregular, rounded trabecular bone. The fossa is 9.7 mm wide and 10.9 mm mesiodistally, with the lowest point distal. It is not possible to discern root apices within it. The bottom of the area rounds out onto the lateral corpus, with a strip of cortical bone 6 mm wide with a small lip laterally demarcating it.

The distal P₄ / mesial M₁ septum is completely absent. The mesial M₂ / distal M₁ septum consists of a small and sharp ridge along the mesial edge of the M₂ mesial root apical socket. These aspects reflect a large granuloma that resulted in the resorption of the mesial, distal and buccal M₁ socket, and then rounding off of the remaining bone. It secondarily involved the P₄ and less so the M₂. It remains uncertain whether the small piece of porous bone on the lingual mesial root socket indicates that the tooth was still in situ at death.

M₂ Right

The alveolus presents complete double root sockets with a normal interradicular septum. The lamina dura is intact. Although slightly broken, the buccal alveolar margin was partially resorbed. The lingual alveolus was broken postmortem. The M₂/M₃ septum is thickened across its width to 4.8 mm.

M₂ Left

The lingual alveolar border was slightly reduced and thickened to 4.2 mm, but the buccal alveolar margin was reduced down to the level of the lateral eminence. The mesial septum is largely absent, reduced to a thin edge that barely projects (see left M₁). The M₂/M₃ septum is thickened, 3.0 mm in its middle, and it is high, probably close to the original alveolar height. The interroot septum is high and 1.4 mm thick, somewhat below the preserved lingual alveolar margin. The lamina dura where present is largely intact, but there is porosity towards the apex and on the lingual side of the distal root socket. The combination of features suggests a tooth tilted modestly towards the absent M₁, in the aftermath of the M₁ loss.

M₃ Right

There is an intact socket with the distal root in place; it was broken off at the lingual alveolar level. There was a clear separation of the two roots, but with a thin interradicular septum. The higher alveolar areas mesial and distal of the socket should both be close to the original “healthy” alveolar level. The lingual and buccal alveoli, however, are resorbed.

M₃ Left

The socket presents intact lamina dura with minimal fine porosity near the apex. There is modest reduction of the lingual alveolus and into the retromolar area. The roots were partially separated near the apex, but mostly there are interradicular septa present along the lingual and buccal margins of the socket.

Table S1. Antemortem versus postmortem loss of the Cro-Magnon 4253 (Cro-Magnon 1) teeth.^{1,2}

	Maxilla Right	Maxilla Left	Mandible Right	Mandible Left
I1	PM	PM	PM	PM
I2	PM	PM	(AM/PM)	PM
C	PM	PM	PM	PM
P3	PM	PM	Root	PM
P4	PM	PM	PM	(PM)
M1	PM	PM	Partial root	(AM/PM)
M2	Partial tooth	(PM)	PM	PM
M3	PM	PM	Partial root	PM

¹ PM indicates probable antemortem or postmortem tooth loss respectively. AM/PM indicates uncertainty as to whether the tooth was lost antemortem or postmortem.

² Parentheses around “AM” or “PM” indicates uncertainty in the assessment.

S3: Cro-Magnon 4254 (Cro-Magnon 2) Maxillary Dentoalveolar Remains

The Cro-Magnon 4254 maxillary alveoli, part of the Cro-Magnon 2 cranium, are largely preserved from the right mesiolingual M³ socket around anteriorly to the left mesial M² alveolus (Fig. S6). The labial surfaces are absent from the right I¹ to the left I², and there is breakage to the buccal right P³ and P⁴ alveoli. The bone is otherwise well preserved, clean of matrix, and retains most of its alveolar crest. There are two largely complete right molars and a root fragment in situ in the left M¹ alveolus.

All of the alveoli either preserve teeth or tooth fragments or are clean and open with normal lamina dura. There is no evidence of antemortem tooth loss. Most of the left M¹ alveolus and all of the left M³ alveolus and adjacent maxilla are absent, providing little or no data on those teeth. The only non-dental anomaly is a wide (3.6 mm) diastema between the I¹s.

I¹ Right

The lingual half of the alveolus with the intact lingual alveolar margin is present. There is no resorption or other alterations, except for a slight rounding of alveolar crests. There is a separation of 3.6 mm between the I¹ alveoli and across the intermaxillary suture.

I¹ Left

The lingual half of the alveolus is present with the intact lingual and mesial alveolar margins. There is no resorption or other alterations, except for a slight rounding of alveolar crests.

I² Right

The alveolus is complete except for a slight loss of the thin bone on the labial margin of the socket. There is a slight irregularity of the mesial and distal interdental alveolar crests.

Figure S6. The Cro-Magnon 4254 (Cro-Magnon 2) maxillae in occlusal (left), anterior (upper right) and right lateral (lower right) views.

P² Left

The lingual and distal sides of the socket are preserved, with breakage to the mesial and labial sides. There is a slight irregularity of the mesial and distal interdental alveolar crests.

C¹ Right

The alveolus presents a large ovoid socket, that extends 15-16 mm up into maxilla, with the apex curving distally at the top over the P³ socket (see right P³). The alveolar crest is intact, if slightly rising on the labial side.

C¹ Left

The large ovoid socket is similar to the right one, but with the labial side broken. The socket is shorter than the right one (14.4 mm from the C¹/P³ septum); it is straight and conical, with none of the apical distal curving evident on the right.

P³ Right

The P³ alveolus is broken away buccally and abraded lingually, but it is otherwise intact. There is a small socket lingually, with its maximum diameter of 5.0 mm oriented obliquely to the tooth row, up against the distolingual C¹ socket. The long axis is mesiolingual to distobuccal. The maximum depth of 5-6 mm may have been constrained by the C¹ root curving above it.

The buccal root was longer but thinner, with its socket extending 12.5 mm from the alveolar crest. It is slightly obliquely oriented, more mesial occlusally and more distal above. The buccal side of the buccal alveolus would have protruded buccally relative to the external sides of the C¹ and P⁴ alveoli.

The P³ was probably a two rooted tooth (as was the left P³), but with markedly asymmetrical buccal and lingual root, the latter being much smaller in diameter and length than the former.

P³ Left

The alveolus exhibits a broad rectangular socket with rounded buccal and lingual margins. The P³ had a clear double root, although the septum is incomplete on the mesial side and largely absent on the distal side until ≈7 mm down from the C¹/P³ septum. There is a little rounding of the alveolar margins, with a slight retraction of the alveolar crest on the lingual side and the buccal margins.

P⁴ Right

The alveolus presents a normal P⁴ single rooted socket, tapering to a rounded apex. It was broken buccally and mesiobuccally, but intact lingually and distally.

P⁴ Left

There is a normal single rooted P⁴ socket, which is relatively shallow (7.9 mm versus 10.5 mm for the right P⁴). There is a small but distinct midline ridge on distal side of the socket, indicating a longitudinal sulcus on the root, but no bifurcation. The distal half of the alveolar crest is a thin and rounded margin.

M¹ Right

The right M¹ presents a complete tooth (despite normal occlusal wear) in situ. The lingual root is exposed near the cervix due to postmortem bone loss, and the buccal roots are almost completely exposed buccally due to postmortem surface bone loss. The tooth is moderately worn (Smith (1984) stage 5a). There are the remains of extensive calculus on the crown and cervix.

M¹ Left

The preserved alveolus consists primarily of the mesial and lingual margins with small portions of the adjacent root sockets. The buccal alveolus is broken, and the buccal two-thirds of the area is plastic filler. The lingual alveolar margin is greatly reduced and descends at the level of the M¹/M² septum almost to the palate. The edge is rounded and irregular, and has a small foramen at its mesial (P⁴/M¹) end. Within the area of the socket, along the inside of the raised lingual edge, there is the ~4.3 mm long apical end of the lingual root.

Therefore, the left M¹ left appears to have experienced serious alveolar resorption, especially lingually, that began mesially in the mid-P⁴ socket and continued through the M¹ to reach close to the level of the M¹ lingual root apex and the palate. Hence the left M¹ was in place at death, but its roots were extensively exposed, especially lingually.

Table S2. Dental mesiodistal (MD) and buccolingual (BL) crown diameters of the sufficiently intact Cro-Magnon teeth compared to those of Early/Mid (E/MUP) and Late (LUP) Upper Paleolithic samples [mean $\pm$ standard deviation (N)], in millimeters.

	4254	4257	4258	E/MUP	LUP	p ¹
P ⁴ MD		7.9		7.1 $\pm$ 0.5 (21)	6.5 $\pm$ 0.7 (10)	0.008*
P ⁴ BL		11.2		9.9 $\pm$ 0.6 (31)	9.6 $\pm$ 0.6 (16)	0.079
M ¹ MD	(11.0)	(13.0)		10.8 $\pm$ 0.7 (46)	10.5 $\pm$ 0.9 (17)	0.206
M ¹ BL	12.4	14.1		12.2 $\pm$ 0.8 (49)	11.8 $\pm$ 1.0 (33)	0.027
M ² MD	(9.5)	(11.6)		10.3 $\pm$ 0.9 (39)	10.0 $\pm$ 0.8 (14)	0.190
M ² BL	(12.5)	13.9		12.4 $\pm$ 0.9 (43)	11.9 $\pm$ 1.1 (31)	0.038
M ₂ MD			(13.0) ²	11.4 $\pm$ 0.8 (44)	11.0 $\pm$ 0.8 (12)	0.166
M ₂ BL			(12.5) ²	11.0 $\pm$ 0.7 (51)	10.8 $\pm$ 0.7 (36)	0.182
M ₃ MD			(11.9)	11.4 $\pm$ 1.0 (20)	10.7 $\pm$ 0.7 (11)	0.052

¹ ANOVA p-values across the two comparative samples. *: Only the P⁴ MD diameters are significantly different at p < 0.05 with a multiple comparison correction.

² The CM 4258 M₂ diameters are the estimated values. The actual values are ≥ 12.5 and ≥ 12.0 mm respectively (see text below).

M² Right

The right M² alveolus retains the complete lingual side, rounding into the M¹/M² septum mesially and the M²/M³ septum distally. The buccal and distal alveolus is absent and partially filled with plaster. The tooth is largely in place, but with a 1.8 mm gap with sediment lingually. The roots and dentin core are largely complete, but the enamel lacks the lingual half and the mesial margin. The tooth shows little wear (Smith stage 3b). There is half of a small distal interproximal wear facet preserved.

The current gap between lingual alveolus and the M² was filled with wax in the 1970s, and the wax had been removed by the 1980s, following photos by ET taken in 1978 and 1985. It

is therefore likely that the tooth was observed and measured in the 1960s by Vallois and Billy (1965) with the wax in place. The lingual half of the crown enamel was absent at both times, and sediment traces on the exposed dentoenamel surface suggests that the enamel was lost prior to 1868. The M² crown diameters of Vallois and Billy (1965), of 12 and 9 mm, are therefore of the reduced tooth; estimation of the missing enamel provides mesiodistal and buccolingual crown diameters of ≈9.5 and ≈12.5 mm respectively. The tooth also exhibits extensive calculus on the crown.

M² Left

The only evidence for the left M² is an edge of its lingual alveolus 7.7 mm long, that continues the resorbed edge of the M¹ alveolus. It is only slightly above the level of the palate and reaches the palatal level distally. There is a hint of the mesial end of its lingual root socket apex.

M³ Right

There is a small area of mesiolingual lamina dura, 3.8 mm wide and 7.8 mm high, distal of the M² socket, for the M³. In combination with the distal interproximal facet on the M², it indicates that the M³ was in occlusion normally.

S4: Cro-Magnon 4256 Mandibular Dentoalveolar Remains

The Cro-Magnon 4256 mandibular corpus retains most of the alveoli of all sixteen mandibular teeth, from the distal right M₃ alveolus to the distal portion of the left M₃ alveolus. There is variable fossilization damage/abrasion, especially buccally, but most of the interdental septa are intact. Thirteen of the sockets are empty without resorption indicating postmortem tooth loss. The other three alveoli, those for the left I₁ and both P₃ sockets, hold broken roots in situ. There is also obscuring matrix in the left I₁, I₂ and P₃ sockets.

The alveoli, however, present a suite of anomalies of dental orientation. The I₂s are rotated mesiolabially, the P₃s are rotated mesiolingually, the M₂s slope mesially, and the right M₃ exhibits an unusual root pattern (Fig. S7; Table S3).

I₁ Right

The alveolus retains a normal mesiodistally narrow socket with loss of the superior half of the labial alveolar bone.

I₁ Left

The left I₁ root is still in situ, and it is a very mesiodistally thin normal root. Distal of the root in the socket there is matrix, in some space between the root and the I₁/I₂ septum.

I₂ Right

The I₂ socket is normal in form with loss of the superior third of the labial bone. The tooth was set largely parallel to the I₁, albeit with the labial side closer to the I₁. The tooth therefore exhibits mild mesiolabial rotation, also present in the left I₂. As a result, the I₂/C₁ septum is triangular, with a broader labial portion, given that the labiolingual axis of the C₁ is perpendicular to the curve of the dental arcade.

I₂ Left

Despite matrix and damage to the I₂/C₁ septum, the left I₂ parallels the right one, in anteroposterior orientation and a resultant triangular I₂/C₁ septum that is labially thick. With the I₁s, the two rotated I₂s would have provided a transverse line of labial incisors, but with labial gaps I₂ to C₁.

C₁ Right

It exhibits a broad and straight socket, with labial bone loss on the superior half of the socket, and a small lip of bone along its lingual side.

C₁ Left

The left C₁ socket is similar to the right one, although less expanded mesiodistally on its labial side.

Figure S7. Details of the Cro-Magnon 4256 alveoli; from left to right: anterior alveoli, right molar alveoli, left molar alveoli. White arrows: rotated I₂s. Yellow arrows: rotated P₃s. Green arrow: mesially sloping M₂.

P₃ Right

The P₃ socket retains a mesiodistally thin root. There is some buccal alveolar resorption. The tooth was rotated $\approx 60^\circ$, lingual to mesial/buccal to distal. The rotation produced a very thin lingually but 5.0 mm thick buccally. C₁/P₃ septum. The P₃/P₄ septum is 2.7 mm buccally and 4.5 mm thick lingually.

P₃ Left

The left P₃ parallels the right one. The socket retains a mesiodistally thin root. There is some buccal alveolar resorption. The tooth was rotated $\approx 70^\circ$ lingual to mesial, resulting in a C₁/P₃ septum which is very thin lingually but 5.5 mm buccally and a P₃/P₄ septum which is 2.9 buccally and 4.4 lingually.

P₄ Right

The alveolus exhibits a normal thicker root socket, oriented correctly. There is minor reduction of the P₄/M₁ alveolar crest.

P₄ Left

The socket is similar the right P₄ one, with the normal lamina dura on the mesial side and some resorption on the distal side.

Table S3. The distribution of rotated incisors, canines and premolars in the Cro-Magnon sample.¹

	I1	I2	C	P3	P4
CM 4253					
Maxilla right	abs	abs	abs	abs	abs
Maxilla left	abs	abs	abs	(pres)	abs
Mandible right	abs	abs	(pres)	pres	abs
Mandible left	abs	abs	abs	abs	abs
CM 4254					
Maxilla right	abs	abs	abs	abs	abs
Maxilla left	abs	abs	abs	abs	abs
CM 4256					
Mandible right	abs	pres	abs	pres	abs
Mandible left	abs	pres	abs	pres	abs
CM 4257					
Maxilla left	abs	abs	abs	pres	abs

¹ (pres) for two of the CM 4253 teeth indicates possible rotation, with uncertainty given resorption and/or damage to the alveoli.

M₁ Right

The M₁ alveolus presents two distinctly separated sockets, with damage to the broad interradicular septum. There is some alveolar resorption along the lingual margin, but it is broken buccally.

M₁ Left

The alveolus has normal paired root sockets, well separated by a high (especially buccally) and thick interradicular septum. There was moderate alveolar resorption lingually, and damage to the buccal margin of the mesial root.

M₂ Right

The M₂ socket presents a single “conical” socket for fused roots, with thin and small crests lingually and buccally for the sulci between the fused roots. However, the hole slopes mesially, such that the distal lamina dura is vertical to the alveolar plane and the mesial one is at a distinct angle to the alveolar plane. There is also a pronounced thickness (4.8 mm) of the

M₁/M₂ septum. This combination of features suggests that the M₂ was erupted to the occlusal plane, but that its crown was angled up against the M₁. It therefore had the root angled distally, resulting in the thick septum between the M₁ and M₂ roots.

M₂ Left

The M₂ socket is partly obscured by thin matrix, but it is similar to the right one; a conical socket for fused roots, a vertical distal septum, an angled mesial septum, and a thickened M₁/M₂ septum. However, the mesial angle is less pronounced, and the thickness of the septum (3.4 mm) is less.

M₃ Right

The root socket pattern for the right M₃ is unusual, although the breakage of the distobuccal alveolus makes its full aspect unclear. There is a mesial midline narrow root (6.5 mm wide versus 8.4 mm for the M₂ socket) socket which then tapers to a narrowing 5.4 mm from the alveolar plane. To the distal on the lingual side, there is an oval socket 4.5 by 3.5 mm, largely vertically oriented, and ≈4 mm deep. The mesial socket should be for a reduced mesial M₃ root, but it is unclear whether the distolingual socket is for a reduced and rotated distal root.

M₃ Left

Only the mesial lamina dura is preserved. It is flat and a normal M₃ mesial root surface, but it slopes slightly mesially, similar to the M₂ mesial root surface.

S5: Cro-Magnon 4257 Maxillary Dentoalveolar Remains

CM 4257 is a complete alveolar and palatal portion of a left maxilla, with the alveoli from the intermaxillary suture mesial of I¹ to the alveolar bone around the missing M³ (Fig. S8). The maxillary portion of the palate is complete, but the labial/buccal portions of the alveoli from I¹ to P⁴ are largely or entirely absent.

The maxilla currently retains the M¹, M² and a P⁴. The conditions of the preserved sockets all indicate postmortem loss of the absent teeth.

In addition, the largely complete P⁴, which has been in the maxilla since the initial description of Broca (1868), does not belong in the maxilla (see below). It is not clear whether it derives from the same individual but is a right P⁴ or it comes from another individual. Its buccolingual crown diameter is unexceptional relative to those of the M¹ or especially of the M², and its degree of occlusal wear matches that of the M², both of which should have the same functional occlusal age. It is therefore conservatively considered to be the right P⁴ of Cro-Magnon 4257.

I¹ Left

Present is the complete lingual third to half of the socket with the intact lamina dura. There is matrix in its apical portion.

I² Left

Present is the complete lingual third of the socket with the intact lamina dura.

C¹ Left

Preserved is the complete lingual half of the socket with the apical portion partly covered labially. There is minor porosity of the lamina dura along the I²/C¹ septum.

Figure S8. Occlusal (left) and buccal (right) views of the Cro-Magnon 4257 left maxilla. Shown are photographs of the maxilla with the P⁴ in its current position and virtual images of the maxilla with the P⁴ removed. Note the slightly more anterolateral than lateral view of the virtual image.

P³ Left

The left P³ alveolus retains its mesial, lingual and distal portions, and presents two sockets with a septum that extends almost to the alveolar margin. As noted by Vallois and Billy (1965), it is best interpreted as a two-rooted P³. It is also rotated almost 90° in the alveolus.

P⁴ Right

As noted above, the complete P⁴ currently in the left P⁴ alveolus was inappropriately placed in that socket, apparently shortly after its discovery. Although the tooth is morphologically a P⁴, with a single root and with buccal and lingual cusps of similar size (the buccal one is slightly larger), it does not fit the CM 4257 left maxilla. Its root is completely pressed into the left P⁴ alveolus, but its occlusal surface projects 2.2 mm above that of the M¹. The very small interproximal facet of the P⁴ does not match the large one on the mesial M¹, and the P⁴ one is above that of M¹. The contour of the distal P⁴ crown does not match that of the M¹, unlike the close fitting of the interproximal facets between the M¹ and the M².

Yet, as noted above, the degree of wear of the P⁴ (Smith stage 5b) is similar to that of the M² (Smith stage 5c). Also, comparisons of the P⁴ versus M¹ and M² buccal crown diameters are unexceptional for Late Pleistocene human (Fig. S9). The tooth cannot be easily sided, given the

symmetry of the crown and its straight root, but it would make an appropriate right P⁴ of the same individual. It is so considered.

The right P⁴ tooth therefore presents an ovoid crown with the remains (after wear) of the mesial and distal marginal ridges and an absence of a developmental groove. It has a single straight root.

Figure S9. The buccolingual diameter of the Cro-Magnon 4257 P⁴ (in mm) compared to the same diameter for its M¹ (left) and M² (right) (Table S2), versus the same comparisons for Early (EUP), Mid (MUP) and Late (LUP) Upper Paleolithic humans.

P⁴ Left

The left P⁴ alveolus, with the right one removed virtually (Fig. S8), presents a normal socket for a single rooted premolar, with small ridges (especially mesially) for the sulci running along the root.

M¹ Left

The in situ M¹ is a complete tooth and alveolus with the loss of thin alveolar bone on the buccal and lingual sides, exposing much of the roots. The occlusal surface is a dentin basin with a continuous ring of enamel around it (Smith stage 7b); the loss on the mesiolingual corner is postmortem breakage. There are postmortem fissures through the crown, with little of the crown dimensions; any expansion of the mesiodistal diameter (the only one likely to be affected) is more than compensated by the interproximal wear (it measures 12.8 mm, rounded off to ≈13.0 mm).

M² Left

The M² is a complete tooth in situ with lingual and especially buccal exposures of most of the roots. It has a tight and congruent mesial interproximal flat contact facet with the M¹, but there is no distal interproximal facet. The occlusal surface exhibits a rounded enamel ring, a dentin basin with a center enamel island connected to the enamel ring only on the mid-buccal side (Smith stage 5c). The tip of the mesiolingual root is exposed through breakage alongside of the M³ crypt (see below); although slightly damaged, the apex of the root was fully closed.

Figure S10. The Cro-Magnon 4257 maxilla in superior view. Note the crypt for the impacted M^3 (red arrow) above the erupted and worn M^2 .

M^3 Left

The M^3 is absent and the retromolar bone extends for only 6.9 mm distal of the M^2 cervix. Superior of the retromolar bone is a crypt 12.2 mm mesiodistal and 8.9 mm buccolingual for the crown of the M^3 (Fig. S10). Because the M^2 and especially the M^1 are heavily worn and the M^2 roots are closed, this space does not represent a crypt for a developing M^3 . It reflects an impacted M^3 crown up against the distal M^2 root, as noted by Vallois and Billy (1965).

S6: Cro-Magnon 4258 Mandibular Dentoalveolar Remains

The Cro-Magnon 4258 mandibular piece consists of the alveolar region from the middle of the M_1 to the ramus (Fig. S11). The alveolar bone is well preserved buccally, especially by the M_2 and M_3 , but it is partially present by the M_1 and absent from the M_2 and the mesial M_3 . All three of the teeth, the M_1 to M_3 , are present. However, the M_1 lost most of its mesial and buccal enamel and the M_2 lost most of its lingual and buccal enamel. The intact M_3 is impacted with its mesial crown against the distal M_2 root and the distal crown not quite at the alveolar plane.

The mandible is labeled “Cro-Magnon n° 4”, possibly based on Pruner-Bey (1865-75), but it remains unclear to which of the crania it might have belonged.

Vallois and Billy (1965) mentioned four teeth associated with the CM 4258 mandible, P_4 to M_3 . There is no current evidence of a premolar with CM 4258, and Pruner-Bey (1865-75) mentioned only the three currently present molars. It is not clear to what premolar Vallois and Billy were referring.

M_1 Right

The M_1 is a heavily worn tooth in situ, with a thin enamel around a dentin surface lingually, distally and on the distal half of the buccal side. The mesial half of the buccal crown and the buccal side of the mesial crown had the enamel worn away antemortem and the dentin rounding down below the cervix. As such it exhibits Smith wear stage 7c. Given damage to the alveolar bone, especially lingually, it is unclear to what extent it may have been resorbed (or the

tooth supererupted), but the M₁/M₂ septum appears largely normal and the alveolar-cervix height (≈ 2.5 mm) is unexceptional for the degree of occlusal wear.

The mesiodistal diameter of the crown is too damaged and worn to measure. The buccolingual diameter as preserved is 12.5 mm; full crown buccolingual diameter prior to wear should have been ≥ 13 mm.

Figure S11. Lateral (left) and medial (right) views of the Cro-Magnon 4258 right mandibular corpus and ramus. See also text Fig. 4 and Fig. S12.

M₂ Right

The M₂ exhibits a dentin occlusal surface with enamel margins preserved mesially and distally; it appears that the enamel ring was complete at death and the missing portions lost subsequently (Smith wear stage 7b). The lingual alveolar bone is absent, but the intact buccal alveolar bone exhibits no resorption. There is a small carious lesion occlusally, slightly lingually of the crown middle, noted by Brennan (1991) and Lacy (2014) (Fig. S12).

The mesiodistal diameter of the crown, as retained with occlusal and interproximal wear, is 12.5 mm. The buccolingual diameter of the crown as worn, estimated continuing the contours of the broken enamel, is ≈ 12.0 mm. Prior to the occlusal and interproximal wear, the two diameters were probably ≈ 13.0 and ≈ 12.5 mm. These values are approximate, but they provide a general assessment of the dimensions of these molar crowns.

M₃ Right

As noted above, the completely formed M₃ is fully present and fully impacted in the mandible. The mesial occlusal crown edge is against the M₂ distal root slightly below the middle of the root. The long (vertical) axis of the tooth is $\approx 35^\circ$ from the alveolar plane. The buccal, distal and distolingual margins of the crypt opening through the alveolus are preserved, but little of the calculus on the distal M₂ appears to have penetrated onto the M₃ crown.

Figure S12. Occlusal views of the Cro-Magnon 4258 right mandibular molars, with the impacted M₃ in its crypt. Green arrow: the rounded mesiobuccal edge of the M₁. Red arrow: the small occlusal carious lesion in the M₂.

S7: Micro-CT Resolution Data

Table S4. Resolutions of the microtomodensitometric (μCT) data for the Cro-Magnon crania and mandibles.

CM 4253 Cranium	Cro-Magnon 1	115.0 μm
CM 4253 Mandible	Cro-Magnon 1	76.6 μm
CM 4254 Cranium	Cro-Magnon 2	110.0 μm
CM 4256 Mandible	--	60.6 μm
CM 4257 Maxilla	--	30.0 μm
CM 4258 Mandible	--	38.2 μm

S8: Proposed Cro-Magnon Associations

Table S5. Proposed associations of the Cro-Magnon adult remains, based on those proposed for the lower limbs by Thibeault and Villotte (2018), for the upper limbs by Villotte et al. (2020), and for the cranial and mandibular remains here. The individuals (Alpha to Delta) are those based on the appendicular remains, restricting the traditional Cro-Magnon 1 to 4 designations to the crania and the one directly associated mandible.

	Alpha	Beta	Gamma	Delta ²
Neurocranium	4253 (#1)	4255 (#3) or 4259 (#4) ¹		4254 (#2)
Maxilla/Mandible	4253 (#1)	4256 or 4257/4258 ¹		4254 (#2)
Clavicle	4290			
Scapula	4292			
Humerus		4294,4295	4293	
Ulna	4299	4301	4300,4302	4297,4298
Radius	4304	4305	4303	
Hip bone	4314a,4314b	4316a,4317,4316b?	4315,4318	
Sacrum		4314c	4319?	
Femur	4323,4327,4325	4321,4324,4329	4322,4323,4328	
Tibia	4331,4332		4330,4333	
Fibula	4335		4334	
Talus			4337	
Calcaneus			4336	

¹ As discussed in the text, the CM 4256 mandible and the CM 4257/4258 maxilla/mandible likely derive from the Beta and Gamma postcranial pair as well as from the CM 4255 and CM 4259 cranial pair. It is not currently possible to determine which way these three pairs might be associated.

² As discussed in the text, the association of CM 4254 cranium with Delta is largely based on its unlikely association with Beta or Gamma, and the assumption of only four adults in the Cro-Magnon sample.

S9: Supporting Information References

- Brennan, M.U., 1991. Health and disease in the Middle and Upper Paleolithic of southwestern France: a bioarcheological study. Ph.D. Thesis. New York University.
- Broca, P., 1868. Sur les crânes et ossements des Eyzies. Bull. Soc. Anthropol. Paris 3, 350–392. <https://doi.org/10.3406/bmsap.1868.9548>
- Lacy, S.A., 2014. Oral Health and its Implications in Late Pleistocene Western Eurasian Humans. Ph.D.Thesis, Washington University in Saint Louis.
- Leonard, A., Bayle, P., Murail, P., Brůžek, J., 2014. Oral exostoses: An assessment of two hundred years of research. Bull. Mém. Soc. Anthropol. Paris 26, 1-22. doi.10.1007/s13219-013-0089-3.
- Pruner-Bey, F., 1865-75. An account of the human bones found in the cave of Cro-Magnon, in Dordogne, in: Lartet, E., Christy, H. (Eds.), Reliquiae Aquitanicae: Being Contributions

- 732 to Archaeology and Palaeontology of Périgord and the Adjoining Provinces of Southern
733 France. Williams and Norgate, London, pp. 73–92.
- 734 Smith, B.H., 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J. Phys.*
735 *Anthropol.* 63, 39-56.
- 736 Vallois, H.V., Billy, G., 1965. Nouvelles recherches sur les hommes fossiles de l’abri de Cro-
737 Magnon. *L’Anthropol.* 69, 47–74.