The challenges of identifying partially digested human teeth : first description of Neandertal remains from the Mousterian site of Marillac (Marillac-le-Franc, Charente, France) and implications for palaeoanthropological research

Les challenges liés à l'identification de dents humaines partiellement digérées : première description de vestiges néandertaliens du site moustérien de Marillac (Marillac-le-Franc, Charente) et implications pour la recherche en paléoanthropologie.

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The challenges of identifying partially digested human teeth: first description of Neandertal remains from the Mousterian site of Marillac (Marillac-le-Franc, Charente, France) and implications for palaeoanthropological research

Bruno MAUREILLE^(a), Sandrine COSTAMAGNO^(b), Cédric BEAUVAL^(c),
Alan E. MANN^(d), María Dolores GARRALDA^(e), Célimène MUSSINI^(a),
Véronique LAROULANDIE^(a), William RENDU^(a), Aurélien ROYER^(f,g),
Guillaume SEGUIN^(h), Bernard VANDERMEERSCH^(a)

Abstract: excavations at the collapsed cave site of Marillac (Marillac-le-Franc, Charente, France)¹, uncovered in the lower half of the stratigraphy, a series of Late Pleistocene sedimentological facies containing a MIS 4/3 fauna. Also discovered were Middle Paleolithic artefacts (Quina Mousterian) and numerous fragmentary Neandertal fossils corresponding to a MNI of seven individuals.

Analyses of the geomorphology of the eastern locus of the site, of the artefacts and especially of the animal bones of the lower part of the stratigraphy, suggest that over the course of time the site was intermittently used by Neandertals for processing animal carcasses. Cave carnivores appear to have sometimes been involved in scavenging activities of the remains abandoned by humans.

Re-examination of two teeth - that were provisionally interpreted as bovid or cervid deciduous incisors by a palaeontologist unfamiliar with Pleistocene mammal fauna - have been identified as Neandertal maxillary permanent incisors. Originally considered as faunal deciduous incisors, what made their identification particularly difficult were the significant modifications to both the crown and roots of these teeth.

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(a) Université de Bordeaux, CNRS, MCC, PACEA UMR5199, FR-33615 Pessac

(b) CNRS, Université Jean Jaurès Toulouse II, TRACES UMR5608, FR-31058 Toulouse cedex

(c) SARL Archéosphère, 2 rue des Noyers, FR-11500 Quirbajou

(d) Department of Anthropology, Princeton University, Princeton, NJ 08544, USA

(e) U. D. de Antropología Física. Facultad de Biología. Universidad Complutense de Madrid. E-28040 Madrid

(f) Université de Bourgogne, CNRS, Biogéosciences UMR6282, FR-21000 Dijon

(g) École Pratique des Hautes Études, Laboratoire EPHE PALEVO, FR-21000 Dijon

(h) Éveha Étude et valorisation archéologique, Route de Larnay, La Tardiverie, FR-86580 Biard

Corresponding authors:

*: bruno.maureille@u-bordeaux.fr

**: costamag@univ-tlse2.fr

(1) The original name for the site was Les Pradelles (David 1934), reflecting the name of the terrain where it is located. Later, during the 1965-1980 Vandermeersch excavations, the site was known as Marillac, the partial name of the village Marillac-le-Franc (Vandermeersch 1965, 1971, 1976a and b). More recently, the name Les Pradelles has been employed during excavations between 2001 and 2013 (Maureille et al. 2004a, 2010). Both site names have been used in publications.

This contribution explores the possible causes for this unusual morphology and, in particular, their ingestion by carnivores. This is the most parsimonious explanation as these teeth possess distinctive modifications clearly indicative of the effects of carnivore gastric secretion, damage which is described here for the first time for human teeth. Finally, a number of straight forward macroscopic features are described that permit the rapid identification of these specific taphonomic modifications on human teeth without the need for microscopy or micro-CT scanning. A literature review indicates that additional hominin teeth, with similar scavenger produced changes, may already have been identified at other sites, especially those dated to the Plio-Pleistocene.

Key-words: Taphonomy, incisor, carnivore, digestion, Quina Mousterian, France.

Résumé : *Les challenges liés à l'identification de dents humaines partiellement digérées : première description de vestiges néandertaliens du site moustérien de Marillac (Marillac-le-Franc, Charente) et implications pour la recherche en paléanthropologie.* Les fouilles du gisement de Marillac (Marillac-le-Franc, Charente) ont autorisé l'identification d'un certain nombre de facies sédimentaires qui, pour la moitié inférieure de la stratigraphie, livrent une faune abondante rapportée au MIS 4/3. Du matériel lithique, bien plus rare, traduisant un techno-complexe moustérien de type Quina ainsi que de nombreux vestiges néandertaliens, correspondant à un NMI de sept individus, ont été mis au jour.

L'étude de l'évolution géomorphologique du locus « est » du site et l'étude du matériel lithique, des vestiges de faune de la moitié basale de la litho-stratigraphie plaident pour des activités de récupération par les Néandertaliens de toutes les ressources exploitables sur les cadavres ou les portions de cadavres de rennes. Ils s'y livrèrent par intermittence et de façon répétée. La fréquentation du gisement par des grands carnivores, qui ont ainsi pu charogner les restes abandonnés par les hommes, a été très sporadique.

Le réexamen des anciennes collections fauniques - précédemment étudiées par un paléontologue non familier avec les faunes du Pléistocène - a permis d'identifier deux dents (des incisives permanentes supérieures). Elles étaient considérées comme des incisives déciduales de bovidé ou de cervidé et sont en fait des incisives permanentes néandertaliennes. Ce qui avait rendu leur identification taxinomique difficile était leur morphologie générale aussi bien au niveau de la couronne que de la racine.

Cet article discute les causes potentielles qui pourraient expliquer ces modifications morphologiques de ces deux dents permanentes et en particulier celle de leur digestion partielle suite à leur ingestion par des carnivores. Cette cause est la plus parcimonieuse puisque ces deux incisives présentent des atteintes qui ne peuvent être que la conséquence de l'effet des attaques enzymatique et acide de l'estomac des carnivores. Nous décrivons donc pour la première fois ces dommages et ces modifications morphologiques sur des dents humaines. Enfin, cette contribution fournit aussi des clefs d'identification macroscopiques, simples et n'utilisant pas de techniques microscopiques, de micro CT-scans, qui permettent d'identifier rapidement ces modifications taphonomiques particulières sur des dents humaines. Ces clefs peuvent aider à trouver, comme nous avons pu le faire avec une revue bibliographique, au sein de collections de vestiges fauniques, de nouveaux fossiles humains du Plio-Pléistocène.

Mots-clés : taphonomie, incisive, carnivore, digestion Moustérien de type Quina, France.

1 - Introduction

Hominin remains are uncommon in the fossil and archaeological record; each find represents another piece of evidence in the reconstruction of extinct patterns of biology and behavior. Without the contribution of newly developed bio-chemical and paleogenetic techniques (Buckley and Collins 2011; Van Door *et al.* 2011; Welker *et al.* 2016), it is oftentimes difficult to recognize fragmentary hominin remains, especially small ones from long bone shafts, amongst a sample of animal bones. Teeth, with their distinctive morphology, are usually easily identified. This, however, is not always the case. Two teeth from the site of Marillac had been modified in such a way that their identification as human was extremely difficult.

Marillac is located in the village of Marillac-le-Franc, Department of the Charente, in the southwest of France, about 20 km east of Angoulême (fig. 1). The site is on the right bank of a very small stream, La Ligonne, a right tributary of the Tardoire River. Although casual activities at the site early in the last century had resulted in the

discovery of a Neandertal mandibular fragment (David 1935; Piveteau 1957), systematic archaeological excavations at Marillac were not undertaken until 1965-1980 (Vandermeersch 1976a). More recent work at the site was carried out between 2001-2013 (Maureille *et al.* 2004a, 2010). Since the 1930s, 87 hominin fossils (corresponding to 109 field fragments), have been discovered, most of them cranial and dental remains plus a few post-cranial pieces. All these hominin specimens possess distinctive morphological attributes of Neandertals and many of them have been published or are available for the scientific community (Piveteau 1951, 1957; Vandermeersch 1976a, 1976b; Mann *et al.* 2002; Maureille *et al.* 2004a, 2004b; Mussini 2011; Mussini *et al.* 2011, 2012; Garalda *et al.* 2014a and b).

Re-examination of the 1965-1980 collection of faunal remains resulted in the discovery of a few hominin fragments, including two anterior teeth, from the same facies, which were previously identified as deciduous incisors of an herbivore, either a bovid or a cervid (fig. 2).

Figure 1 - Location (# 17) of Marillac and others sites in the ancient Poitou-Charentes French Region where Neandertal lineage remains have been discovered are also shown.

Figure 1 - Localisation (n° 17) de Marillac et d'autres sites de l'ancienne région de Poitou-Charentes qui ont livré des restes humains appartenant à la lignée néandertalienne.

The existence of these teeth, with their ambiguous morphology modified in such a way as to make their recognition, as hominin, extremely difficult, has prompted the presentation of this report.

2 - Site context

The site has a complex geological and sedimentological history. Presently it is a large rectangular depression, some 12 meters long, 9 meters wide and about 3 to 9 meters deep

representing the remains of a Bajocian limestone collapsed karstic cave. Figure 3 presents the eastern site locus from which the majority of hominin fossils have been recovered, including the two teeth presented in this article. At the base of the profile, sedimentological facies 2a to 4b (which are clast-supported limestone deposits associated to a clayey matrix; fig. 3) contain the most important archaeological remains, including lithics of the Quina Mousterian techno-complex (Meignen and Vandermeersch, 1986; Bourguignon, 1997). Reindeer largely dominate the associated ungulate

Figure 2 - The two permanent regurgitated Neandertal incisors. A to F: upper right central incisor (M72 c.10 E11 # 336), G to L: upper right lateral incisor (M70 c.10 F12 # 54). A and G: buccal view, B and H: lingual view, C and J: mesial view, D and I: distal view, E and K: apical view, F and L: occlusal view. Scale = 10 mm. Note that the layer 10 (c.10) defined by B. Vandermeersch is equivalent to a part of facies 2a of the 2001-13 excavations.

Figure 2 - Les deux incisives permanentes néandertaliennes régurgitées. A à F : incisive centrale supérieure droite (M72 c.10 E11 n° 336), G à L : incisive latérale supérieure droite (M70 c.10 F12 n° 54). A et G : vue vestibulaire, B et H : vue linguale, C et J : vue mésiale, D et I : vue distale, E et K : vue apicale, F et L : vue occlusale. Echelle = 10 mm. Notez que la couche 10 (c.10) définie par B. Vandermeersch est équivalente à une partie du facies 2a des fouilles 2001-2013.

fauna (NISP close to 95 %). A small number of carnivore bones of cave hyena, cave lion, wolf and fox have also been recovered from these levels (Costamagno *et al.* 2005). Some complete coprolites, gnaw marks on herbivore bones as well as some regurgitated bone fragments, reindeer petrous bones and cervid or hyena teeth in the base of facies 2a and facies 4b document some active involvement of carnivores in either primary accumulation or in secondary scavenging related to hominin activities. In much of facies 2a and facies 2b, small pieces of coprolites and a few partially digested bone fragments (no more than 37 numbered fragments from a total sample of 3423; this does not include the numerous very small bone/ tooth fragments from this facies) also attest to the presence of carnivores, most probably cave hyena rather other Pleistocene carnivores (Mann *et al.* 2005).

The detailed chronological results of the site are presented in Frouin *et al.* (submitted this volume) which demonstrate that the age of the Neanderthal fossils is around ~55 ka, and dates the Quina occupations between the end of Marine Isotope Stage (MIS) 4 and into the MIS 3 (see also Royer 2013; Royer *et al.* 2013; Frouin 2014).

3 - Description of the two teeth (fig. 4a and 4b)

They are an upper permanent central incisor, perhaps right side (M72 c.10 E11 # 336) and an upper permanent lateral

right incisor (M70 c.10 F12 # 54), both discovered in layer 10 (equivalent to a part of facies 2a). Both possess marked occlusal attrition, stage 4 for the central incisor and 3 for the lateral one following the analysis of dental attrition published by Murphy in Smith (1984). Given the differences in occlusal wear on the two teeth, and the observed differences in wear between incisors in any Neandertal jaw, it is not possible to state with certainty that they derive from the same individual. A detailed description of the morphological traits, crown and root characteristics and diameters of these teeth as well as micro CT-scans and 3D dental tissue proportions will be presented by Garralda *et al.* (in preparation).

These teeth present numerous unusual features (figure 4a and 4b). Techniques such as scanning electronic microscopy and CT scanning provide a large corpus of useful information but the amassing of this data it is not the main aim of this article. Here the focus is essentially on their gross morphology and the external aspects of the enamel and dentine; the goal is to provide the essential macroscopic features to identify partially digested human teeth. The unusual features of the two Marillac incisors are:

- 1) The relative proportions between crown and root diameters, specifically for the central incisor, are not those of a permanent tooth. They are more appropriate in a deciduous tooth with an almost completely calcified root;
- 2) The roots of both teeth are very flat mesio-distally and bucco-lingually. This morphology is more accentuated on

Figure 3 - Eastern locus of Marillac/Les Pradelles with the identified lithofacies related to 2001-2013 excavations. 1: silty endokarstic clays with large blocks embedded, sterile; 2a: clast-supported deposits associated to a clayey matrix, abundant archaeological material; 2b: clast supported deposits with voids partially filled in, abundant archaeological material; 3: recent sedimentation related to the present plateau topography, clast-supported deposits associated to sandy and clayey redeposited matrix, mixing of prehistorical and historical sediments, very rare archaeological material; 4a: clast-supported deposits associated to a clayey matrix, abundant archaeological material; 4b: compacted clast-supported deposits associated to a clayey matrix, less abundant archaeological material; 4d: cemented clast-supported deposits associated to a clayey matrix, abundant archaeological material; 5: clast supported deposits with voids partially filled in, rare archaeological material, carnivore occupations; 6: solifluxion layer, alternation of pebbly levels, clast-supported, and matrix-supported levels, very rare faunal remains; 7: slabs and clast supported deposits associated to an heterogeneous matrix, sterile; 8: recent soil with bioturbation.

Figure 3 - Locus est de Marillac/Les Pradelles avec les facies sédimentaires identifiés durant les fouilles 2001-2013. 1 : argiles limoneuses endokarstiques avec parfois quelques blocs de calcaire de taille variable, stérile; 2a : cailloutis colmatés par une matrice argilo-limoneuse, matériel archéologique abondant ; 2b : cailloutis peu ou non colmatés (vides entre les blocs), matériel archéologique abondant ; 3 : dépôt sédimentaire très récent relié à l'actuelle topographie, cailloutis colmatés inclus dans une matrice sablo-argileuse hétérogène : mélanges de sédiments anciens et récents, matériel archéologique très rare ; 4a : fragments rocheux hétérométriques jointifs avec une matrice sablo-argileuse, couleur jaunâtre, matériel archéologique abondant ; 4b : fragments rocheux hétérométriques jointifs avec une matrice sablo-argileuse, couleur brune, matériel archéologique moins abondant ; 4d : fragments rocheux hétérométriques jointifs et cimentés associés à une matrice très fine, matériel archéologique abondant ; 5 : éboulis hétérométriques à structure ouverte à semi-ouverte, matériel archéologique rare, repaire de carnivore ; 6 : dépôts stratifiés, coulées de solifluxion avec alternance de niveaux de blocailles, de cailloutis et de sédiments plus fins, restes fauniques très rares ; 7 : dalles calcaires et de cailloux très hétérométriques inclus dans une matrice sablo-argileuse hétérogène, stérile; 8 : Sol récent et bioturbé.

the central than on the lateral incisor and is unusual for a permanent tooth;

3) The two root apices are open and very large for teeth with such marked attrition. An almost completely calcified permanent (or deciduous) incisor does not possess an open apex of this size. Note that such a size is also inappropriate for a partially resorbed deciduous incisor root;

4) Atypical too are the polished root surfaces lacking cementum;

5) The dentine exposures on the occlusal surface of both teeth have a polished patina. In contrast, the borders of the enamel appears more irregular;

6) Finally and more intriguing, the apical limits of the enamel of both incisors (figure 4a and 4b: open arrow) are not

Figure 4a - Upper right central incisor (M72 c.10 E11 # 336): lingual and occlusal views. Open arrow: apical limit of the enamel, solid arrow: anatomical cervix. Scale in millimeters, each gradation = 2 mm.

Figure 4a - Incisive centrale supérieure droite (M72 c.10 E11 n° 336) : vues linguale et occlusale. Flèche blanche : limite apicale de l'émail, flèche noire : limite anatomique du collet. Échelle en millimètres, chaque graduation = 2 mm.

Figure 4b - Upper right lateral incisor (M70 c.10 F12 # 54): buccal and apical views. Open arrow: apical limit of the enamel, solid arrow: anatomical cervix. Scale in millimeters, each gradation = 2 mm.

Figure 4b - Incisive latérale supérieure droite (M70 c.10 F12 n° 54): vues vestibulaire et apicale. Flèche blanche : limite apicale de l'émail, flèche noire : limite anatomique du collet. Échelle en millimètres, chaque graduation = 2 mm.

located at their normal positions, i.e. the anatomical cervix (fig. 4a and 4b: solid arrow). They terminate well away from them. Note also that the central incisor possesses a very irregular cervical border, while the border on the lateral incisor, though smooth and regular, has an abnormal convexity.

Although this unusual suite of features is not present to the same degree of development/extension on the two incisors and does not have the same modifying impact on their normal morphology, their overall modifications are similar. This indicates they were subject to the same taphonomic processes.

Significant research has been undertaken to more fully understand the various modifications observed on the faunal and human remains from archaeological sites (i.e. Horwitz and Smith 1988; Fisher 1995; Brugal *et al.* 1997; Selvaggio 2001; Egeland *et al.* 2004; Domínguez-Rodrigo and Piqueras 2003). Taphonomic modifications include abrasion, weathering, the action of vegetation, animals and soil acidity (for example, Lyman 1994; Hedges and Millard 1995; Nicholson 1998; Nielsen-Marsh and Hedges 2000; Pickering *et al.* 2004; Fernández-Jalvo and Andrews 2016). Because the three hard dental tissues (enamel, dentin and cementum) composing a tooth are characterized by distinct compositions and structures (enamel is the most mineralized of the tissues, dentin and cementum less so; i.e. Hillson 2014), some of these processes would differentially act on a tooth.

4 - Potential pathology

A literature review (Hillson 1996, 2014; Piette and Goldberg 2001) failed to discover any pathological conditions that

could explain such unusual crown and root morphology on human permanent incisors or any other tooth type.

5 - Soil acidity (fig. 5)

Soil acidity is one possible agent that might produce modifications on teeth. Enamel is the most mineralized hard tissue in the body, with its mineral structure and crystallinity organized to resist to corrosive effects of dietary and digestive acids (Dawes 2003 ; Pasteris *et al.* 2008). However, to assess the possibility that soil acidity might have been responsible for the modifications observed on the Neandertal incisors, modern deciduous and permanent bovid isolated molars were placed in a 10% formic acid solution (PH = 2.91). This obviously is not a precise measure of the soil acidity at Marillac, and while formic acid at this concentration is considered an irritant and not corrosive, it nevertheless represents a reasonable way to observe the reaction of the various parts of the teeth to the action of an acid. Figure 5 illustrates the teeth before immersion in the formic acid and after 22 hours in this acid solution. Note the decrease of the mesio-distal diameter of the crown: 5.8% for the deciduous tooth, 3.3% for the permanent molar as well as the more limited loss of tissue at the cervix: 0.74% for the deciduous tooth, 0.66% for the permanent molar.

The acid treatment produced obvious changes on the morphology of the teeth: the heavily mineralized enamel crowns have been markedly transformed by immersion in the formic acid solution while the root, composed of less mineralized dentine, shows little change. The acid worked primarily on the mineralized portion of the dental tissues. The reduction in the size of the crowns is greater than in the roots. These changes to root and crown sizes are exactly

Figure 5 - Deciduous and permanent bovid molars (buccal view). Left, before acid immersion. Right, after 22 hours in a 10% solution of formic acid. Scale in centimeters, each gradation = 10 mm.

Figure 5 - Molaires déciduale et permanente de bovidé (vue vestibulaire). À gauche, avant l'immersion dans l'acide. À droite, après 22 heures dans une solution à 10 % d'acide formique. Échelle en centimètres, chaque graduation = 10 mm.

opposite from the modifications observed on the Neandertal incisors from Marillac; that is to say, those teeth showed greater loss of root dentine tissue and less on the more heavily mineralized crown.

Many isolated faunal and human teeth are known from Marillac (and from many Upper Pleistocene sites from the south-west of France) and virtually all of them possess normal morphology. Thus, it is extremely unlikely that soil acidity, never very important within the high pH limestone karstic caves, could be the main factor that produced these unusual dental modifications.

6 - Partial digestion by carnivores (fig. 6)

Research (Sutcliffe 1970; Binford 1981; Andrews 1990, 1995; Cruz-Urbe 1991; d'Errico and Villa 1997; Dauphin *et al.* 2003; Pickering *et al.* 2004; Backwell *et al.* 2009; Camarós *et al.* 2017) provides evidence for another taphonomic process that results in modifications to hard tissues: the action of digestive enzymes and acids during consumption by a variety of animals including birds (eagles, vultures), reptiles (crocodiles) and mammalian carnivores (lion, wolf, hyena). The combination of digestive acids, enzymes and time (Denys *et al.* 1995) generally leads to the destruction to both mineral and organic components of the tooth (Fernández-Jalvo and Andrews 2016); the soft tissues (the organic material) will disappear first (with some variability; Pickering 2001).

To assess the potential that digestive processes might have on dental tissues, the two incisors were compared to a sample of partially digested faunal teeth directly associated with hyena occupations (i. e. Villa *et al.* 2004; Fourvel 2012; Fourvel *et al.* 2015) from the French Pleistocene sites of Les Plumettes (Airvaux 1987) and les Rochers-de-Villeneuve (Beauval *et al.* 2005). The major modifications on these faunal teeth are a differential erosion of dentine and enamel, especially at the cervix, a reduction in the

Figure 6 - Bovid regurgitated teeth from Marillac with similar or more pronounced modifications than the two Neandertal incisors. The difference between the anatomical cervix and the present one is very clear on the tooth on the left. For the three teeth, the root apices are largely opened. The tooth in the middle no longer possesses enamel and the dentine crown has been affected by the process. It explains why the asymmetry between the crown and the root breadth seems less pronounced. The tooth on the right presents the same degree of modifications as the left one but with more preserved enamel and a shorter root. It was probably not the same incisor number. All three teeth possess marked opening of the root apex. Scale in centimeters, Each gradation = 10 mm.

Figure 6 - Dents régurgitées de bovidés de Marillac avec des modifications similaires ou plus accentuées que les deux incisives néandertaliennes. Sur la dent à gauche, la différence entre collet anatomique et extension de l'émail est bien visible. La dent du milieu ne montre plus du tout d'émail et la dentine coronaire a aussi été affectée, ce qui diminue la dissymétrie couronne-collet. La dent de droite présente les mêmes caractéristiques que celle de gauche avec un émail mieux conservé mais une racine plus courte. Elle n'est probablement pas du même rang. Pour les trois dents, l'apex de la racine est largement ouvert. Échelle en centimètres, chaque graduation = 10 mm.

diameter and length of the root, and a significant widening of the root apex. This is the result of both digestive enzymes, like pepsin, which break down the collagen component of the less mineralized dentin and cementum and digestive acids which decalcify the mineral portion of both enamel and dentin.

It is clear from this examination of teeth from Pleistocene hyena dens that the morphological modifications produced by their partial digestion are the same as those observed on both Neandertal teeth from Marillac. Figure 6 illustrates three bovid incisors from Marillac with the same modifications, at different stages of the process, produced by carnivore partial digestion.

7 - Discussion

Archaeological analysis of the remains from facies 2a and 2b of Marillac strongly suggests that this site served repetitively over time as a hunting camp. Many reindeer carcasses, as well as those of several horses and bison, were butchered and prepared for transport and storage to another location for consumption (Costamagno *et al.* 2006; Meignen *et al.* 2010).

There is also evidence at Marillac of human manipulation of dead Neandertals (Vandermeersch 1971, 1976a; Le Mort 1987, 1988; Garraalda *et al.* 2005; Garraalda 2008; Mussini 2011). More than 35 % of the Marillac Neandertal cranial and infracranial pieces (both mature and juvenile individuals) present unquestionable cut-marks (indicative of scoring with a stone tool), percussion pits and incipient fracture lines. Internal vault releases (White 1992) are also identifiable on different skull fragments. These observations document butchery practices on these humans. The presence of butchered Neandertal bones may indicate cannibalism at Marillac (Maureille *et al.* 2010; Mussini 2011), or some other cultural practice that did not involve consumption (Garraalda and Vandermeersch 2000; Garraalda *et al.* 2005; Garraalda 2008; Pettitt 2011).

The most parsimonious explanation to account for the partial digestion of human teeth is that faunal elements left after butchery, as well as hominin remains, were abandoned and subsequently scavenged by carnivores.

Since the initial identification of partially digested incisors at Marillac (Costamagno *et al.* 2003), five other teeth at the same site, a left lower second permanent molar (M71 c.9/10), a first left premolar (M72 c.11 I10 # 22), a first left lower deciduous molar (M73 c.10 E10), a germ of a lateral left upper incisor (M75 c.11 H9 # 3) have also been identified. Descriptions, as well as 3D and virtual reconstructions of the Marillac teeth are being prepared for publication (Garraalda *et al.*, in preparation).

8 - Conclusion

The examination of some difficult to interpret morphological features on two isolated teeth from the Marillac site that had been previously identified as those of a bovid or a cervid deciduous teeth has resulted in their identification as partially digested Neandertal maxillary incisors.

This contribution gives also macroscopic key features to identify such peculiar taphonomic modifications on isolated human teeth and which could help to find, within faunal collection samples, new human fossils. The description of the complete set of regurgitated Neandertal teeth from Marillac will perhaps also help to discuss the impact of the partial digestion by carnivores of partial human maxillas or mandibles.

An implication of this research is that more attention ought to be directed to faunal samples from sites where large predators may have been involved in their accumulation. Hyena dens were a frequent feature in Western Europe at the end of Mousterian times (Discamps 2011; Discamps 2014). For some of them, for example Rochelot (Tournepiche and Couture 1999), Les Rochers-de-Villeneuve (Beauval *et al.* 2005), partially gnawed hominin bones (humerus, femur) and isolated teeth have been discovered. It is likely that additional examples of regurgitated hominin teeth are present in the faunal collections from similar sites, but may not have been considered human, identified instead as deciduous teeth of a medium or large mammal. Bovid and cervid anterior teeth with notable occlusal attrition but with an open (and large) root apex can be more carefully examined for a discrepancy between the crown's apical border and the tooth cervix, the partial absence of enamel, an abnormal enamel thickness or the asymmetry between the breadth of the crown and the root. A polished luster over the entire tooth and a relative lack of cementum are also useful signs.

A literature review has resulted in the discovery of similar modifications on hominin posterior teeth from the Upper Pleistocene sites of Grotte du Bison (Yonne, figure 3 in Tillier *et al.* 2013a) and Grotte des Hyènes at Arcy-sur-Cure (Yonne, Auy H D6 Iva, unpublished, pers. obs.). Moreover, a left deciduous central incisor of *Paranthropus robustus* (SWT3-2433) from Member 3 of Swartkrans (South Africa; figure 2 in Pickering *et al.* 2016) also appears to possess the same modifications. Note that the authors of these articles provide crown diameters of the teeth, but apparently do not take into consideration the possible reduction of their crown dimensions. However, such a taphonomic process has a real influence on the metrical dimensions of the crown and root. This was emphasized by Tillier *et al.* (2013b) for an upper permanent third molar which may very well have been partially digested. It is worth noting that all these teeth were identified as hominin, indicating it is essentially incisors and canines where carnivore digestive processes have resulted in changes in crown and root morphology that make recognition as hominin difficult and confusing.

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