

Cutmarked human remains bearing Neandertal features and modern human remains associated with the Aurignacian at Les Rois

Fernando V. Ramirez Rozzi¹, Francesco d'Errico², Marian Vanhaeren³, Pieter M. Grootes⁴, Bertrand Kerautret⁵ & Véronique Dujardin⁶

- 1) UPR 2147, *Dynamique de l'Evolution Humaine*, CNRS, 44 Rue de l'Amiral Mouchez, 75014 Paris, France
e-mail: fernando.ramirez-rozzi@evolhum.cnrs.fr
- 2) UMR 5199 PACEA, CNRS, Institut de Préhistoire et de Géologie du Quaternaire, Avenue des Facultés, 33405 Talence, France
- 3) UMR 7041 ArScAn, *Ethnologie préhistorique*, CNRS, 21 allée de l'université, F-92023 Nanterre, France
- 4) Leibniz Labor für Altersbestimmung und Isotopenforschung Universität Kiel, Max-Eyth-Strasse 11-13, 24118 Kiel, Germany
- 5) IUT St Dié - LORIA - ADAGIo Team, Campus Scientifique, B.P. 239, 54506 Vandoeuvre-Lès-Nancy cedex, France
- 6) DRAC Poitou-Charente, 102 Grand'Rue, 86020 Poitiers, France

Summary - *The view that Aurignacian technologies and their associated symbolic manifestations represent the archaeological proxy for the spread of Anatomically Modern Humans into Europe, is supported by few diagnostic human remains, including those from the Aurignacian site of Les Rois in south-western France. Here we reassess the taxonomic attribution of the human remains, their cultural affiliation, and provide five new radiocarbon dates for the site. Patterns of tooth growth along with the morphological and morphometric analysis of the human remains indicate that a juvenile mandible showing cutmarks presents some Neandertal features, whereas another mandible is attributed to Anatomically Modern Humans. Reappraisal of the archaeological sequence demonstrates that human remains derive from two layers dated to 28–30 kyr BP attributed to the Aurignacian, the only cultural tradition detected at the site. Three possible explanations may account for this unexpected evidence. The first one is that the Aurignacian was exclusively produced by AMH and that the child mandible from unit A2 represents evidence for consumption or, more likely, symbolic use of a Neandertal child by Aurignacian AMH. The second possible explanation is that Aurignacian technologies were produced at Les Rois by human groups bearing both AMH and Neandertal features. Human remains from Les Rois would be in this case the first evidence of a biological contact between the two human groups. The third possibility is that all human remains from Les Rois represent an AMH population with conserved plesiomorphic characters suggesting a larger variation in modern humans from the Upper Palaeolithic.*

Keywords - *Contact, Upper Palaeolithic, Modern Human Variation, Tooth Morphology, Tooth Growth.*

Introduction

Biological and cultural interactions between Neandertals and Anatomically Modern Humans (AMH) in Europe during the Middle-to-Upper-Palaeolithic transition are the subjects of a lively debate (Bar-Yosef & Pilbeam, 2000; Churchill & Smith, 2001; Stringer, 2002; Zilhão & d'Errico, 2003; d'Errico, 2003; Conard *et al.*, 2004; Zilhão, 2006; Finlayson *et al.*, 2006; Gravina *et al.*, 2006; Mellars 2004, 2006; Zilhão *et al.*, 2006). Distinction between these two human groups has recently been emphasized by geometric morphometrics analysis of tooth morphology (Martinón-Torres *et al.*, 2006; Gómez-Robles *et al.*, 2007, 2008) as well as by the recognition of different evolutionary trajectories in brain expansion and cranial growth (Bruner *et al.*, 2003; Ponce de León & Zollikofer, 2001; Ponce de León *et al.*, 2008). However, the small number of human remains associated with archaeological material dated to this transition represents a major problem for testing hypotheses regarding the nature, extent, and chronology of relationships between the two human types. Furthermore, several human remains previously assigned to the Early Aurignacian yielded recently younger radiocarbon dates and they have to be assigned to more recent periods (Conard *et al.*, 2004; Zilhão & d'Errico, 2003; Svoboda *et al.*, 2002) hence reducing to very few the diagnostic AMH remains associated with the first phase of this culture (Churchill & Smith, 2001; Svoboda *et al.*, 2002). Other remains lack archaeological context (Churchill & Smith, 2001; Trinkaus *et al.*, 1999). Taxonomic attribution for the makers of the other Early Upper Palaeolithic (EUP) technologies is equally ambiguous. Widely accepted for the Châtelperronian, the only cultural tradition associated with diagnostic Neandertal remains (Lévêque & Vandermeersch, 1981; Hublin *et al.*, 1996; Bailey & Hublin, 2005), the Neandertal authorship of other EUP technologies, even if plausible, remains undemonstrated. Here we reappraise the taxonomic diagnosis, cultural affiliation, and chronological attribution of the human remains from Les Rois (Mouton & Joffroy, 1958), one of the few sites with Aurignacian artefacts and

human remains frequently cited to support the association of AMH with Aurignacian technologies (Mellars, 2004, 2006; Churchill & Smith, 2001; Trinkaus *et al.*, 1999).

Archaeological context

The Les Rois cave is located 2 km south of the village of Mouthier-sur-Boëme, Charente, France. The site was discovered in the late 1920s by the abbé Coiffard (1937), who collected a few human teeth, now lost, from inside the cave. Between 1930 and 1939, a test pit was dug at the entrance of the cave by a local amateur, Charles Potut. Little is known about this excavation, which remains unpublished. According to Jean Morel, who visited the site in August 1935 (Dujardin, 2000), Potut identified three layers that yielded Aurignacian lithic and bone artefacts comparable to those found at the nearby site of La Quina (Henry Martin, 1925, 1931). At the invitation of Potut, the deposit outside the cave was systematically excavated between 1948 and 1952 by Mouton and Joffroy (see Fig 1 in Mouton & Joffroy, 1958). The excavation extended over 45 m² and reached a depth of between 1 and 2.50 m. Mouton & Joffroy (1958) recognised three main archaeological units below a humus layer containing few reworked artefacts (Fig. 1 Suppl. Mat.). Basal unit B, overlying the bedrock, yielded an exceptionally abundant faunal assemblage, mostly composed of fractured reindeer mandibles and limb bones (more than 220 individuals represented), which has been interpreted as an accumulation of butchery waste. Separated at places from unit B by a sterile layer, the overlying sub-unit A2 β is dominated by reindeer and, to a lesser extent, fractured horse remains as also found in unit B. Following another sterile layer, called A2 α , the top unit A1 provided less abundant faunal remains with reindeer and horse in equal proportions. Three hearths were identified in A2 and one in A1 (see Fig 5 in Mouton & Joffroy, 1958). The stone tool assemblage from unit B is dominated by crenated scrapers and end-scrapers on Aurignacian blades (Fig. 1).

Numerous lozenge-shaped antler spear points with elliptical cross-sections, characteristic of an advanced phase of the Aurignacian, were recovered from this unit, which also yielded a varied collection of personal ornaments. Stone tool types from units A1-2 are the same as in unit B with a gradual increase in busked burins and a reduction in the proportion of Aurignacian blades (Fig. 2). The bone industry is characterised by lozenge-shaped points that are rectangular-in-section. A single AMS ^{14}C age of $28,715 \pm 145$ BP (Lyon-2171 OxA) obtained from burnt bone from unit B was available before the present study (Dujardin & Tymula, 2004).

Human remains

Vallois states that two human mandibles and 36 isolated teeth were discovered at Les Rois (Fig. 3) (Vallois, 1958). However, 37 teeth are described in his paper. Mandible A, from the basal unit B, consists of a right and left body broken on both sides at the level of the M_2 socket and preserving right and left C, P_3 , M_1 , and dm_2 ; incisors were lost post-mortem. Vallois (1958) attributes to this mandible an isolated lower LM2, R51 #6. Two other lower molars (R50#31 and R51#30) were found in the same layer. Mandible B, found in a fireplace from sub-unit A2 β but showing no signs of burning, comprises a portion of the alveolar margin from right I_2 to right P_4 , with right P_3 and P_4 preserved, and shows a horizontal break below the tooth sockets. Isolated teeth come from the same unit. Vallois (1958) provides the tooth type assignment and, in most cases, the number and description of each tooth. We present here the list of isolated teeth after Vallois (1958):

- four upper incisors: left I1 (R50 #45), right I1 (without number), left I1 (without number), and left I (1?) (R50 #5),
- eight lower incisors: RI1 (R51 #12), LI1 (R50 #13), LI2 (R51 #11), LI2 (R51 #17), LI1 (R50 #24), LI (without number), RI2 (#35), and I1 (#31),
- two lower canines: RC (R40) and LC (A3 #10),
- three lower premolars: LP3 (R51 #22), LP4 (R51 #23), and LP3 (R50),
- two upper premolars: LP4 (R50) and RP4 (R51 #29),
- ten lower molars: RM1 (R50 #40), LM2/3 (R50 #3), RM2 (R50 #31), RM3 (R50 #9), RM1/2 (without number), LM1/2 (without number), LM1/2 (R51 #30), LM (without number), RM1 (R51 #14), RM (R51 #15),
- four upper molars: RM1/2 (#54), RM1/2 (R53 P), RM3 (R50 #21A), and RM3 (R51 #16).
- one lower Ldm2 (R50).

Two other isolated teeth, a lower RC and RI2, are attributed by him to mandible B, and a lower LM2 (R51 #6) to mandible A. This gives a total of 37 teeth. In the same paper, Vallois provides a plan of 2m² in which mandible B and nine isolated teeth were found (Vallois, 1958, Fig. 4). The lower incisors R51 #11, R51 #12, and R50 #13 were found 30 cm away from mandible B, and assigned, after comparison with the anterior teeth from this mandible, to the same individual (Vallois, 1958). One additional heavily worn incisor from A2 has its root perforated in order to be used as a pendant.

Vallois identified primitive traits on both mandibles, particularly on mandible B, and also reported the presence of cut-marks on this specimen (Mouton & Joffroy, 1958; Vallois, 1958). After Mouton & Joffroy's work (1958), archaeological remains from Les Rois were reviewed in two works focused on South-west France (Perpère, 1972; Leroy-Prost, 1985). The human remains from Les Rois have since been considered as representing AMH from the Early Upper Palaeolithic of France (Gambier, 1989).

Methodology

The entire available anthropological and archaeological collections from Les Rois were reappraised in the framework of the present



Fig.1 - Aurignacian artefacts from Les Rois unit B: a-f: fragmentary spear points made of antler, g: decorated antler, h-j: fragments of ivory sticks, k: preform of an ivory basket-bead, l: tubular bone bead, m: fragment of an antler decorated stick, n: pointed antler pendant, o-w: perforated horse incisor (o), fox canine (p), reindeer incisor (q), reindeer canine (r), hind canine (s), stag canine (t), bovid incisor (u), and wolf canine (v-w), x: perforated gastropod mould, y: perforated urchin, aa: carenated end scraper, bb: shouldered scrapers, cc: retouched blade, dd: double end scraper, ee: nosed end scraper, ff-ii and kk: end scrapers on retouched blades, ll: dihedral burin.

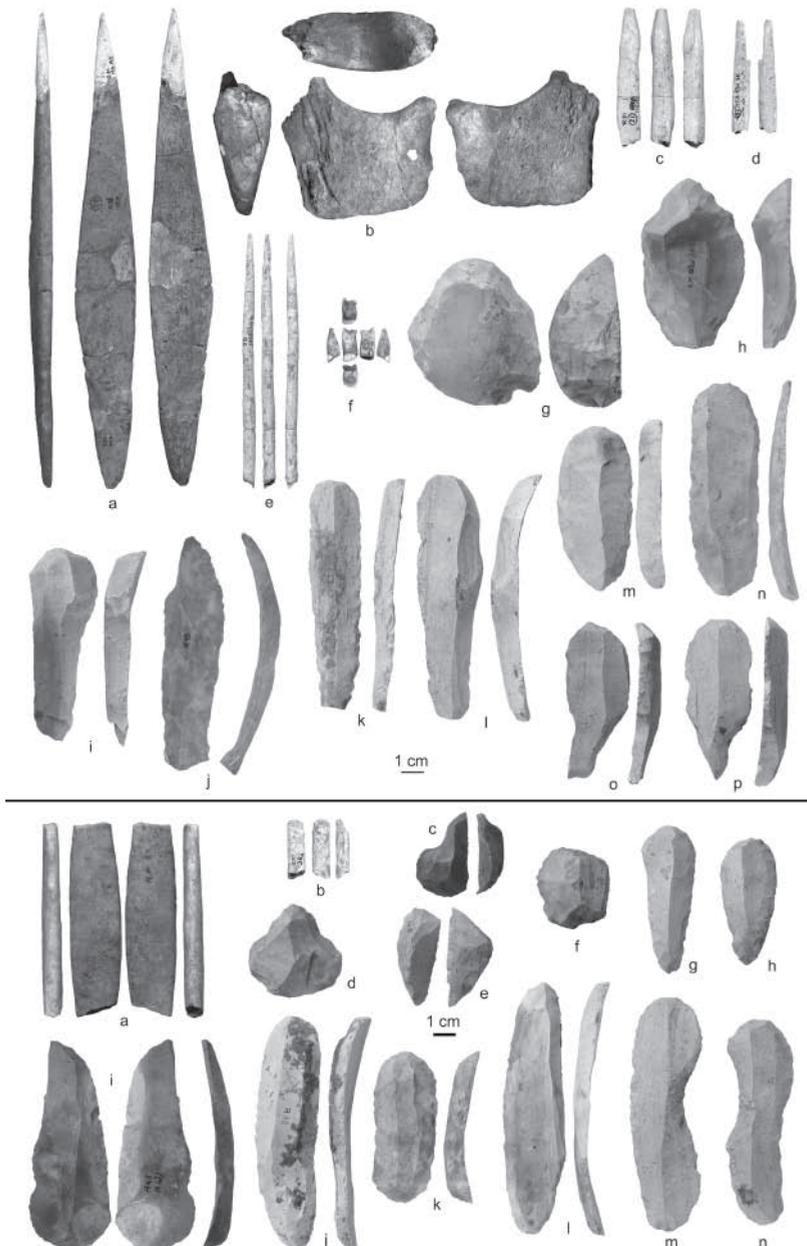


Fig. 2 - Aurignacian artefacts from Les Rois unit A2 (top) and A1 (bottom). Top, a: lozenge-shaped antler spear point, b: fragment of perforated antler, c-d: bone awls, e: bone pin, f: perforated human tooth, g: carenated end scrapers, h: nosed end scraper, i: end scraper, j: burin on a retouched blade, k-l: end scrapers on blades, m-n: double end scrapers, o-p: burins-end scrapers. Bottom, a: fragment of a lozenge-shaped antler spear point, b: fragment of an antler stick, c: busqué burin, d: nosed end scraper, e-f: carenated end-scraper, g-h: end scrapers on retouched blades, i: end scraper-perforator, j-k: double end scrapers, l: retouched blades, m-n: end scrapers on Aurignacian "strangled" blades.

study. Human remains are presented in Figure 3. The human and some faunal remains found by Joffroy and Mouton are housed at the Institut de Paléontologie Humaine (IPH), Paris; and the lithic and bone tools as well as the personal ornaments are housed at the Musée d'Archéologie Nationale, Saint-Germain-en-Laye. We were unable to locate the remainder of the faunal remains analysed by Bouchud (1958), and we could not analyse four small samples of loose sediment preserved in sealed bottles housed at the Musée d'Archéologie Nationale. With the exception of the Mouton & Joffroy's monograph (1958) and Vallois' paper (1958), no other documents are available on the 1948- 1952 excavations.

The retouched tools, cores, debitage and bone tools were analysed for i) features characteristic of specific *facies* or chronocultural phases of the Aurignacian in order to narrow the cultural attribution of the three units, ii) pieces diagnostic of Middle- or other Upper Palaeolithic technocomplexes in order to verify the monocultural nature of the human occupation. Reappraisal of the lithics was conducted using the criteria suggested by Pelegrin (1995), Bordes & Lenoble (2002), Bon (2002), Connet (2002), and summarized by Zilhão *et al.* (2006). Bone tools were analysed according to criteria suggested by Sonnevile-Bordes (1966) and Liolios (1999). Personal ornament association was compared to that reported from the other Aurignacian sites (Vanhaeren & d'Errico, 2006). All human remains, bone tools and personal ornaments as well as a representative sample of the lithics from each unit were photographed.

Recent works have suggested that Neandertal and AMH teeth differ in their morphology (Bailey, 2002, 2004; Bailey & Lynch, 2005), as well as in the number and pattern of distribution of incremental lines in anterior teeth (Ramirez Rozzi & Bermudez de Castro, 2004; Guatelli-Steinberg *et al.*, 2005). Although overlap exists between these two human groups in all variables, these traits can be used to suggest a probable attribution as either AMH or Neandertal in otherwise not-assignable isolated teeth and mandible/maxilla fragments.

Bailey (2000, 2002, 2004), Bailey & Lynch (2005) and Bailey & Hublin (2006) have observed that some morphological dental characters are particularly diagnostic of Neandertals. These include the lingual tubercle in the second upper incisor, the asymmetric shape of the mandibular fourth premolar, the cusp relationships in maxillary molars, and the mid-trigonid crest - frequently present in Neandertal and frequently absent in AMH lower first molars. Other relevant dental traits are present in both groups but are expressed with greater frequency in Neandertals, such as the shovelling and lingual tubercles of upper incisors, the distal accessory ridge in lower canines, the multiple lingual cusps, the mesiolingual groove and the crown asymmetry in lower third premolars, the distolingual cusp, the transverse crest in lower fourth premolars, the Cusp 6 in lower first molars, the Y pattern, the Cusp 6, the mid trigonid crest, and the anterior fovea in the second lower molars (Bailey & Hublin, 2006). These non-metric characters were recorded in teeth from Les Rois using the Arizona State University Dental Anthropology System (ASUDAS) (Turner *et al.*, 1991). Those traits absent in ASUDAS were scored as outlined in Bailey (2002) and Bailey & Hublin, 2006. The presence/absence assessment of these dental characters was established using the breakpoint suggested by Bailey (2002) and Bailey & Hublin (2006).

The occurrence of subvertical grooves was also recorded. Subvertical grooves on the wear facets of posterior teeth have been observed in modern and extinct human groups (Villa & Giacobini, 1995). Although high frequency of these grooves is observed in Australian aborigines (Kaidonis *et al.*, 1992), they show a higher occurrence in Neandertals than in any other hominid group (Perez-Perez *et al.*, 2003; Villa & Giacobini, 1995).

Mesio-distal and bucca-lingual diameters of teeth from Les Rois were recorded with digital calipers and were used to establish the crown base area (CBA), which is a measure of tooth robusticity (Smith, 1989; Bermudez de Castro, 1993). Instead of the CBA, Bailey & Hublin (2006) employed the bucco-lingual breadth to compare Neandertals and modern humans from the Upper

Palaeolithic. Bucco-lingual diameter and CBA of teeth from Les Rois were compared with data from Neandertals and early Upper Palaeolithic modern humans (EUP). For Neandertals, the reference data are from Bailey & Hublin (2006) and Bermudez de Castro (1993). The Neandertal sample in Bailey & Hublin include individuals attributed to the OIS 7-3 from Europe and Middle East. The Neandertal sample studied by Bermudez de Castro (1993) includes OIS 7-3 individuals found in Europe solely. Upper Palaeolithic Modern Humans data, kindly provided by C. Verna, comes from bibliographic data for individuals associated to Aurignacian and Gravettian contexts (see Appendix 1). Bailey (2005) has suggested that root length provides additional taxonomic information that may be useful in diagnosing dental remains, in particular for lower first incisor, lower fourth premolars, upper first incisors and upper canines. Root length have been measured in teeth from Les Rois and compared to values for Neandertals and anatomically modern humans. Root measurements were taken on the lingual aspect of anterior teeth and premolars, and on the mesial root of molars (Bailey, 2005; Bailey & Hublin, 2006).

Dental growth presents strong genetic basis and it can be characterized by incremental lines in enamel (Jernvall & Thesleff, 2000; Smith, 2008). One type of incremental line, the striae of Retzius, reaches the enamel surface and manifests itself as smooth grooves called perikymata, which have a modal periodicity of 8 or 9 days (range 6–12 days) in humans (Fitzgerald, 1998; Reid & Dean, 2000; Schwartz & Dean, 2001). A similar periodicity of 7-8 days was found in Neandertals (Dean *et al.*, 2001; Macchiarelli *et al.*, 2006; Smith *et al.*, 2007).

Although the study of enamel microanatomy failed to establish a taxonomic attribution of Plio-Pleistocene hominid premolars and molars from Omo (Ramirez Rozzi, 1998), the pattern of perikymata distribution on anterior teeth has been shown to be different between *Paranthropus* and *Australopithecus* anterior teeth (Dean, 1987; Beynon & Dean, 1988; Dean *et al.*, 2001). The study of incremental lines in enamel in the largest

sample of Neandertal and Upper Palaeolithic-Mesolithic AMH (UPAMH) anterior teeth to date has revealed significant differences between these two populations in the number and packing pattern of perikymata (Ramirez Rozzi & Bermudez de Castro, 2004). Indeed, significant differences in perikymata number are found in the last (cervical) third or the last fourth of the crown depending on tooth type (Ramirez Rozzi & Bermudez de Castro, 2004: 936). Differences in the perikymata packing pattern are also found when Neandertals are compared with modern human populations (Guatelli-Steinberg *et al.*, 2007). The latter study, however, does not identify significant differences between Neandertal and some modern populations in the total number of perikymata.

In the present work, we analyze the number and pattern of perikymata distribution on the anterior teeth as well as on the P_3 from the two mandibles and isolated teeth from Les Rois. Results from a previous study of anterior teeth in Neandertals and Upper Palaeolithic-Mesolithic AMH (Ramirez Rozzi & Bermudez de Castro, 2004) are compared to those obtained from Les Rois. We expand on this approach to include information on P_3 . We add results for the P_3 in Neandertals from Genay (n=2), Hortus (n=1), Zafarraya (n=1), Petit-Puymoyen (n=2), Sidron (n=3), Krapina (n=2), la Chapelle aux Saints (n=1), le Moustier (n=2), Circeo III (n=1), La Quina (n=2), and modern humans from the Upper Palaeolithic to historical times: Pataud (n=1), La Madeleine (n=1), Laugerie Basse (n=1), Lachaud 4 (n=1), Lespugues (n=2), Aurignac (n=1), historical times (n=6).

Wear prevented the study of perikymata in a lower canine (R40 w/# LRC), four fragmentary upper first incisors (R50 #45 LI¹, w/# RI¹, w/# RI¹, R50 #5 LI¹), the lower isolated premolars (R51 #22 LP₃, R50 LP₃, R51 #23 LP₄) and the perforated incisor from unit A2 at Les Rois. Environmental stress can produce enamel hypoplasia affecting the enamel surface. Linear hypoplasias represent a dysfunction in enamel organ function that may or may not be accompanied by an alteration in the distance between adjacent perikymata (Cunha *et al.*, 2004). This alteration,

when occurs, is locally placed and do not affect the entire hypoplastic enamel but is located at the limit of it and thus do not alter the number of perikymata neither the perikymata packing pattern. Teeth from Les Rois do not present hypoplasia. Only unworn teeth and teeth with a wear not higher than stage 3 (Hooper *et al.*, 2004), i.e. a loss of ca 15% of crown height and exposure of a small area of dentine on the occlusal surface (Ramirez Rozzi & Sardi, 2007, Fig. 1), were selected for perikymata analysis.

Each tooth was individually cleaned prior to this study. Perikymata counts were made directly on the original specimens. The starting step of perikymata analysis consists of measuring the crown height, which was done using a Vernier micrometer eye-piece connected to a digital ocular measure that was linked to a calculator-meter-printer RZD-DO (Leica). Values of buccal crown height of anterior teeth and P₃ from Les Rois were divided into ten equal divisions (deciles) from the first formed enamel at the cusp to the last forming or cervical enamel as already described (Reid & Dean, 2000; Schwartz & Dean, 2001; Ramirez Rozzi & Bermudez de Castro, 2004). Perikymata counts were made in each of the 10 divisions of the crown height. In order to test if perikymata number in the Les Rois teeth is closer to Neandertal or UPAMH teeth, each decile in each tooth class was compared with results from a sub-sample of teeth included in Ramirez Rozzi & Bermudez de Castro's work (2004). This sub-sample is comprised of anterior teeth showing comparable degree of wear to that present in the Les Rois specimens. Ellipses of probability at 95% were constructed. Data were processed statistically using StatView and Systat 9 software.

Cut-marks on mandible B were replicated by using the addition-curing silicone Coltene President putty and light body moulds. Epoxy resin replicas were made from each mould (Beynon, 1987) and observed with a Scanning Electron Microscope (SEM). The Les Rois faunal collection kept at the Institut de Paléontologie Humaine, mostly composed of reindeer mandibles, was also analyzed under the microscope to investigate possible anthropogenic modifications,

including the locations and orientations of cutmarks, which were recorded and photographed.

Radiocarbon Dating

Five faunal elements from units A and B, hold at the Musée d'Archéologie Nationale, were dated by accelerator mass spectrometer (AMS) at the Leibniz Laboratory. All remains showed cutmarks or traces of use as retouchers. Collagen extraction followed an extensive and rigorous pretreatment (Grootes *et al.*, 2004) designed to remove soluble contaminants by chemical extraction and insoluble ones by filtering the collagen dissolved as gelatine, a commonly used method. Small samples of about 2 mg of bone were collected and their nitrogen concentration, determined by colorimetry as nitrate, was used to calculate the collagen concentration of the bone. These values estimate the collagen preservation in the bone and were used to calculate the mass of bone needed for AMS ¹⁴C dating, which minimized sampling damage.

The samples were checked and mechanically cleaned under the microscope. Surface contamination was removed with a scalpel; signs of glue or other contaminants were noted and avoided. Samples of crushed material (<3 mm) were first treated with acetone and rinsed with demineralised water to remove fatty coatings, which might make subsequent acid and alkali extractions less effective. A particle size of just below 3 mm was chosen to reduce diffusion pathways for the demineralisation and extraction of the interior of the sample material, yet avoid fine dust, which would increase extraction losses. Because glue had been used on the reindeer mandible, KIA 25246, this sample was subjected to sequential soxhlet type serial extraction to remove organic contaminants (Bruhn *et al.*, 2001). In sequence, sample KIA 25246 was extracted three times each with boiling tetrahydrofuran (THF), chloroform, petroleum-ether, acetone, and methanol and then rinsed with demineralized water. These solvents were chosen for their efficiency in removing a wide range of hydrophobic organic substances used in order of

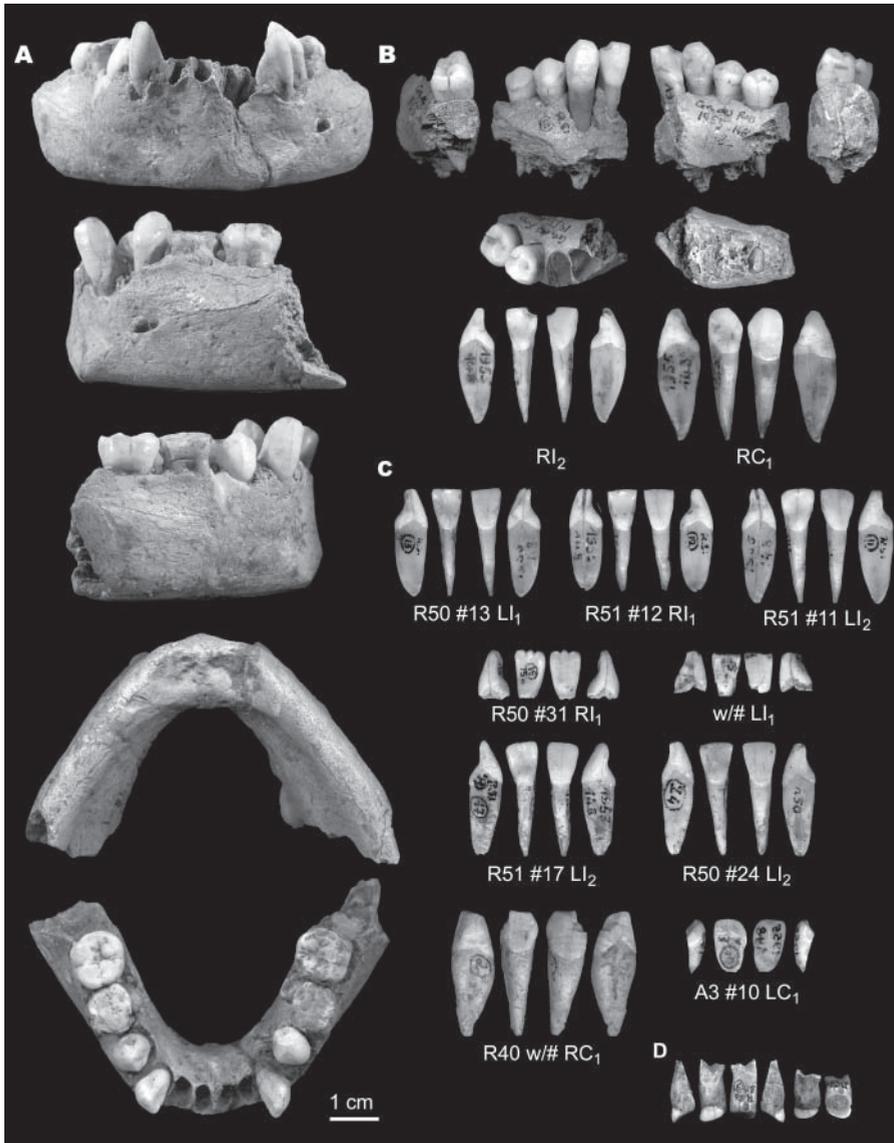


Fig. 3 - Human remains from Les Rois. A. From top to bottom: frontal, right, left, occlusal, and basal views of mandible A from unit B. Note the chin is formed by a vertical keel along the symphysis becoming more prominent inferiorly to form the mental protuberance, and the associated mental fossae, both characteristic of *H. sapiens* (Schwartz & Tattersall, 2000). B. From left to right and top to bottom: occlusal, distal, frontal, lingual, mesial, and basal views of mandible B, loose right lateral incisor (LRI2) and canine (LRC) from this mandible from unit A2. The change in orientation of the mandibular surface at the canine level evokes a flat or slightly arched anterior mandibular surface, characteristic of Neandertals (Schwartz & Tattersall, 2000). The fragmentary nature of the specimen, however, precludes a taxonomic diagnosis only on this basis. C. Mesial, lingual, buccal, and distal views of isolated lower incisors and canines from unit A2. Three isolated teeth (#11, #12, #13) are attributed to mandible B. D. Lateral, lingual, buccal, lateral, and occlusal views of a perforated human incisor from unit A2 (Continued on page 10).

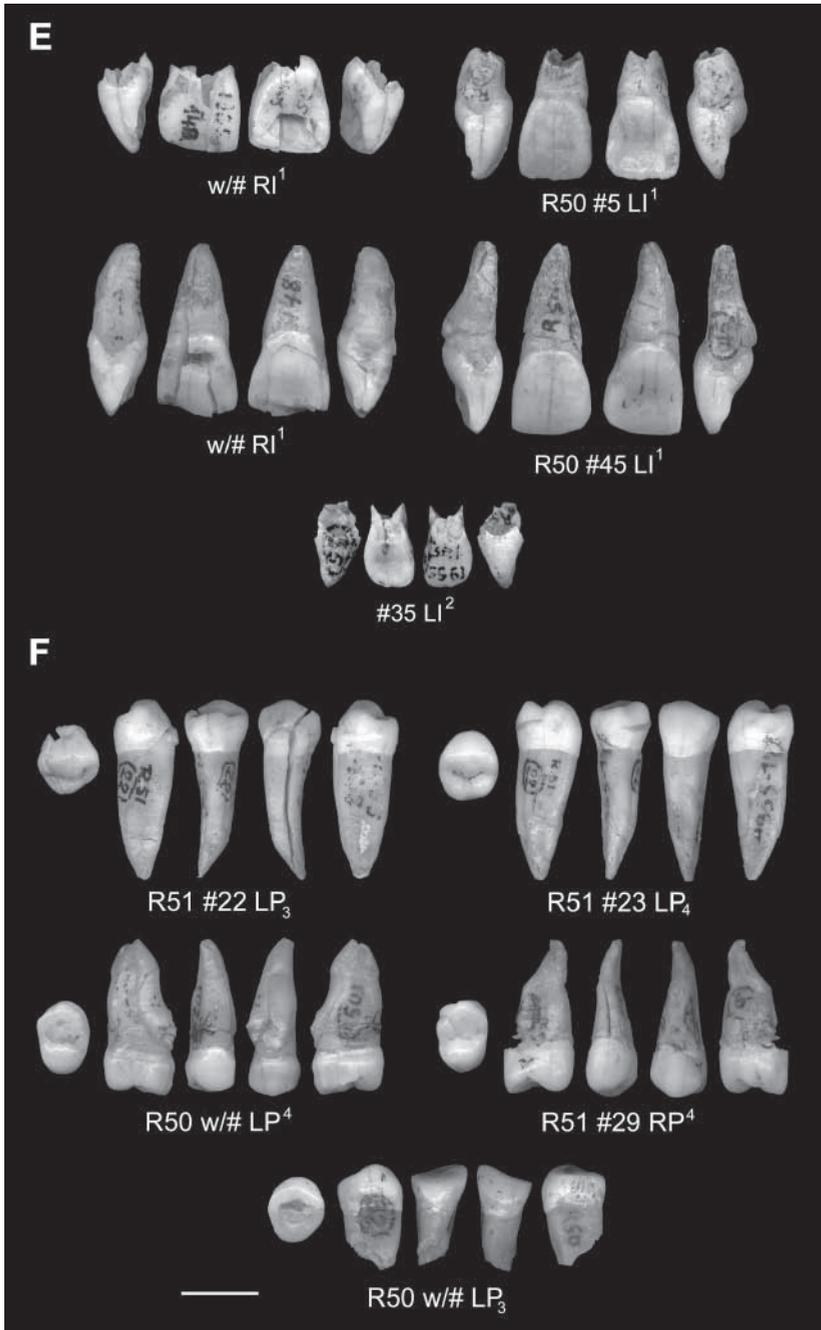


Fig. 3 (continued) - E. Mesial, lingual, buccal, and distal views of isolated upper incisors from unit A2. Vallois (1958) attribution of teeth to tooth classes was reviewed. R50 #24 is attributed here to a LI2 instead than to a LI1 and #35 to a LI2 instead than to a RI2. **F.** Occlusal (buccal face up), mesial, lingual, buccal, and distal views of isolated premolars.

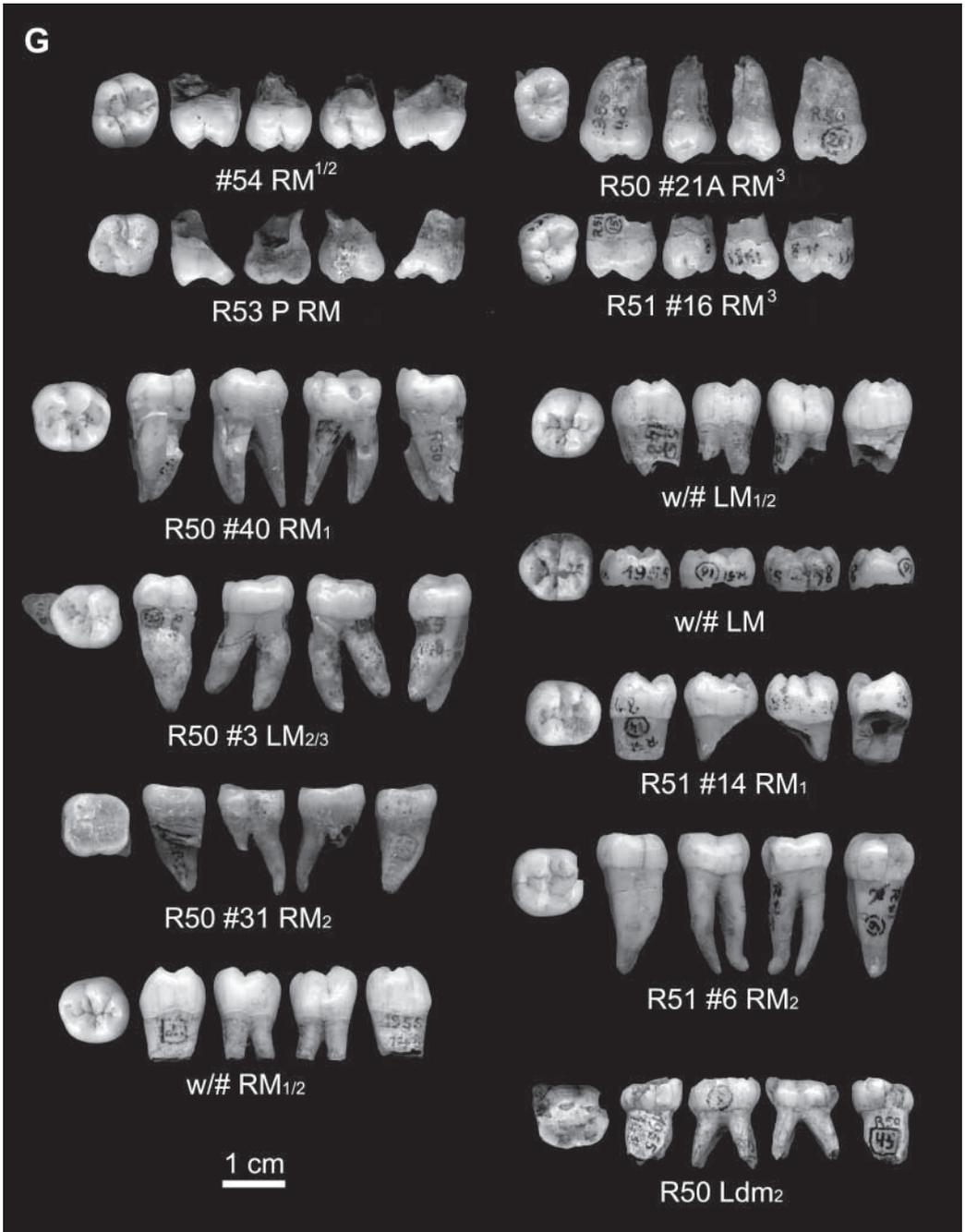


Fig. 3 (continued) - G. Idem molars. # refers to the number given by Vallois (1958); w/#: without number. Three molars described by Vallois were not identified among the remnant teeth labelled as 'Les Rois' (see text).

decreasing hydrophobicity, also effectively removing previous extraction solvents.

The samples were subsequently demineralised in HCl (ca. 1 %). Initially ca. 10 ml 1 % HCl is added. When the pH shows that most of the acid has reacted, concentrated acid is added to bring the solution back to ca. 1 % (pH < 1) until the pH stays below 1. Then the solution is siphoned off and the sample is washed repeatedly with deionized water until the pH is above four. This removes not only carbonates, salts, and the extracting acid, but also the water/acid soluble organic components designated as the fulvic acid fraction. As these are water soluble, they are mobile in the soil and are thus likely contaminants.

To remove mobile humic acids, the demineralised bone material was treated with 1 wt% NaOH (at 20°C, for 1 h) and subsequently washed repeatedly with demineralised water until the pH is below 9. The sample is then again treated with 1 % HCl (20°C, 1 h) and washed to remove atmospheric CO₂, which may have dissolved into the alkali solution.

The preferred dating material, bone collagen, was dissolved overnight as gelatine in demineralised water at 85 °C and pH = 3. The non-soluble fraction, including insoluble bone protein and possible contamination, was filtered through a 0.45 µm pore silver filter, which had been pre-cleaned by bake-out at 900°C. The gelatine solution was freeze dried, and the gelatin was combusted as the “bone sample”. In addition, we also dated the gelatinization-insoluble fraction on the filter (bone residue) to obtain an indication of the presence or absence of non-collagenous contaminants in the bone sample.

The combustion to CO₂ of all fractions was performed at 900°C in a closed pre-combusted quartz tube together with precombusted CuO and silver wool. The sample CO₂ was reduced with H₂ over Fe powder as catalyst, and the resulting carbon/iron mixture was pressed into a pellet in the target holder. CO₂ to yield 1 mg of carbon was reduced on 2 mg Fe. The CO₂ of all the small bone was reduced on 1 mg Fe to approach a C:Fe weight ratio of 1 to 2 for these smaller-size fractions.

The above protocol is effective in producing reliable ages for most bone samples because the process deals sequentially with particulates, conservation chemicals and hydrophobic compounds, carbonates, fulvic acids, humic acids, and finally non-collagen particulate organic matter.

A two-fraction AMS measurement of a bone sample, which not only reveals the presence of contamination but also gives an indication of its severity, is very useful. If one makes a mass balance calculation of the amount of contamination involved, one may estimate how likely it is that the measured age is significantly influenced.

A ¹³C/¹²C ratio was obtained during the AMS measurement of the ¹⁴C/¹²C ratio. This δ¹³C value does not have the same accuracy as traditional stable isotope ratio analysis (SIRA), but is suitable for the ¹³C fractionation correction and provides information on collagen composition and the presence of glues and other foreign compounds.

Results

Archaeology

Analysis of the lithic assemblages, including pieces with no stratigraphic assignment or coming from the very base of the sequence, confirms the excavators' diagnosis that all the lithics can be attributed to the Aurignacian. Mousterian and Châtelperronian tools, debitage, and cores are absent. The highly selective nature of the collection makes it difficult to propose a more precise cultural attribution. Retouched bladelets (Font-Yves, Dufour of the Dufour, and Roc-de-Combe subtypes,) characteristic of the various facies/phases of the Aurignacian are absent in the assemblage, which seems incompatible with the relative abundance in all units of carinated “scrapers” from which suitable blanks were certainly detached. Debitage is almost entirely restricted to large unbroken blades, which is inconsistent with the numerous recovered flake cores. In spite of these limitations, the presence of an Archaic Aurignacian (Bon, 2000) can be excluded considering the absence of unipolar prismatic bladelet cores. The abundance of large retouched blades

with a curved profile, particularly in unit B, and the increase of the busked burins and nosed end-scrapers in unit A supports a tentative attribution of the two main units, B and A, to the Early and Evolved Aurignacian, respectively. However, the richness, in all units, of lozenge-shaped antler points, characteristic of the Evolved Aurignacian, and the absence of split base antler points in unit B, seem to indicate that the site does not record the earliest phase of the Early Aurignacian. The analysis of the personal ornaments (Figs. 1 and 2) identifies cultural links with northern Aurignacian groups. Three out of the thirteen ornament types from unit B (perforated reindeer canine and incisor, gastropod mould) are found only at Les Rois, five others (perforated hyena canine, human tooth, urchin, pointed antler pendant, ivory basket bead) are found at other sites from southwestern France. Seven other types (perforated red deer, fox, wolf canines, horse and bovid incisors, tubular bone bead, antler diadem) are common at both sites from this last region, and in northern Europe. The only personal ornament from unit A, a perforated human incisor, corresponds to a type whose distribution is restricted to the south-western France. Apart from the perforated red deer canine, which is the most ubiquitous Aurignacian ornament, none of the ornament types found at Les Rois occur at Mediterranean sites.

Chronology

The collagen content for each sample from Les Rois is shown in Table 1. The bone organic material has thus largely disappeared, but the remaining concentrations are, in our experience, sufficient for precise radiocarbon ages.

Collagen extracted from the bones provides dates ranging between ca. 27.3 kyr and 30.4 ¹⁴C kyr BP (1 kyr = 1,000 years) for both units. Supplemental dating of the organic bone residue, remaining after the extraction of the collagen as dissolved gelatin, yielded ages between 13.4 and 20.3 ¹⁴C kyr BP. This shows the –not unexpected– presence of younger contaminants. The age differences between the collagen and the insoluble residue fractions are large but unfortunately not out of the ordinary for old bones. Yet, the

sensitivity to young contamination for the Les Rois samples is not as large as for very old samples near 40 kyr, because the ¹⁴C concentrations are still in the range of 2 to 3 percent of modern carbon (Tab. 1). As can be seen, the amount of carbon in the insoluble residues (calculated from the CO₂ pressure after combustion) was much smaller than the amount of carbon in the collagen fractions (from 1 % to 10 % (KIA 25246) of the collagen fraction). The chemical extraction of the collagen after the acid-alkali-acid pre-treatment—as gelatin in solution through a silver filter—aims to prepare a pure gelatin sample and concentrate possible remaining non-soluble contaminants in the insoluble fraction. Table 1 shows the amount of young (100 percent modern carbon (pMC)) contaminant needed to bring the ¹⁴C concentration of the rest fraction from that of the collagen/gelatin to its measured value. As expected little is needed (24 to 212 µg). The question is how effectively the 0.45 µm silver-filter eliminates non-soluble contaminants (soluble ones were dealt with before in the acid-alkali-acid extraction and washing).

Considering a scenario where 10 % of the amount of contamination concentrated in the insoluble fraction would have passed the filter and remained in the collagen (which is unlikely), the “real” age of the collagen fraction would be from 60 yr to 190 yr older –corresponds with 0.3σ and 1.0σ for KIA 25247 and KIA 25250 respectively – than reported, well within the ± 2σ uncertainty range of the measurement (95.4 % confidence probability). Based on these considerations we are confident that the residue ages (and masses of that fraction) indicate a fairly light contamination and thus support the reliability of the ages obtained for the collagen.

The δ¹³C values of the collagen (Tab. 1) are in the normal range and do not indicate contamination. The insoluble fractions are somewhat more negative, which could indicate some minor influence of contaminating plant material consistent with Table 1. The small insoluble fraction of KIA 25247 shows a quite different δ¹³C and must be mostly contamination. Considering the calculation of the amount of modern contaminant needed to

Tab. 1 - Radiocarbon dating of faunal remains from Les Rois.

Lab No	Specimen	Stratum	Cc (%) ¹	Bone used (mg)	Cy (mg C) ²	Wt.fraction of bone (%)	insoluble organics (mg C)
KIA 25250	shaft fragment with impact notch	A1	5.9	1064	28.3	5.7	1.1
KIA 25249	shaft fragment with fresh bone break	A1	5.6	562	26.5	9.6	~0.4
KIA 25246 ⁴	reindeer mandible with cutmarks	B	2.3	820	5	1.3	0.5
Ly (OxA) 2171	burnt shaft fragment	B	N/A				
KIA 25247	shaft fragment utilised as retoucher	B	4.5	1050	16.8	3.4	0.2
KIA 25248	shaft fragment with cut marks	B	6.5	686	20.3	6.3	0.8

Lab No	¹⁴ C age gelatin (¹⁴ C yrs BP) $\delta^{13}\text{C}(\text{‰-VPDB})^3$	¹⁴ C age insol. organics (¹⁴ C yrs BP) $\delta^{13}\text{C}(\text{‰-VPDB})^3$	Collagen fraction (mg C)	pMC	insoluble residue (mg C)	pMC	carbon of 100 pMC in r (mg)
KIA 25250	27,790+200/-190 -18.8 ± 0.2	13,440+190/-180 -22.8 ± 0.5	28.3	3.15 ± 0.10	1.1	18.78 ± 0.43	0.212
KIA 25249	30,250±220 -19.1±0.1	N/A	26.5	2.32 ± 0.06	~0.4	N/A	N/A
KIA 25246 ⁴	27,270+240/-230 -19.0 ± 0.3	20,330+330/-320 -22.9 ± 0.2	5	3.35 ± 0.10	0.5	7.96 ± 0.32	0.024
Ly (OxA) 2171	28715±145 N/A	N/A					
KIA 25247	28,960±210 -20.4 ± 0.2	13,900+420/-400 -31.8 ± 0.3	16.8	2.72 ± 0.07	0.2	17.71 ± 0.90	0.031
KIA 25248	30,440+290/-280 -20.1 ± 0.2	19,200+200/-190 -22.8 ± 0.3	20.3	2.26 ± 0.08	0.8	9.16 ± 0.22	0.056

¹ Collagen content (Cc) was calculated from the concentration of nitrogen, determined by colorimetry as nitrate; fresh defatted dried bone tissue contains 20-27 %.

² Collagen yields (Cy) were all sufficient for reliable radiocarbon measurements. These ages should reflect the actual radiocarbon age of the human remains.

³ ± 1 s.d. N/A : non available.

⁴ Because glue had been used on the reindeer mandible, KIA 25246 was subjected to a soxhlet-type serial extraction with, in sequence, boiling tetrahydrofurane (THF), chloroform, petroleum-ether, acetone, and methanol and then rinsed with demineralized water.

produce the observed age discrepancies, the non-collagen material in the insoluble fraction must be composed primarily of old plant material.

Proof that contamination has been fully removed is, unfortunately, difficult if not impossible to provide and an earlier age for these units cannot be ruled out.

Human remains

Matching isolated teeth from the Les Rois collection with those listed by Vallois is made difficult by the fact that some catalogue numbers have rubbed off and the same numbers are present on more than one tooth. We were able to identify incisors, canines, premolars and upper molars with the help of Vallois description. Eight out of eleven isolated lower molars were identified in the same way. A degree of uncertainty remains about the others. Surprisingly, four previously unidentified teeth were found in the box containing the Les Rois remains. These specimens do not appear in Vallois original reports and thus were excluded from the analysis.

Vallois (1958) assigned the isolated lower RM2 R51 #6, found by Mouton and Joffroy in reworked layers, to mandible A. The alveolar socket of this tooth is reduced to a small area of the mesial wall, which makes this matching questionable. Four isolated lower teeth, two premolars and two molars, were found close to mandible B and attributed to the same individual by Vallois (1958). The two premolars (R51 #22 LP₃, R51 #23 LP₄) were found in the square adjacent to the one that has yielded mandible B. Morphological comparison indicates that they certainly derive from this mandible. Both P3 have a similar asymmetric outline shape and a transverse crest. In both P4, the metaconid has a mesial position when compared to the protoconid and both show a small distolingual cusp.

The two molars found in the same square as mandible B are R51 #14 RM₁ and R51 #15 LRM. R51 #14 RM₁ cannot be assigned to mandible B since the root of the lower RM1 does not fit the alveolar wall and the proximal wear facet does not correspond to that observed on the lower P4 in the mandible. The lower RM (R51

#15), described as a tooth germ by Vallois (1958) could not be located.

Vallois (1958) attribution of teeth to tooth classes was reviewed. R50 #24 is attributed here to a LI₂ instead than to a LI₁ and #35 to a LI² instead than to a RI₂.

Inspection of dental morphological characters reveals the following aspects:

- in the upper incisors, the shovel shape is absent or, as in R50 #5, does not reach the breakpoint; a right I¹ (w/#) is the only upper incisor that presents a lingual tubercle.
- R40 w/# LRC and the canine of mandible B show a distal accessory ridge not present in A3 #10 LLC neither in the canine of mandible A
- lower third premolars do not present multiple lingual cusps nor mesiolingual grooves. Crown asymmetry cannot be assessed confidently, but it is difficult to assign a symmetric crown shape to P3 of mandible B and R51 #22;
- the transverse crest is absent in lower P4; the mesial position of the metaconid relative to the protoconid in the P4 of mandible B and R51 #23 creates an asymmetrical crown shape in occlusal view;
- the Cusp 6 is absent in the isolated lower first molars but present in the right M1 of mandible A (the left M1 is broken distally); the mid-trigonid crest is absent but in one tooth (R50 #40) the anterior fovea is well developed;
- the Cusp 6 and the mid-trigonid crest are absent in lower second molars; the anterior fovea is only present in R51 #6, a right M2; the Y pattern is observed in three isolated lower M2 (R50 #3 and the two without number), however the attribution of these teeth as M2 is uncertain.
- subvertical grooves on wear facets were observed on the mesial face of the LP⁴ w/#, RM₂ R51 #6, and R50 #31. Their absence in the other molars, all unworn or with a low degree of wear, is not significant considering that these features only occur on teeth showing an advanced degree of wear.

Anterior teeth diameters (ATD) and crown base area (CBA) for Les Rois teeth and for Neandertal and AMH from the early Upper Palaeolithic (EUP) are presented in Appendix 1. The range of variation in ATD and CBA differ between Neandertals and EUP while showing large overlaps. The mesio-distal diameter in teeth from Les Rois falls in the range of both populations (Appendix 1). CBA of teeth from mandible A are systematically closer to EUP than to Neandertal averages. In contrast CBA of incisors and P4 from mandible B are closer to Neandertal than to EUP means. In isolated incisor and the lower P3 (#22) and P4 (#23), CBA is also closer to Neandertal than EUP means. In six molars, CBA is closer to EUP. In three others the opposite is observed.

The bucco-lingual diameter (BL), a variable considered particularly diagnostic by Bailey & Hublin (2006), reveals an interesting difference between the two mandibles. Values for mandible A fall in the range of both populations (Neandertals and AMH from the Upper Palaeolithic [UPAMH]) but are, with the exception of the right canine, closer to mean values observed in UPAMH (Appendix 1). BL values for the first incisors from mandible B fall outside the individual range of UPAMH and is, in all anterior teeth, closer to Neandertal means. In isolated anterior teeth and premolars, BL is closer to values recorded on UPAMH than in Neandertals; in molars, some are closer to Neandertals, other to UPAMH values (Appendix 1).

Root length cannot be measured on teeth from mandible A. In mandible B (Tab. 2), root length in incisors lays outside or close to the lower limit of root length variation in Neandertals, and inside the range observed in Upper Palaeolithic AMH. Root length of lower C from mandible B is close to Neandertal average value and at the limit of AMH variation. That of the lower P4 in mandible B falls in the variation in both reference populations but is closer to the average of AMH. Root length in isolated anterior teeth falls outside Neandertal and fit well in AMH variation. In isolated premolars attributed to mandible B (R51 #22, R51 # 23) root length is

closer to Neandertal average values; in premolars and molar R50 #40, values are also close to Neandertals' and not comprised in UPAMH variation (Tab. 2). R50 w/# LP⁴ show an intermediate value falling outside Neandertal and UPAMH variation.

Comparison between Neandertal and UPAMH teeth with low degree of wear shows that significant difference (Mann-Whitney *U*-test) exist in the number of perikymata in the last deciles (Tab. 1 Suppl. Mat.). Ramirez-Rozzi & Bermudez de Castro (2004) found significant differences between the two groups in the last four deciles of the I1, while in the subsample analyzed here, significant differences were found only in the last two deciles. Crown height reconstruction in worn teeth included in Ramirez Rozzi & Bermudez de Castro's work (2004) can be responsible for this discrepancy. However, it could also, and most likely, result from a type II error in the statistical analyses. Indeed, only three Neandertal teeth are used for comparison. It is worth noting that the greater the number of teeth compared, the greater the number of deciles showing significant differences in perikymata number between the two human groups.

The number of perikymata in canines and P₃ from mandible A fall within AMH, and outside Neandertal, variation (Tab. 3). In contrast, incisors, and P₃ from mandible B provide values closer to those in Neandertals. The number of perikymata, which is lower than the Neandertal averages, is incompatible with an attribution to UPAMH. The lower canine from this same mandible falls well within the Neandertal values, and below the UPAMH variation. All isolated incisors and canine from unit A2, coming from at least two individuals, have a number of perikymata well in the range of Neandertals or even lower and, only in two cases, at the limit of UPAMH variation. In decile by decile comparison, the same distinction is observed. Isolated teeth and teeth from mandible B correspond more closely to Neandertal distribution, whereas teeth from mandible A are closer to UPAMH distribution (Figs. 2 Suppl. Mat). When ellipses

Tab. 2 - Root length in teeth from Les Rois compared to those in Neandertals and anatomically modern humans from the Upper Palaeolithic.

Tooth	Rois		UPAMH*	Neandertal*
I ₁	Md B right	14.1	13.3 (11.7-14.1)	16.1 (15.7-16.6)
	Md B left	12.9	13.3 (11.7-14.1)	16.1 (15.7-16.6)
I ₂	Md B right	15.2	15.0 (13.6-16.3)	17.1 (15.3-17.9)
	Md B left	15.2	15.0 (13.6-16.3)	17.1 (15.3-17.9)
C	Md B right	18.5	16.2 (13.1-19.0)	19.4 (16.3-23.2)
P ₄	Md B right	16.1	15.0 (12.6-17.1)	18.7 (14.5-22.6)
I ¹	R50 #45	13.6	12.5 (10.4-15.2)	17.5 (15.7-19.7)
	w/#	11.7	12.5 (10.4-15.2)	17.5 (15.7-19.7)
P ⁴	R50 w/#	13.7	11.9 (10.5-13.3)	17.6 (16.2-19.0)
	R51 #29	13.3	11.9 (10.5-13.3)	17.6 (16.2-19.0)
I ₂	R50 #24	14.8	15.0 (13.6-16.3)	17.1 (15.3-17.9)
	R51 #17	14.6	15.0 (13.6-16.3)	17.1 (15.3-17.9)
C	R40 w/#	16.9	16.2 (13.1-19.0)	19.4 (16.3-23.2)
P ₃	R51 #22	16.4	13.7 (11.4-16.3)	16.6 (14.5-18.1)
P ₄	R51 #23	17.0	15.0 (12.6-17.1)	18.7 (14.5-22.6)
M ₁	R50 #40	15.6	13.2 (11.6-14.0)	14.3 (12.2-16.8)
M ₂	R50 #3	16.9	13.7 (11.3-16.8)	15.3 (14.3-16.5)
	R51 #6	16.9	13.7 (11.3-16.8)	15.3 (14.3-16.5)

Measurements in mm.

* averages and ranges from Bailey 2005. In bold, the average value closest to result for Les Rois tooth. The root length of the P⁴ R50 is closer to the average of UPAMH than to that of Neandertal, but it is not marked in bold because it falls outside the UPAMH variation.

of probability at P=0.95 are generated for each tooth type and decile, the number of perikymata in isolated teeth and in teeth from mandible B are included in the Neandertal ellipse, whereas values for teeth from mandible A accommodate in the UPAMH ellipse (Figs. 3 Suppl. Mat). The perikymata packing pattern in incisors from mandible B matches closely that observed in Neandertals, characterised by a homogenous

distribution of perikymata through deciles (Guatelli-Steinberg *et al.*, 2007). In canines and P3, the perikymata packing pattern does not reveal significant differences between mandible A and mandible B (Fig. 4).

Morphologically, mandible B shows a change in the orientation of the mandibular surface at the canine level evoking a flat or slightly arched anterior mandibular surface, a feature described

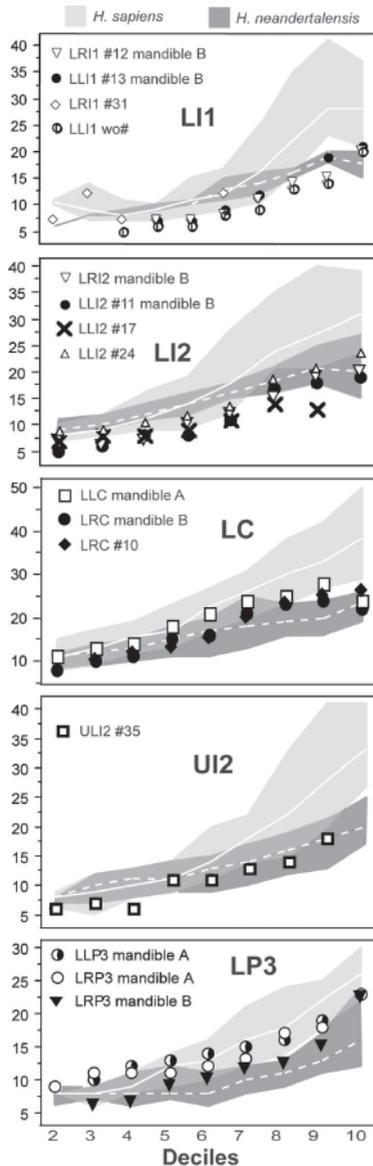


Fig. 4 - Perikymata packing pattern in anterior teeth from Les Rois compared to the range (grey areas) and the mean of the same character in (a sub-sample of) UPAMH (solid line) and Neandertals (dotted line) teeth showing comparable degree of tooth wear to those from Les Rois. Overlap exists between the two human groups, however values distribution are clearly different in Neandertals and UPAMH in cervical deciles (see Table 1 Suppl. Mat., Fig 2 & 3 Suppl. Mat.).

in Neandertal mandibles (Schwartz & Tattersall, 2000), while mandible A presents a typical AMH chin formed by a vertical keel along the symphysis becoming more prominent inferiorly to form the mental protuberance, and the associated mental fossae (Schwartz & Tattersall, 2000).

Cutmarks

Microscopic analysis confirms the presence of cutmarks on mandible B and their absence on mandible A. Cutmarks on mandible B consist of three parallel striations located on the lingual aspect, below the right lateral canine and P3 (Fig. 5 and Fig. 4 Suppl. Mat.). Two of them bear diagnostic features of flint cutting-edge generated marks in form of v-shaped cross sections, “barbs” and, in one case, a typical splitting (Fisher 1995).

The faunal sample available for comparison is composed of 48 fragmentary reindeer mandibles. All show fresh bone fractures along the mandibular canal, suggesting deliberate smashing for marrow extraction, a practice repeatedly observed ethnographically (Binford, 1978). Twenty-five mandibles (52%) bear percussion marks located on the vestibular aspect midway between cheek teeth and the mandible base (Fig. 4 Suppl. Mat.). Eleven mandibles (23%) display cutmarks on their lingual aspect located below the premolars and oriented obliquely with respect to the mandible base. A single specimen has cutmarks on the vestibular aspect below the M_1 and M_2 .

Discussion

Human remains associated with Aurignacian contexts are rare. With the exception of Mladeč, which includes cranial, dental, and postcranial elements (Wild *et al.*, 2005) dating to ca. 31.000 BP, the remaining human fossils securely associated with the Aurignacian are, for the most part, undiagnostic, poorly dated, or both (Churchill & Smith, 2000). Les Rois is one of the few sites where the association of the human remains with the Aurignacian is unambiguous. This situation has led some authors to suggest that there are no definite bases to conclude that anatomically

Tab. 3- Number of perikymata (N pk) in anterior teeth and lower P3 from Les Rois.

	Unit	Deciles analysed	N pk	Homo sapiens		Homo neandertalensis		
				range ²	mean ³	range ²	mean ³	
Mandible A								
Md A RC	B	2 - 10	178	157 - 262	205	115 - 177	148	
Md A LC	B	2 - 10	178	157 - 262	205	115 - 177	148	
Md A RP ₃	B	1 - 10	136	114 - 170	142	81 - 127	99	
Md A LP ₃	B	3 - 10	122	99 - 150	124	66 - 109	82	
Mandible B								
Md B LI ₁ #13	A2	4 - 10	88	94 - 180	126	90 - 109	100	
Md B RI ₁ #12	A2	4 - 10	82	94 - 180	126	90 - 109	100	
Md B RI ₂	A2	2 - 10	102	118 - 211	152	111 - 154	129	
Md B LI ₂ #11	A2	3 - 10	92	111 - 199	142	104 - 144	120	
Md B RC	A2	2 - 10	150	157 - 262	205	115 - 177	148	
Md B RP ₃	A2	3 - 10	95	99 - 150	124	66 - 109	82	
Isolated teeth¹								
w/# LI ₁	A2	4 - 10	98	94 - 180	126	90 - 109	100	
#31 RI ₁	A2	1 - 9	90	97 - 179	126	97 - 112	105	
R51 #17 LI ₂	A2	2 - 9	82	92 - 168	119	75 - 131	101	
R50 #24 LI ₂	A2	3 - 10	114	107 - 196	139	82 - 148	111	
#35 LI ²	A2	2 - 9	86	88 - 164	120	75 - 119	101	
A3 #10 LLC	A2	3 - 10	144	149 - 247	194	105 - 165	137	

¹ The accession numbers of teeth correspond to those given in Vallois (1958). w/#: unlabelled

² The number of perikymata gives the results for the deciles analysed indicated in the second column and does not correspond to the total number of perikymata of the tooth.

³ The two values represent the sum of the minimum and maximum number of perikymata observed for the same deciles as those analysed on Les Rois teeth.

⁴ Values correspond to the sum of the means for each decile. In bold, the value closest to those observed on Les Rois teeth.

modern humans were the makers, or the only makers, of the Aurignacian (Conrad *et al.*, 2004). Recently, Henry-Gambier *et al.*, (2004) conducted a morphological and morphometric analysis of teeth from Brassempouy, a site dated to 30-34 ky BP, and concluded that the taxonomic status of these fossils is uncertain. This

conclusion was criticised by Bailey & Hublin (2005) who proposed, based on a combination of morphological and morphometric criteria, that the teeth from Brassempouy are clearly affiliated with AMH.

Taxonomic diagnosis of isolated teeth requires the combined use of different criteria,

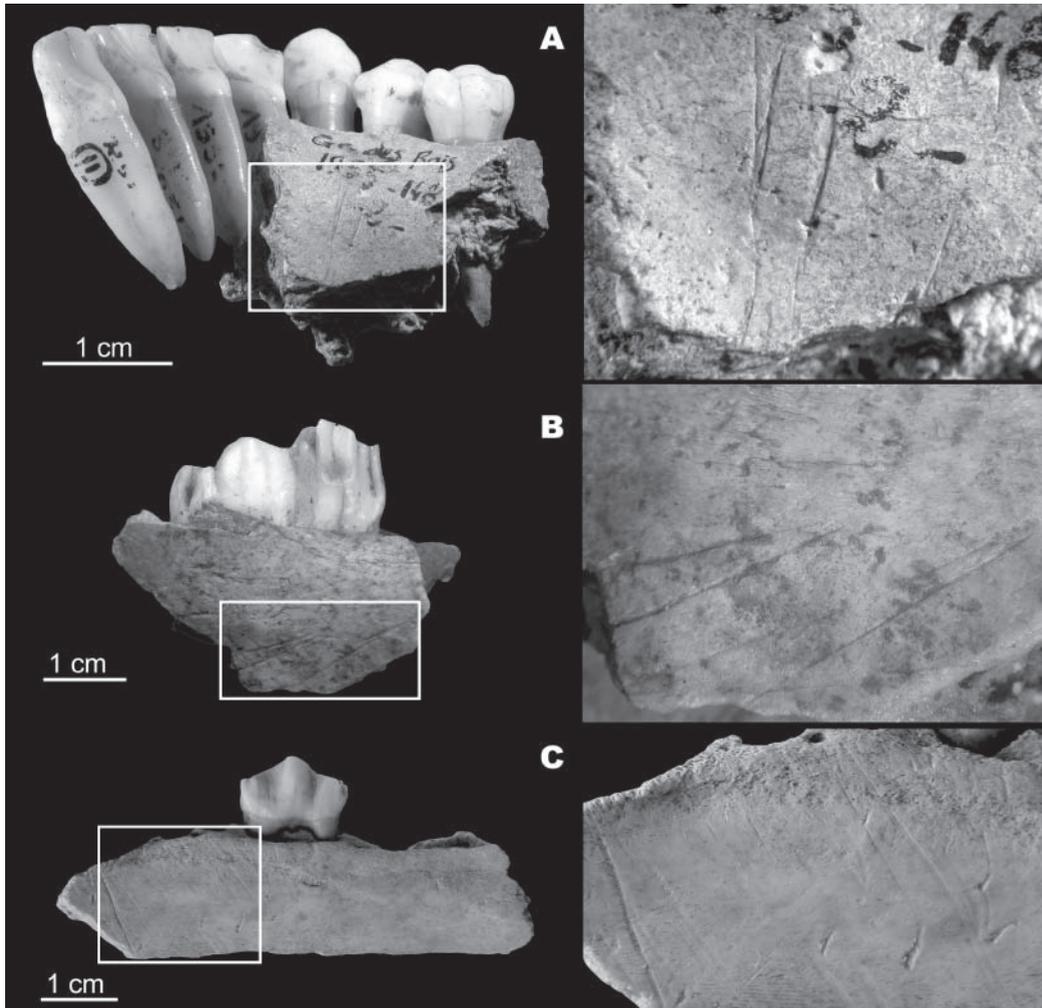


Fig. 5 - A. Lingual aspect of Les Rois mandible B from unit A2 with cutmarks produced by multiple strokes of a sharp stone tool. **B-C.** Cutmarks on the lingual aspect of reindeer mandible fragments from the same unit. Rectangles on the left identify areas magnified on the right.

the pertinence of which ultimately resides in the robustness of reference data. Here we have followed this path and recorded morphological, morphometric and tooth growth information on isolated teeth and on teeth in mandibles from Les Rois. Morphologically, teeth from Les Rois are closer to AMH than to Neandertal teeth. However, non-metrical traits common in Neandertals are recorded: the distal accessory ridge on mandible B canine (67% in Neandertals,

27% in AMH) and the anterior fovea in R51 #6 RM_2 (88% in Neandertals, 53% in AMH) which presents subvertical grooves. Two of the most diagnostic non-metric traits of Neandertal teeth are the asymmetric shape of the mandibular fourth premolar and the presence of the mid-trigonid crest in lower first molar (Bailey, 2002; Bailey & Hublin, 2005). The asymmetric shape of the mandibular fourth premolar can be accompanied with a well-developed, mesially-

placed lingual cusp (metaconid) and an uninterrupted crest joining the metaconid to the buccal (protoconid) cusp. Approximately 35% of Neandertals possess at least two P4 traits, a combination observed in only 2.4% of modern humans (Bailey, 2002, p. 152). A well developed mid-trigonid crest in lower first molar shows high frequency in Neandertals (98%) and low frequency in AMH (0%) (Bailey, 2002). The cusps of the P₄ from Les Rois mandible B and #23 are clearly separated by the mesio-distal groove, but the mesial position of the metaconid relative to the protoconid creates a non-symmetrical shape in occlusal view, which recalls the Neandertal morphology. In R50 #40, a lower M₁, the anterior fovea is limited distally by a bridge between the two mesial cusps but the protoconid ridge does not contact the metaconid ridge, a condition which seems to be below the breakpoint assigned by Bailey (2002) to attribute this tooth to Neandertals.

Teeth from mandible B as well as isolated incisors, canine and P₃ from Les Rois show a particular perikymata packing pattern. Such a pattern fits better with Neandertal variation range than it does for that of UPAMH range (Ramirez Rozzi & Bermudez de Castro, 2004). Although it is now clear that overlap in the number of perikymata in Neandertal and modern human teeth exists (Ramírez Rozzi & Bermúdez de Castro, 2004; Ramírez Rozzi, 2005; Guatelli-Steinberg *et al.*, 2005) perikymata number can be used as a good probabilistic criterion to distinguish between distinct human populations. The recorded differences for perikymata number between Neandertals and UPAMH may reflect population affiliation.

Both Ramirez Rozzi & Bermudez de Castro (2004), and Guatelli-Steinberg *et al.* (2007) agree that perikymata distributions are different between Neandertals and AMH. Neandertals are characterised by a homogenous distribution of perikymata i.e., the number of perikymata does not change abruptly from one decile to another. This is the pattern observed for the incisors from mandible B and some isolated anterior teeth

(w/# LI₁, #31 RI₁, R51 #17 LI₂, R50 #24 LI₂, A3 #10 LC, #35 LI₂).

In summary, three teeth from mandible A (C and right and left P3) and four isolated teeth (R50 #5 LI₁, R50 LP₃, #54 RM^{1/2} and R51 #16 RM³) are attributed to a taxon (UPAMH) by converging independent observations resulting from the application of a variety of methods. Results indicate a clear affinity of mandible A with AMH from the Upper Palaeolithic. Differently, in mandible B, BL diameter in anterior teeth and in P4 as well as perikymata numbers and CBA in incisor suggest an attribution of this mandible to Neandertals. Root length would indicate an affinity of mandible B with UPAMH, however it is worth indicating that the reference data on root length that we have used (Bailey, 2005) is based on a reduced sample and include Les Rois teeth in the UPAMH sample. If teeth from Les Rois were excluded, the upper limit of the variation in AMH would have been lower and Les Rois teeth would lie outside the individual range of AMH.

Perikymata numbers and CBA place isolated anterior teeth with Neandertals. Non-metric traits, BL and, where possible, root length suggest affinity with UPAMH. The same is true for isolated premolars, excepted R51 #23 – interpreted as coming from mandible B – in which BL is close to UPAMH, the other traits to Neandertals. In general isolated molars fit well UPAMH variation. However, R50 #40 RM₁ has a long “neandertal” root and an undiagnostic BL. The same is valid for R51 #6 RM₂, which exhibits an anterior fovea and subvertical grooves.

Providing a univocal interpretation for the presence of cutmarks on mandible B is not an easy task. Secondary burial practices and cannibalism are the two alternative explanations traditionally proposed to account for modifications on prehistoric human bones. When insightfully argued, the latter is based on the demonstration that faunal and hominin remains were subjected to similar treatment and, ideally, that contemporary mortuary practices resulted in modifications on bone significantly different from those interpreted as the product of alimentary consumption. This requires data on depositional context,

a fairly large sample of animal and human remains, including post-cranial, and information on local mortuary practices (Villa *et al.*, 1986; White, 1992). A consistent number of reindeer mandibles from Mouton and Joffroy's excavation show cut-marks located and oriented similarly to those recorded on mandible B. Considering their location and orientation, these cut-marks may have resulted from slicing through the geniohyoid muscle to remove the tongue. Mandible B and associated teeth were apparently found in a fireplace located close to a pavement of burnt pebbles, but this is all we know about their depositional context. Similarly located and oriented cutmarks are observed on the juvenile Neandertal mandible from the Mousterian site of Moulaguercy (France) and interpreted, like those on the other human remains found at this site, as evidence for cannibalism (Defleur *et al.*, 1999). In our case, however, contextual pieces of information needed to favour the cannibalistic interpretation are missing. Three other reasons make Les Rois evidence ambiguous. Firstly, cranial bones are the less appropriate remains to assess the consumption hypothesis because skinning of the skull and removal of underlying muscles is common in practices of trophy keeping and secondary burials (Pickering, 1989; Villa, 1992). Secondly, no convincing Aurignacian primary burials are known (Churchill & Smith, 2000) that may suggest the existence of mortuary practices distinct and contemporary with cannibalistic practices. Thirdly, a number of cranial and mandible fragments from Upper Palaeolithic sites (Saint-Germain-la-Rivière, Isturitz, Bedeilhac, Placard, etc.) reveal modifications in the form of perforations, engravings, and scraping, indicating that they were given special treatment (Le Mort 1981; Buisson & Gambier 1991). Four Aurignacian sites (Vanhaeren & d'Errico, 2006), including Les Rois, have yielded perforated human teeth, which confirms the interest in using human bone, and teeth in particular, by Aurignacians, for symbolic purposes. Fractures of the maxilla compatible with it being broken with intent to extract teeth and processing marks on the extracted teeth to be used as personal

ornaments are reported from the Aurignacian site of Brassempuy (Haenry-Gambier *et al.*, 2004). The only known other Aurignacian youth mandible with cut-marks, found at Fontechevalde (Gambier, 2000), occurs in isolation. This fits the pattern seen at Les Rois and Brassempuy. In summary, although the possibility that the young individual bearing Neandertal features was consumed cannot be discarded, available data on the treatment and symbolic use of human remains during the Aurignacian do not appear to support this interpretation.

Conclusion

Reappraisal of the Les Rois sequence indicates that Aurignacians must be considered solely responsible for the accumulation of the archaeological and human remains dated to 28–30 kyr BP. Morphological and morphometric analyses, and number and packing of perikymata on Les Rois teeth indicate UPAMH affinities for the juvenile mandible A from the lowest unit B. Taxonomic assignation of isolated teeth remains uncertain although most of them conform well to UPAMH variability. As regards the juvenile mandible B from overlying unit A2, the taxonomic assignation remains also uncertain. Indeed, most of morphological features of teeth suggest an attribution to EUR, however dental size and perikymata packing pattern indicate a Neandertal affinity for the mandible B.

Three possibilities may account for this unexpected evidence. The first one is that the Aurignacian was exclusively produced by AMH and that the child mandible from unit A2 represents evidence for consumption and/or symbolic use of a Neandertal child by Aurignacian AMH. The second possibility is that Aurignacian technologies were produced at Les Rois by human groups bearing both AMH and Neandertal features. Human remains from Les Rois would be in this case the first evidence of a biological contact between the two human groups. The third possibility is that all human remains from Les Rois represent an AMH population with conserved

plesiomorphic characters suggesting a larger variation in modern humans from the Upper Palaeolithic.

The first possibility implies that Neandertals communities bearing Mousterian or “transitional” cultures, such as the Châtelperronian in France, persisted in the region for several millennia after the arrival of Aurignacian AMHs. This scenario has been proposed to explain the age of ca. 29–28 ka obtained for two Neandertal remains from level G1 of Vindija, Croatia (Smith *et al.*, 1999), the dates of ca. 24–30 ka for the Mousterian level IV at Gorham’s Cave, Gibraltar (Finlayson *et al.*, 2006), and the cultural innovations associated with Châtelperronian Neandertals (Mellars, 1999, 2005; Gravina *et al.*, 2005). However, these claims are now dismissed or considered uncertain for a number of reasons. The Vindija Neandertals have been re-dated to 32–33 ka and possibly earlier (Higham *et al.*, 2005). A reappraisal of the Gorham’s Cave data suggests that the most parsimonious explanation for layer IV and associated ^{14}C determinations is that they represent a Middle Palaeolithic occupation up to, but not beyond, ca. 32–30 ka (Zilhao & Pettitt, 2006). A revision of purported interstratifications of Aurignacian/Châtelperronian layers, such as those at Grotte des Fées, and available ^{14}C ages indicates that the Châtelperronian is significantly earlier than the Aurignacian and may be seen as a largely independent Neandertal cultural development (d’Errico *et al.*, 1998; Zilhao & d’Errico, 1999; Zilhao *et al.*, 2006).

As far as the archaeological record of south-western France is concerned, no Châtelperronian or Late Mousterian sites have produced reliable ^{14}C ages younger than 35 ka (d’Errico & Sanchez Goñi, 2003). Even though the ^{14}C dates obtained from Les Rois may represent an underestimation of the real age of the site, a gap of at least 2,000 to 3,000 years remains between the latest recorded presence of the Mousterian or the Châtelperronian in the region and the chronological attribution of the Les Rois layer that yielded the child’s mandible bearing Neandertal features, thereby contradicting our second proposed suggestion.

Considering the age (ca. 30–28 ka), the cultural attribution of the archaeological layers (ancient Aurignacian with no split base points) and the apparent admixture of Neandertal and UPAMH characters in some human remains, the second possibility implies that a certain degree of cultural and biological exchange did occur between the two populations in order for individuals of an Aurignacian community to inherit Neandertal traits. A Neandertal genetic and cultural contribution to Europe earliest modern human societies has been proposed repeatedly (see Zilhao 2006 for a synthesis), and human remains such as those from Lagar Velho (Duarte *et al.*, 1999; Trinkaus & Zilhao, 2002), Mladeč (Wolpoff, 1999; Wild *et al.*, 2005), and Oase (Trinkaus *et al.*, 2003; Soficaru *et al.*, 2006) have been interpreted as bearing inherited Neandertal features. The mtDNA sequences obtained thus far from a dozen Neandertal specimens lie outside the range of variation of modern Europeans (Krings *et al.*, 1997; Lalueza-Fox *et al.*, 2005; Ovchinnikov *et al.*, 2000; Schmitz *et al.*, 2002; Serre *et al.*, 2004), suggesting that Neandertals did not contribute significantly to the present mtDNA gene pool. Also, recent work on nuclear DNA suggests that Neandertal and AMH lineages split around 500 ka (Noonan *et al.*, 2006; Green *et al.*, 2006). These results, however, do not exclude the possibility of gene flow from modern humans into Neandertals or a genetic Neandertal input to the gene pool of early modern colonisers, later eliminated by bottleneck and replacement events. No consensus exists, however, on what potential rate of admixture between the two populations is compatible with the available paleogenetic data. Templeton (2002, 2005) and Serre (Serre *et al.*, 2004) accepts the possibility of up to 10% admixture, but the majority of authors exclude an interbreeding rate higher than 1% (Krings *et al.*, 2000; Ovchinnikov *et al.*, 2000; Caramelli *et al.*, 2003; Currat & Excoffier, 2004). In the current state of affairs, the possibility that makers of the Aurignacian bore Neandertal features is compatible with, but not supported by, the available genetic evidence.

The interpretation that Neandertal features in AMHUP result for a some degree of biological contact between these two human groups have been challenged by a number of authors who suggest that features interpreted as evidence of admixture, are, in reality, plesiomorphic features, or that the anatomical traits have been studied without paying adequate attention to their developmental context (Tattersal & Schwartz, 1999; see Trinkaus, 2006). It is possible that morphological features in human remains from Les Rois with values outside of the AMHUP range of variation result by the retention of plesiomorphic characters (third possibility). Works based on external cranial and dental features suggest that modern humans appear in Africa between 150 000 and 200 000 years ago by morphological transition from a more primitive form, i.e. *H. heidelbergensis*/*H. ergaster* (Hublin 2001; McDougall *et al.*, 2005). These *Homo* species present large tooth size, which is thus the plesiomorphic condition of *Homo sapiens*. This latter species has since experienced a trend towards tooth size reduction, although this is not a universal trend as some dimensions in modern human teeth from the Middle Stone Age are reduced, whereas others are not and approach values reported for Neandertals (Grine *et al.*, 2002). The pattern observed in teeth from Les Rois in which typical characteristics of later AMHUP are accompanied by more robust features exemplifies this scenario. Further, big tooth dimensions have been reported for the earliest modern human remains in Europe (Trinkaus *et al.*, 2003a,b). It is possible that the first modern humans in Europe still preserved plesiomorphic features and that a general reduction in tooth size appeared later in time, leading to a clearer separation from the more robust Neandertal teeth.

In contrast with morphological features, aspects of dental development could not be explained by a plesiomorphic retention. Smith *et al.*, (2007) have suggested that the modern humans pattern on dental growth appeared 200 000 years ago and that this pattern differs from that of Neandertals. It is worth to note that the perikymata packing pattern in Neandertals differs from that of AMHUP

and also from that of *H. heidelbergensis* (Ramirez Rozzi & Bermudez de Castro, 2004). Despite the known geographical, ecological, and growth patterns diversity observed in recent modern human populations, tooth structure and dental growth seem to have remained constant during the last 60 000 years of the Palaeolithic (Smith *et al.*, 2006). Therefore, it is difficult to interpret aspects of the dental developmental (e.g. perikymta packing pattern) in teeth from Les Rois as a retention of the plesiomorphic condition, suggesting that they have to be considered most likely as characteristics of a particular population.

Given the paucity of human remains from the early Upper Palaeolithic and the relative antiquity of the excavations, which were not conducted to modern standards, it is difficult to reach a definite conclusion. One of the main goals of the new excavations that we recently initiated at Les Rois is to recover diagnostic human remains in well-defined cultural contexts in order to better characterise the skeletal morphology of the inhabitants of south-western France during the accumulation of the two Aurignacian layers.

Acknowledgements

Special thanks are given to C. Verna for sharing her database on Upper Paleolithic individuals and for her suggestions on previous version of this paper. We are grateful to D. Grimaud-Hervé, M. Patou-Mathis, and C. Schwab for providing access to the Les Rois material curated at the Institut de Paléontologie Humaine, Paris and the Musée des Antiquités Nationales, Saint-Germain-en-Laye, M.-J. Nadeau for discussion and preparation of the dated samples, B. Pinilla-Pérez, A. Pérez-Pérez, S. Lalueze, D. Fouchier, R. Lacruz, and M. Tersis for their assistance. We also thank E. Trinkaus for fruitful comments on a previous manuscript, and W. Banks for careful editing of the final manuscript. This work was funded by the Origin of Man, Language and Languages program of the European Science Foundation, the French Ministry of Research, and a post-doctoral grant of the Centre National de la Recherche Scientifique.

References

- Bailey S.E. 2000. Dental morphological affinities among late Pleistocene and recent humans. *Dent. Anthropol.*, 14:1–8
- Bailey S.E. 2002. A closer look at Neandertal postcanine dental morphology, I, the mandibular dentition. *New Anatomist*, 269:148-156.
- Bailey S.E. 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominids. *J. Hum. Evol.*, 47:183-198.
- Bailey S.E. 2005. Diagnostic dental differences between Neandertals and Upper Paleolithic modern humans: Getting to the root of the matter. In E. Zadzińska (ed): *Current Trends in Dental Morphology Research*, pp. 201-210. University of Lodz, Lodz, Poland.
- Bailey S.E. & Lynch J.M. 2005. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. *Am. J. Phys. Anthropol.*, 126:268-277.
- Bailey S.E. & Hublin J.J. 2005. Who made the early Aurignacian? A reconsideration of the Brassempouy dental remains. *Bull. Mém. Soc. Anthropol. Paris*, 17:115-121.
- Bailey S.E. & Hublin J.J. 2006. Dental remains from Grotte du Renne at Arcy-sur-Cure (Yonne). *J. Hum. Evol.*, 50:485-508.
- Bar-Yosef O. 2002. The Upper Paleolithic revolution. *Annu. Rev. Anthropol.*, 31:363-393.
- Bar-Yosef O. & Pilbeam, D. (eds) 2000. *The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean*. Peabody Museum, Harvard Univ., Cambridge, Massachusetts.
- Bermúdez de Castro J.M. 1993. The Atapuerca dental remains. New evidence (1987-1991 excavations) and interpretations. *J. Hum. Evol.*, 24:339-371.
- Beynon A.D. 1987. Replication technique for studying microstructure in fossil enamel. *Scanning Microsc.*, 1:663-669.
- Beynon A.D. & Dean M.C. 1988. Distinct dental development patterns in early fossil hominids. *Nature*, 335:509-514.
- Billy G. 1975. Étude Anthropologique des Restes Humains de l'Abri Pataud. In H.L. Movius (ed): *Excavation of the Abri Pataud, les Eyzies (Dordogne)*, pp. 201-261. Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, Massachusetts.
- Binford L.R. 1978. *Nunamiut ethnoarchaeology*. Academic Press, New York.
- Bon F. 2002. *L'Aurignacien entre Mer et Océan. Réflexion Sur l'Unité des Phases Anciennes de l'Aurignacien dans le Sud de la France*. Mémoire 29, Société Préhistorique Française, Paris.
- Bordes J.-G. & Lenoble A. 2002. La lamelle Caminade: un nouvel outil lithique aurignacien? (The Caminade bladelet : a new Aurignacian lithic tool?). *Bulletin de la Société Préhistorique Française*, 99:735-749.
- Bouchud in Mouton P. & Joffroy R. 1958. *Le gisement aurignacien des Rois à Mouthiers (Charente)*. Suppl. à Gallia Préhistoire IX, CNRS.
- Bruhn F., Duhr A., Grootes P.M., Mintrop A. & Nadeau M.-J. 2001. Chemical removal of conservation substances by "Soxhlet"-type extraction. *Radiocarbon*, 43:229-237.
- Bruner E., Manzi G. & Arsuaga J. L. 2003. Encephalization and allometric trajectories in the genus Homo: evidence from the Neandertal and modern lineages. *Proc. Natl. Acad. Sci. U.S.A.*, 100:15335-15340.
- Buisson D. & Gambier D. 1991. Façonnage et gravures sur des os humains d'Isturitz (Pyrenées-Atlantiques). *Bulletin de la Société Préhistorique Française*, 88:172-177.
- Caramelli D., Lalueza-Fox C., Vernesi C., Lari M., Casoli A., Mallegni F., Chiarelli B., Dupanloup I., Bertranpetit J., Barbujani G., Bertorelle G. et al., 2003. Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans. *Proc. Natl. Acad. Sci. U.S.A.*, 100:6593–6597.
- Churchill S. E. & Smith F. H. 2001. Makers of the Early Aurignacian of Europe. *Yearb. Phys. Anthropol.*, 43:61–115.
- Coiffard J. 1937. L'Aurignacien en Charente. *Bulletin et Mémoire de la Société de Archéologie et Historique de Charente*, 113-128.
- Conard N. J., Grootes P. M. & Smith F. H. 2004. Unexpectedly recent dates for human remains

- from Vogelherd. *Nature*, 430:198-201.
- Connet N. 2002. *Le Châtelperronien: Réflexions sur l'unité et l'identité techno-économique de l'industrie*. Ph.D. dissertation. University of Lille I, France.
- Cunha E., Ramirez Rozzi F., Bermúdez de Castro J.M., Martínón-Torres M., Wasterlain S.N. & Sarmiento S. 2004. A new look into enamel hypoplasias: evidence from the Sima de los Huesos Middle Pleistocene site. *Am. J. Phys. Anthropol.*, 125:220-231.
- Curat M. & Excoffier L., 2004. Modern humans did not admix with Neandertals during their range expansion into Europe. *PLoS Biol.*, 2:2264-2274.
- d'Errico F. 2003. The invisible frontier. A multiple species model for the origin of behavioural modernity. *Evol. Anthropol.*, 12:188-202.
- d'Errico F. & Sanchez Goni M. F. 2003. Neandertal extinction and the millennial scale climatic variability of OIS 3. *Quat. Sc. Rev.*, 22:769-788.
- d'Errico F., Zilhao J., Baffier, D., Julien M. & Pelegrin, J. 1998. Neandertal acculturation in western Europe? a critical review of the evidence and its interpretation. *Curr. Anthropol.*, 39:1-44.
- Dean M.C. 1987. The dental developmental status of six East African juvenile fossil hominids. *J. Hum. Evol.*, 16:197-213.
- Dean M.C., Leakey M.G., Reid D., Schrenk F., Schwartz G., Stringer C. & Walker A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature*, 414:628-631.
- Defleur A., White T., Valensi P., Slimak L. & Crégut-Bonnoure E. 1999. Neandertal cannibalism at Moula-Guercy, Ardèche, France. *Science*, 286:128-131.
- Duarte C., Maurício J., Pettitt P., Souto P., Trinkaus E., van der Plicht H. & Zilhão J. 1999. The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proc. Natl. Acad. Sci. U.S.A.*, 96:7604-7609.
- Dujardin V. & Tymula S. 2004. Relecture chronologique de sites anciennement fouillés : datation des sites paléolithiques et épipaléolithiques de Poitou-Charentes. 129e Congrès des Travaux historiques et scientifiques, Besançon. *Bulletin de la Société Préhistorique Française*, 102:771-88.
- Dujardin V. 2000. Une excursion en Charente préhistorique en 1935... D'après les cahiers de Jean Morel. *Bulletin et Mémoire de la Société de Archéologie et Historique de Charente*, 1:35-48.
- Finlayson C., Pacheco F.G., Rodríguez-Vidal J., Fa D.A., Gutierrez López J.M., Pérez A.S., Finlayson G., Allue E., Baena Preysler J., Cáceres I., Carrión J.S., Fernández Jalvo Y., Gleed-Owen C.P., Jimenez Espejo F.J., López P., López Sáez J.A., Riquelme Cantal J.A., Sánchez Marco A., Giles Guzman F., Brown K., Fuentes N., Valarino C.A., Villalpando A., Stringer C.B., Martínez Ruiz F. & Sakamoto T., 2006. Late survival of Neandertals at the southernmost extreme of Europe. *Nature*, 443:850-853.
- Fisher J.W. 1995. Bone surface modifications in zooarchaeology. *J. Arch. Met. & Th.*, 2:7-67.
- Fitzgerald C. M. 1998. Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. *J. Hum. Evol.*, 35:371-386.
- Fraye D.W. 1977. Metric dental change in the European Upper Paleolithic and Mesolithic. *Am. J. Phys. Anthropol.*, 46:109-120.
- Fraye D.W. 1978. *Evolution of the Dentition in Upper Paleolithic and Mesolithic Europe*. Publications in Anthropology, 10. University of Kansas, Lawrence, Kansas.
- Gambier D. 1989. Fossil Hominids from the Early Upper Paleolithic (Aurignacian) of France. In P. Mellars, C. B. Stringer (eds): *The Human Revolution: behavioural and biological perspectives on the Origins of Modern Humans*, pp. 298-320. Princeton University Press.
- Gambier D. 2000. Aurignacian children and mortuary practice in Western Europe. *Anthropologie*, 38:5-21.
- Gómez-Robles A., Martínón-Torres M., Bermúdez de Castro J. M., Margvelashvili A., Bastir M., Arsuaga J. L., Pérez-Pérez A., Estebananz

- F. & Martinez L. 2007. A geometric morphometric analysis of hominin upper first molar shape. *J. Hum. Evol.*, 53:272-285.
- Gómez-Robles A., Martín-Torres M., Bermúdez de Castro J. M., Prado L., Sarmiento S. & Arsuaga J. L. 2008. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *Homo*. *J. Hum. Evol.*, 55:627-638.
- Gravina B., Mellars P.A. & Bronk Ramsey C., 2005. Radiocarbon dating of interstratified Neandertal and early modern human occupations at the Chatelperronian type-site. *Nature*, 438:51-56.
- Green R.E., Krause J., Ptak S.E., Briggs A.W., Ronan M.T., Simons J.F., Du L., Egholm M., Rothberg J.M., Paunovic & M., Paäbo S. 2006. Analysis of one million base pairs of Neandertal DNA. *Nature*, 444:330-336.
- Grine F.E. & Henshilwood C.S. 2002 Additional human remains from Blombos Cave, South Africa: (1999-2000 excavations). *J. Hum. Evol.*, 42:293-302.
- Grootes P.M., Nadeau M.-J. & Rieck A. 2004. ¹⁴C-AMS at the Leibniz-Labor: Radiometric dating and isotope research. *Nucl. Instr. Meth.*, B223-224:55-61.
- Guatelli-Steinberg D. & Reid D.J. 2008. What molars contribute to an emerging understanding of lateral enamel formation in Neandertals vs. modern humans? *J. Hum. Evol.*, 54:236-250.
- Guatelli-Steinberg D., Reid D.J., Bishop T.A. & Larsen C.S. 2005. Anterior tooth growth periods in Neandertals were comparable to those of modern humans. *Proc. Natl. Acad. Sc. U.S.A.*, 102:14197-14202.
- Guatelli-Steinberg D., Reid D.J. & Bishop T.A. 2007. Did the lateral enamel of Neandertal anterior teeth grow differently from that of modern humans? *J. Hum. Evol.*, 52:72-84.
- Henri-Martin L. 1925. La station aurignacienne de la Quina, Charente. *Bull. Mém. Soc. Anthropol. Paris*, 6:10-17
- Henri-Martin L. 1931. La station aurignacienne de la Quina. *Bulletin et Mémoire de la Société de Archéologie et Historique de Charente pour l'année 1930*, t. XX, 77 p., 8 Fig., 24 pl. h.t.
- Henry-Gambier D., Maureille B. & White R. 2004. Vestiges humains des niveaux de l'Aurignacien ancien du site de Brassempouy (Landes). *Bull. Mém. Soc. Anthropol. Paris n.s.*, 6:49-87.
- Higham T., Ramsey C.B., Karavanic I., Smith F.H. & Trinkaus E. 2006. Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neandertals. *Proc. Natl. Acad. Sc. U.S.A.*, 103:553-557.
- Hillson S. & Trinkaus E. 2002. Comparative dental crown metrics. In J. Zilhão, E. Trinkaus (eds): *Portrait of the Artist as a Child. The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archeological Context*, pp. 355-364. *Trabalhos de Arqueologia*, 22. Instituto Português de Arqueologia, Lisbonne.
- Hooper S.M., Meredith N., Jagger D.C. 2004. The development of a new index for measurement of incisal/occlusal tooth wear. *J. Oral Rehabilitation*, 31:206-212.
- Hublin J.J. 2001. Northwestern African Middle Pleistocene hominids and their bearing on the emergence of *Homo sapiens*. In L. Barham, K. Robson-Brown (eds): *Human Roots*, pp. 99-121. Western Academic and Specialist Press, Bristol.
- Hublin J.J., Spoor F., Braun M., Zonneveld F. & Condemi S. 1996. A late Neandertal associated with Upper Palaeolithic artefacts. *Nature*, 381:224-226.
- Jelínek J., Pelisek J. & Valoch K. 1959. Der fossile Mensch Brno II. *Anthropos*, 9, (n.s. 1): 7-30.
- Jernvall J. & Thesleff I. 2000. Reiterative signaling and patterning in mammalian tooth morphogenesis. *Mech. Dev.*, 92:19-29.
- Kaidonis J.A., Townsend G.C. & Richards L.C. 1992. Brief communication: Interproximal tooth wear: a new observation. *Am. J. Phys. Anthropol.*, 88:105-107.
- Krings M., Capelli C., Tschentscher F., Geisert H, Meyer S. et al., 2000. A view of Neandertal genetic diversity. *Nat. Genet.*, 26:144-146.
- Krings M., Stone A., Schmitz R.W., Krainitzki

- H., Stoneking M. & Paabo, S. 1997. Neanderthal DNA sequences and the origin of modern humans. *Cell*, 90:19-30.
- Lalueza-Fox C., Sampietro M.L., Caramelli D., Puder Y., Lari M., Calafell F., Martinez-Maza C., Bastir M., Fortera J., de la Rasilla M., Bertranpetit & J., Rosas A. 2005. Neanderthal evolutionary genetics; mitochondrial DNA data from the Iberian peninsula. *Mol. Biol. Evol.*, 22:1077-1081.
- Le Mort F. 1981. *Degradation artificielles sur des os humains du Paléolithique*. Unpublished PhD. Université Pierre and Marie Curie.
- Leroy-Prost C. 1985. L'industrie osseuse aurignacienne; essai regional de classification: Poitou, Charente, Périgord. *Gallia Préhistoire*, 18:65-156.
- Lévêque E. & Vandermeersch B., 1981. Le Néandertalien de Saint-Césaire. *La Recherche*, 12:242-244.
- Liolios D. 1999. *Variabilité et caractéristiques du travail des matières osseuses au début de l'Aurignacien: approche technologique et économique*. PhD Dissertation, University Paris X, Nanterre.
- Macchiarelli R., Bondioli L., Debénath A., Mazurier A., Tournepiche J.-F., Birch W. & Dean C. 2006. How Neanderthal molar teeth grew. *Nature*, 444:748-751.
- Martinón-Torres M., Bastir M., Bermúdez de Castro J. M., Gómez A., Sarmiento S., Muela A. & Arsuaga J. L. 2006. Hominin lower second premolar morphology: evolutionary inferences through geometric morphometric analysis. *J. Hum. Evol.*, 50:523-533.
- Matiegka J. 1934. *L'Homme fossile de Předmostí en Moravie (Tchécoslovaquie). I. Les crânes*. Académie Tchèque des Sciences et des Arts, Prague.
- McDougall I., Brown F. & Fleagle J.G. 2005. Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature*, 433:733-736.
- Mellars P.A. 1999. The Neanderthal problem continued. *Curr. Anthropol.*, 40:341-364.
- Mellars P.A. 2005. The impossible coincidence: a single-species model for the origins of modern human behavior in Europe. *Evol. Anthropol.*, 14:12-27.
- Mellars P.A. 2004. Neandertals and the modern human colonisation of Europe. *Nature*, 432:461-465.
- Mouton P. & Joffroy R. 1958. *Le gisement aurignacien des Rois à Mouthiers (Charente)*. Suppl. à Gallia Préhistoire IX, CNRS.
- Noonan J.P., Coop G., Kudaravalli S., Smith D., Krause J., Alessi J., Chen F., Platt D., Pääbo S., Pritchard J.K. & Rubin E.M. 2006. Sequencing and Analysis of Neanderthal Genomic DNA. *Science*, 314:1113-1118.
- Ovchinnikov I.V., Götherström A, Romanova G.P., Kharitonov V. M., Liden K. *et al.*, 2000. Molecular analysis of Neanderthal DNA from the northern Caucasus. *Nature*, 404:490-493.
- Pelegrin J. 1995. *Technologie lithique: le Châtelperronien de Roc-de Combe (Lot) et de la Côte (Dordogne)*. Centre National de la Recherche Scientifique, Paris.
- Pérez-Pérez A., Espurz V., Bermudez de Castro J.M., De Lumley M.A. & Turbón D. 2003. Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. *J. Hum. Evol.*, 44:497-513.
- Perpère M. 1972. Remarques sur l'Aurignacien en Poitou-Charente. *L'Anthropologie*, 76:387-425.
- Pickering M.P. 1989. Food for thought: an alternative to "Cannibalism in the Neolithic. *Australian Archaeology*, 28:35-39.
- Ponce de León M. S., Golovanova L., Doronichev V., Romanova G., Akazawa T., Kondo O., Ishida H. & Zollikofer C. P. E. 2008. Neanderthal brain size at birth provides insights into the evolution of human life history. *Proc. Natl. Acad. Sci. U.S.A.*, 105:13764-13768.
- Ponce de León M. S. & Zollikofer C. P. E. 2001. Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature*, 412:534-538.
- Ramírez Rozzi F.V. 1998. Can enamel microstructure be used to establish the presence of different species of Plio-Pleistocene hominids from Omo, Ethiopia? *J. Hum. Evol.*, 35:543-576.

- Ramírez Rozzi F.V. 2005. Age au décès de l'enfant néandertalien de l'Hortus. *Bull. Mém. Soc. Anthropol. Paris*, 17:47-55.
- Ramírez Rozzi F.V. & Bermudez de Castro J. M. 2004. Surprisingly rapid growth in Neanderthals. *Nature*, 428:936-939.
- Ramírez Rozzi F.V. & Sardi, M. 2007. Crown formation time in Neandertal anterior teeth revisited. *J. Hum. Evol.*, 53:108-113.
- Reid D.J. & Dean M.C. 2000. Brief communication: The timing of linear hypoplasia on human anterior teeth. *Am. J. Phys. Anthropol.*, 113:135-139.
- Reid D.J., Guatelli-Steinberg D & Walton P. 2008. Variation in modern human premolar enamel formation times: Implications for Neandertals. *J. Hum. Evol.*, 54:225-235.
- Schmitz R.W., Serre D., Bonani G., Feine S., Hillgruber F., Krainitzki H., Paabo S. & Smith F.H. 2002. The Neandertal type site revisited: Interdisciplinary investigations of skeletal remains from the Neander Valley, Germany. *Proc. Natl. Acad. Sci. U.S.A.*, 99:13342-13347.
- Schwartz G.T. & Dean M.C. 2001. The ontogeny of canine dimorphism in extant hominoids. *Am. J. Phys. Anthropol.*, 115:269-283.
- Schwartz J.H. & Tattersall I. 2000. The human chin revisited: what is it and who has it? *J. Hum. Evol.*, 38:367-409.
- Serre D., Langaney A., Chech M., Teschler-Nicola M., Paunović M., Mennecier P., Hofreiter M., Possnert G. & Pääbo S. 2004. No evidence of Neandertal mtDNA contribution to early modern humans. *PLoS Biol.*, 2:313-317.
- Sládek V., Trinkaus E., Hillson S.W. & Holliday T.W. 2000. *The People of the pavlovian. Skeletal Catalogue and Osteometrics of the Gravettian Fossil Hominids from Dolní Vestonice and Pavlov. The Dolní Vestonice Studies*, 5. J. Svoboda, Institute of Archaeology, Academy of Sciences of the Czech Republic, Brno.
- Smith B.H. 1991. Dental development and the evolution of life history in Hominidae. *Am. J. Phys. Anthropol.*, 86:157-174.
- Smith F.H., Trinkaus E., Pettitt P.B., Karavanic I. & Paunovic M. 1999. Direct radiocarbon dates for Vindija G₁ and Velika Pečina Late Pleistocene hominid remains. *Proc. Natl. Acad. Sci. U.S.A.*, 96:12281-12286.
- Smith P. 1989. Dental evidence for phylogenetic relationships of middle Palaeolithic hominids. In M. Otte (ed): *L'Homme de Neandertal, vol. 7 L'extinction*, pp. 111-120. Etudes et Recherches Archéologiques de l'Université de Liège.
- Smith T. 2008. Incremental dental development: methods and applications in hominid evolutionary studies. *J. Hum. Evol.*, 54:205-224.
- Smith T. Olejniczak A.J., Tafforeau P., Reid D.J., Grine F.E. & Hublin J.-J. 2006. Molar crown thickness, volume, and development in South African Middle Stone Age humans. *South African Journal of Science*, 102:1-5.
- Smith T.M., Tafforeau P.T., Reid D.J., Grün R., Eggen S., Boutakiout M. & Hublin J.-J. 2007. Earliest evidence of modern human life history in North African early Homo sapiens. *Proc. Natl. Acad. Sci. U.S.A.*, 104:6128-6133.
- Smith T.M., Toussaint M., Reid D.J., Olejniczak J. & Hublin J.-J. 2007. Rapid dental development in a Middle Paleolithic Belgian Neandertal. *Proc. Natl. Acad. Sci. U.S.A.*, 104:20220-20225.
- Soficaru A., Doboş A. & Trinkaus E., 2006. Early modern humans from the Petreşra Muierii, Baia de Fier, Romania. *Proc. Natl. Acad. Sci. U.S.A.*, 103:17196-17201.
- Sonneville-Bordes D. 1966. L'évolution du Paléolithique supérieur en Europe Occidentale et sa signification. *Bulletin de la Société Préhistorique Française*, 63:3-34.
- Stringer C. 2002. Modern human origins: progress and prospects. *Phil. Trans. R. Soc. Lond. B*, 357:563-579.
- Svoboda J., van der Plicht J. & Kuzelka V. 2002. Upper Palaeolithic and Mesolithic human fossil from Moravia and Bohemia (Czech Republic): some new ¹⁴C dates. *Antiquity*, 76:957-962.
- Tattersall I. & Schwartz J.H. 1999. Hominids and hybrids: The place of Neandertals in human evolution. *Proc. Natl. Acad. Sci. U.S.A.*, 96:7117-7119.
- Templeton A.R. 2002. Out of Africa again and again. *Nature*, 416:45-50.
- Templeton A.R. 2005. Haplotype trees and

- modern human origins. *Yearb. Phys. Anthropol.*, 48:33-59.
- Trinkaus E. 2005. Early modern humans. *Annu. Rev. Anthropol.*, 34:207-230.
- Trinkaus E. 2006. Modern human versus Neandertal evolutionary distinctiveness. *Curr. Anthropol.*, 47:597-620.
- Trinkaus E., Moldovan O., Milota S., Bilgar A., Sarcina L., Athreya S., Bailey S.E., Rodrigo R., Gherase M., Higham T., Bronk Ramsey C. & van der Plicht J. 2003a. An early modern human from the Peștera cu Oase, Romania. *Proc. Natl. Acad. Sci. U.S.A.*, 100:11231-11236.
- Trinkaus, E., Milota Ș., Rodrigo R., Mircea G. & Moldovan, O. 2003b. Early modern human cranial remains from the Peștera cu Oase, Romania. *J. Hum. Evol.*, 45:245-253.
- Turner II C.G., Nichol C.R. & Scott G.R., 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University Dental Anthropology System. In M. Kelley & C. S. Larsen (eds): *Advances in Dental Anthropology*, pp. 13-31. Wiley Liss, New York.
- Vallois H. V. 1958. Les restes humains d'âge aurignacien de la grotte des Rois, Charente. *Bull. Mém. Soc. Anthropol. Paris*, 9, série X:138-159.
- Vanhaeren M. & d'Errico F. 2006. Aurignacian ethno-linguistic geography of Europe revealed by personal ornaments. *J. Archaeol. Sci.*, 33:1105-1128.
- Verneau R. 1906. *Les grottes de Grimaldi, Baoussé-Roussé*. Anthropologie, II. Monaco.
- Villa G. & Giacobini G. 1995. Subvertical grooves of interproximal facets in Neandertal posterior teeth. *Am. J. Phys. Anthropol.*, 96:51-62.
- Villa P. 1992. Cannibalism in prehistoric Europe. *Evol. Anthropol.*, 1:93-104.
- Villa P. C. Bouville, Courtin J., Helmer D., Mahieu E., Shipman P., Belluomini G. & Branca M. 1986. Cannibalism in the Neolithic. *Science*, 233:431-437.
- Voelker A.H.L., Grootes P.M., Nadeau M.-J. & Sarnthein M. 2000. Radiocarbon levels in the Iceland Sea from 25-53 kyr and their link to the earth's magnetic field intensity. *Radiocarbon*, 42:437-452.
- White T. 1992. *Prehistoric cannibalism at Mancos 5MTUMR-2346*. Princeton Univ. Press, Princeton.
- Wild E.M., Teschler-Nicola M., Kutschera W., Steier P., Trinkaus E. & Wanek W. 2005. Direct dating of Early Upper Palaeolithic human remains from Mladeč. *Nature*, 435:332-335.
- Wolpoff M.H. 1999. *Paleoanthropology*. McGraw-Hill, New York.
- Wolpoff M.H. 1979. The Krapina Dental Remains. *Am. J. Phys. Anthropol.*, 50:67-113.
- Zilhão J. 2006. Neandertals and moderns mixed, and it matters. *Evol. Anthropol.*, 15:183-195.
- Zilhão J. & d'Errico, F. (eds) 2003. *The chronology of the Aurignacian and of the transitional technocomplexes. Dating, stratigraphies, cultural implications*. Portuguese Institute of Archaeology (IPA), Trabalhos de Arqueologia, Lisbon.
- Zilhão J. & d'Errico F. 1999. The chronology and taphonomy of the earliest Aurignacian and its implications for the understanding of Neandertal extinction. *J. World Prehist.*, 13:1-68.
- Zilhão J., d'Errico F., Bordes J.-G., Lenoble A., Texier J.-P. & Rigaud J.-P. 2006. Analysis of Aurignacian interstratification at the Châtelperronian-type site and implications for the behavioral modernity of Neandertals. *Proc. Natl. Acad. Sci. U.S.A.*, 103:12643-12648.
- Zilhão J. & Pettitt P. 2006. On the new dates for Gorham's Cave and the late survival of Iberian Neandertals. *Before Farming* 3, article 3:1-9.
- Zilhão J. & Trinkaus, E. (eds) 2002. *Portrait of the Artist as a Child. The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archeological Context*. Trabalhos de Arqueologia Vol. 22. Lisbon.

Appendix 1- Tooth dimensions in teeth from Les Rois.

Les Rois	diameters CBA			EUP ¹		H. neandertalensis ²		UPAMH ³ BL diam x (range)	Neand ³ BL diam x (range)
				diameters range	CBA x range	diameters range	CBA x range		
Mandible A									
Md A RC	MD	6.9	59.3	6.1-8.0	63.6	6.8-8.8	71.6	8.2	8.5
	BL	8.6		7.8-10		47.6-80.0			
Md A LC	MD	6.7	54.3	6.8-8.3	66.5	6.8-8.8	71.6	8.2	8.5
	BL	8.1		8.0-9.8		57.3-78.4			
Md A RP ₃	MD	7.2	60.5	6.0-8.0	61.2	7.0-9.0	70.9	8.4*	9.0 °
	BL	8.4		7.7-9.0		46.2-68.0			
Md A LP ₃	MD	7.1	60.4	6.0-8.0	60.1	7.0-9.0	70.9	8.5*	9.0 °
	BL	8.5		7.7-9.5		46.8-66.5			
Md A Rdm2	MD	-						10.8	10.8
	BL	9.5							
Md A RM1	MD	11.3	118.6	10.3-13	131.0	10.0-13.6	127.4	10.8	10.8
	BL	10.5		10.0-12.5		103.0-150.2			
Md A LM1	MD	-		10.3-13	131.0	10.0-13.6	127.4	8.2	8.5
	BL	10.3		10.0-12.5		103.0-150.2			
Mandible B									
Md B LI ₁ (R50 #13)	MD	6.4	44.8	3.7-6.5	30.9	5.1-6.3	43.1	6.2*	7.4 °
	BL	7.0		5.4-6.9		21.5-42.2			
Md B RI ₁ (R51 #12)	MD	6.3	44.1	3.7-6.1	30.6	5.1-6.3	43.1	6.2*	7.4 °
	BL	7.0		5.4-6.9		20.9-42.1			
Md B RI2	MD	-		5.0-7.3	42.4	6.1-7.5	51.7	6.7	7.5
	BL	7.2		6.0-7.5		33.6-52.6			
Md B LI ₃ (R51 #11)	MD	7.1	51.8	4.1-7.2	42.4	6.1-7.5	51.7	6.7	7.5
	BL	7.3		6.6-7.6		27.1-51.1			
Md B RC	MD	7.3	65.0	6.1-8.0	63.6	6.8-8.8	71.6	8.2	8.5
	BL	8.9		7.8-10		47.6-80.0			
Md B RP ₃	MD	7.4	61.4	6.0-8.0	61.2	7.0-9.0	70.9	8.4*	9.0 °
	BL	8.3		7.7-9.0		46.2-68.0			
Md B RP ₄	MD	7.6	66.9	6.6-8.5	65.0	6.9-9.4	69.5	8.3	8.9
	BL	8.8		7.8-9.5		54.4-78.8			
Isolated teeth⁴									
R50 #45 LI ¹	MD	10.2	75.5	7.7-10.0	69.9	8.2-12.0	81.6	7.6*	8.6 °
	BL	7.4		7.0- 8.3		60.0-81.0			
w/# RI ¹	MD	10.6		7.9-10.0	69.9	8.2-12.0	81.6		
	BL	-		7.1-8.2		60.0-81.0			

Appendix 1- Tooth dimensions in teeth from Les Rois (continued).

Les Rois	diameters	CBA	EUP ¹		H. neandertalensis ²		UPAMH ³ BL diam x (range)	Neand ³ BL diam x (range)	
			diameters range	CBA x range	diameters range	CBA x range			
Isolated teeth¹ (Continued)									
w/# RI ¹	MD BL	10.6 7.7	81.6	7.9-10.0 7.1-8.2	69.9 60.0-81.0	8.2-12.0 7.4-9.7	81.6 63.3-105.7	7.7*	8.6 ° (7.4-9.7)
R50 #5 LI ¹ (?)	MD BL	9.5 7.3	69.4	7.7-10.0 7.0- 8.3	69.9 60.0-81.0	8.2-12.0 7.4-9.7	81.6 63.3-105.7	7.7*	8.6 ° (7.4-9.7)
w/# LI ₁	MD BL	6.1 6.9	42.1	3.7-6.5 5.4-6.9	30.9 21.5-42.2	5.1-6.3 6.8-8.2	43.1 36.2-51.3	6.2*	7.4 ° (6.8-8.2)
#31 RI ₁	MD BL	6.3 6.5	41.0	3.7-6.1 5.4-6.9	30.6 20.9-42.1	5.1-6.3 6.8-8.2	43.1 36.2-51.3	6.2*	7.4 ° (6.8-8.2)
#35 LI ²	MD BL	6.9 -		5.8-8.8 6.3-8.1	51.5 41.7-66.0	6.3-9.3 7.7-9.9	68.0 51.0-81.4		
R51 #17 LI ₂	MD BL	6.9 7.0	48.3	4.1-7.2 6.6-7.6	42.4 27.1-51.1	6.1-7.5 6.7-9.0	51.7 40.8-65.6	6.7 (6.0-7.5)	7.5 (6.0-8.0)
R50 #24 LI ₂	MD BL	7.1 6.9	49.0	4.1-7.2 6.6-7.6	42.4 27.1-51.1	6.1-7.5 6.7-9.0	51.7 40.8-65.6	6.7 (6.0-7.5)	7.5 (6.0-8.0)
A3 #10 LLC	MD BL	6.9 -		5.8-8.3 8.0-9.8	66.5 57.3-78.4	6.8-8.8 7.5-10.3	71.6 54.4-90.1		
R40 w/# LRC	MD BL	- 9.0		6.1-8.0 7.8-10	63.6 47.6-80.0	6.8-8.8 7.5-10.3	71.6 54.4-90.1	8.2 (7.7-9.5)	8.5 (5.6-9.8)
R51 #22 LP ₃	MD BL	8.2 7.9	64.8	6.0-8.0 7.7-9.5	60.1 46.8-66.5	7.0-9.0 7.3-10.3	70.9 51.8-91.7	8.5*	9.0 ° (7.3-10.3)
R50 LP ₃	MD BL	7.3 8.4	61.3	6.0-8.0 7.7-9.5	60.1 46.8-66.5	7.0-9.0 7.3-10.3	70.9 51.8-91.7	8.5*	9.0 ° (7.3-10.3)
R51 #29 RP ⁴	MD BL	6.4 9.1	58.2	5.9-7.9 8.8-11.2	69.4 54.7-88.5	6.4-8.8 9.0-11.7	73.6 58.5-102.9	9.6 (8.8-10.5)	10.3 (8.2-11.3)
R50 LP ⁴	MD BL	6.3 9.3	58.6	5.9-7.9 8.8-11.2	69.4 54.7-88.5	6.4-8.8 9.0-11.7	73.6 58.5-102.9	9.6 (8.8-10.5)	10.3 (8.2-11.3)
R51 #23 LP ₄	MD BL	7.9 8.7	68.7	6.6-8.5 7.8-9.5	65.0 51.2-75.5	6.9-9.4 7.1-10.5	69.5 50.4-86.6	8.3 (7.1-9.2)	8.9 (7.6-10.5)
#54 RM ^{1/2}	MD BL	10.6 11.8	125.1	9.2-12.0 11.0-14.0	131.2 102.1- 165.2	10.0-13.4 11.1-14.2	138.8 113.2- 185.3	12.1*-	12.2 ° (11.1-14.2)
R53 P RM ^{1/2}	MD BL	10.9 -		9.2-12.0 11.0-14.0	131.2 102.1- 165.2	10.0-13.4 11.1-14.2	138.8 113.2- 185.3		
R50 #21A RM ³	MD BL	8.7 12.3	107.0	8.3-11.1 9.2-13.2	113.2 78.2-145.3	8.3-11.4 10.0-14.0	121.7 84.7-148.5	11.6*	12.2 ° (10-14)
R51 #16 RM ³	MD BL	8.9 11.2	99.7	8.3-11.1 9.2-13.2	113.2 78.2-145.3	8.3-11.4 10.0-14.0	121.7 84.7-148.5	11.6*	12.2 ° (10-14)
R50 #40 RM ₁	MD BL	12.4 10.9	135.2	10.3-13 10.0-12.5	131.0 103.0- 150.2	10.0-13.6 9.6-12.9	127.4 102.7- 174.8	10.8 (9.8-11.9)	10.8 (9.7-11.8)
R50 #3 LM _{2/3}	MD BL	11.3 10.1	114.1	9.2-12.8 9.8-12.0	125.1 92.0-150.0	10.5-14.0 9.6-12.4	130.8 102.7- 172.4	10.6 (9.8-12.3)	10.8 (9.9-12.1)

Appendix 1- Tooth dimensions in teeth from Les Rois (continued).

Les Rois	diameters	CBA	EUP ¹		<i>H. neandertalensis</i> ²		UPAMH ³	Neand ³
			diameters range	CBA x range	diameters range	CBA x range	BL diam x (range)	BL diam x (range)
Isolated teeth¹ (Continued)								
R50 #31	MD	-	9.2-12.8	125.1	10.5-14.0	130.8	10.6	10.8
RM ₂	BL	10.0	9.8-12.0	92.0-150.0	9.6-12.4	102.7-172.4	(9.8-12.3)	(9.9-12.1)
w/# RM _{1/2}	MD	11.0	118.8	10.3-13	131.0	10.0-13.6	127.4	10.8
	BL	10.8		10.0-12.5	103.0-150.2	9.6-12.9	102.7-174.8	(9.8-11.9) (9.7-11.8)
w/# LM _{1/2}	MD	11.2	123.2	10.3-13	131.0	10.0-13.6	127.4	10.8
	BL	11.0		10.0-12.5	103.0-150.2	9.6-12.9	102.7-174.8	(9.8-11.9) (9.7-11.8)
w/# LM	MD	11.8	125.1					
	BL	10.6						
R51 #14	MD	11.9	120.2	10.3-13	131.0	10.0-13.6	127.4	10.8
RM ₁	BL	10.1		10.0-12.5	103.0-150.2	9.6-12.9	102.7-174.8	(9.8-11.9) (9.7-11.8)
R51 #6	MD	11.4	124.3	9.2-12.8	125.1	10.5-14.0	130.8	10.6
RM ₂	BL	10.9		9.8-12.0	92.0-150.0	9.6-12.4	102.7-172.4	(9.8-12.3) (9.9-12.1)
R50 Ldm ₂	MD	11.6	109.0					
	BL	9.4						

¹ Tooth dimensions range and CBA in early Upper Palaeolithic humans (EUP) from Abri Pataud, Brno, Dolní Vestonice, Grotte des enfants, Mladeč, Pavlov, Předmostí and Brassempouy-grotte des hyènes (Billy 1975, Frayer 1977, 1978, Hillson & Trinkaus 2002, Henry-Gambier et al., 2004, Jelinek et al., 1959, Matiegka 1934, Sládek et al., 2000, Verneau 1906) (Data provided by C. Verna). Values for EUP were obtained separately for left and right antimers.

² Tooth dimensions and CBA in Neandertals (Bermudez de Castro 1993). CBA: crown base area (MD x BL). In bold, the CBA closest to Les Rois value.

³ Bucco-lingual diameter (BL diam) from Bailey & Hublin (2006), excepted ° from Bermúdez de Castro (1993) and * average from our results EUP. In bold, the average value closest to the measure in teeth from Les Rois.

