Isolated teeth from La Ferrassie: reassessment of the old collections, new remains and their implications

G. Becam[a], C. Verna[a], A. Gómez-Robles[b], A. Gómez-Olivencia[c,d,e,a], L. Albessard[a], J. Arnaud[f], M.A. Frelat[g], S. Madelaine[h,i], C. Schwab[j], C. Souday[a], A. Turq[h,i], A. Balzeau[a,k]

[a] Musée de l'Homme, UMR 7194 CNRS, Université de Perpignan "Via Domitia", EPCC-CERP de Tautavel, Département Homme et environnement, Muséum national d'Histoire naturelle, Paris, France.

[b] Department of Anthropology, University College London, 14 Taviton Street, London WC1H 0BW, UK. [c] Dept. Estratigrafía y Paleontología, Facultad de Ciencia y Tecnología, Universidad del País Vasco-Euskal Herriko Unibertsitatea (UPV/EHU). Barrio Sarriena s/n. 48940 Leioa, Spain.

[d] IKERBASQUE. Basque Foundation for Science. 48013 Bilbao, Spain.

[e] Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos. Avda. Monforte de Lemos, 5. Madrid 28029, Spain.

[f] Dipartimento di Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Università degli Studi di Ferrara, C.so Ercole I d'Este, 32, 44121 Ferrara, Italy.

[g] UMR 7268 ADES, Aix-Marseille Université/EFS/CNRS, Equipe 1 – Paléoanthropologie et Bioarchéologie, France.

[h] Musée national de Préhistoire, 1 rue du Musée, 24620 Les Eyzies de Tayac-Sireuil, France.

[i] UMR 5199 PACEA, Université de Bordeaux, Bâtiment B8, Allée Geoffroy Saint Hilaire, CS 50023 33615 Pessac cedex, France.

[j] Musée d'Archéologie Nationale, Saint-Germain-en-Laye, France.

[k] Department of African Zoology, Royal Museum for Central Africa, B-3080 Tervuren, Belgium.

Corresponding authors: gael.becam@cerptautavel.com (G. B.), abalzeau@mnhn.fr (A. B.)

Abstract

Objectives We provide the description and comparative analysis of six new teeth from the site of La Ferrassie. Our goal is to discuss their taxonomic attribution, and to provide an updated inventory of Neandertal and modern human remains from La Ferrassie in their associated archaeological context.

Materials and Methods We use external and internal anatomy, classic morphometrics, and geometric morphometrics. The teeth from La Ferrassie are compared to several samples of contemporary Neandertals and upper Paleolithic modern humans as well as to recent modern humans.

Results Three specimens are classified as Neandertals, two as modern humans and one remains unclassified.

Discussion Based on the previously known fossil samples and the new teeth reported here there are currently a minimum of four adult and five immature Neandertal individuals coming from the "Grand Abri" as well as a minimum of two modern human adult individuals: one from "Grand Abri" and one from "Grotte". It is noteworthy that the spatial distribution of the recovered Neandertal remains is not restricted to the area where the LF1 to LF 8 were found but now covers the full extension of the excavated area. Moreover, while both Neandertal and modern human occupations have yielded isolated human remains, the partial-to-complete skeletons only belong to Neandertals. These considerations open new perspectives for the understanding of the occupation and use of the La Ferrassie site.

Keywords: Neandertal, Anatomically modern humans/*Homo sapiens*, Pleistocene/Palaeolithic, patrimonial collections, microtomography, enamel-dentine junction

Introduction

The site of La Ferrassie preserves a long cultural sequence that yielded rich Middle and Upper Paleolithic lithic and faunal assemblages resulting from the use of this site by both Neandertals and modern humans (Delporte, 1984; Laville & Tuffreau, 1984). The site is a group of localities including a "Grotte" (cave), a "Petit Abri" (small rockshelter) and the well-known "Grand Abri" (large rockshelter). Since its discovery at the end of the 19th, three main excavation seasons were undertaken under the direction of L. Capitan and D. Peyrony, H. Delporte and recently by A. Turq (Turq et al., 2012). The remains found at the Grand Abri comprise five immature partial (Heim, 1982a) and two adult Neandertal skeletons (Heim, 1976, 1982b), the latter likely dated to~43–45 ka (Guérin et al., 2015). A first review of the faunal remains from the old excavations and curated at Musée National de Préhistoire (les Eyzies-de-Tayac, France – noted MNP hereafter) identified three isolated permanent teeth attributed to an Upper Paleolithic context. A preliminary study briefly described these teeth (Gambier, Hoüet & Tillier, 1990; Gambier, 1992) and concluded that one of them (an upper central incisor) shows affinity with modern humans, whereas no taxonomic assignment could be reached for a second and a third lower molars. A recent re-assessment (2013-2014) of the faunal material from La Ferrassie, curated at the Musée d'Archéologie Nationale (Saint-Germain-en-Laye, France, MAN hereafter) and Muséum national d'Histoire naturelle (Paris, MNHN hereafter), resulted in the identification of additional human remains ascribed to the LF8 infant (Gómez-Olivencia, Crevecoeur & Balzeau, 2015) and LF1 adult and to the description of the ear ossicles of the LF1 skull (Gómez-Olivencia et al., 2018). This re-assessment also led to the identification of three new isolated human teeth: an upper canine, an upper fourth premolar and a lower third premolar.

We provide the description and comparative analysis of these three newly identified human teeth as well as a detailed re-assessment and comparative analysis of the three teeth described by D. Henry-Gambier (Gambier, Hoüet & Tillier, 1990; Gambier, 1992). Our goal is to discuss their taxonomic attribution by using external and internal anatomy, classic morphometrics, and geometric morphometrics. We also provide an updated inventory of Neandertal and modern human remains from La Ferrassie in their associated archaeological context and the minimum number of individuals they represent.

Material

The sample from LF includes five permanent teeth from the "Grand Abri" and one permanent tooth from the "Grotte" (Figure 1). The teeth from "Grand Abri" are numbered serially following their identification date: an upper right fourth premolar (URP4; LF7), an upper right central incisor (URI1; LF9), a lower right third molar (LRM3; LF10), an upper left canine (ULC; LF11) and a lower right third premolar (LRP3; LF12) (Figure 2).The lower right second molar (LRM2) from the cave is named La Ferrassie "Grotte" 1 (LFG1). LF9, LFG1 and LF10 were already reported by Gambier et al. (1990) and Gambier (1992) while LF7, LF11 and LF12 are the newly identified teeth.

The morphological features and measurements of the LF teeth are primarily compared to samples of Neandertals and Late Pleistocene modern humans. The Neandertal sample encompasses specimens found in Europe and southwest Asia attributed to the marine isotope stages (MIS) 5d to 3. Early modern humans include MIS 5-4 remains from southwest Asia and Africa (AAEMH) as well as MIS 3-2 Upper Paleolithic modern humans from Europe (UPMH). Various samples of recent modern humans (RMH) are used in our comparative analyses. Detailed descriptions of these comparative samples are provided in the supplementary information (Supporting Information B- Detailed material, Tables B.1 to B.6).

Methods

The teeth from La Ferrassie were scanned at the AST-RX platform (MNHN, Paris) using the microfocus tube of the micro-CT scanner "v|tome|x L 240" (GE Sensing & Inspection Technologies Phoenix X|ray). LF7 was scanned with resolution of 12.20 µm, the other teeth were scanned together with a resolution of 16.39 µm. The segmentation of the dental tissues was realized with the "watershed" tool of Avizo 7® software. These microCT scans are available for scientific research without restrictions (requests should be made to A.Balzeau).

In the description of the teeth, the dental attrition was scored following the stages defined by Molnar (1971). Dental crown metrics include the maximum mesiodistal (MD) and buccolingual (BL) crown diameters (M81 and M81(1); Braüer, 1988), measured with calipers, as well as the crown base areas in mm² (CBA = MD × BL). LF data were compared to our

reference samples using adjusted z-scores (Azs) following Maureille *et al*. (2001). Data for right and left sides, when available, were averaged prior to the assessment of the distributions. Bivariate plots of crown diameters were created with Statistica 7.0 software (see details Supporting Information B - Detailed methods).

The description of non-metric traits at the outer enamel surface (OES) and enamel dentine junction (EDJ) is based on the Arizona State University Dental Anthropology System (ASUDAS; Turner, Nichol & Scott, 1991; Scott & Turner, 1997), supplemented by Bailey (2002, 2006) and Martinón-Torres *et al*. (2012). Trigonid crests at the OES and EDJ of lower molars are classified following Martínez de Pinillos et al. (2014).

The occlusal morphology of premolars and molars was evaluated using a landmark- and semilandmark-based geometric morphometric approach (Supporting Information 2, Table B6; Gómez-Robles et al., 2008; Gómez-Robles, Olejniczack, Martinón-Torres, Prado-Simón & Bermúdez de Castro, 2011a; Gómez-Robles, Bermúdez de Castro, Martinón-Torres, Prado-Simón & Arsuaga 2015). Detailed definitions of landmarks and semilandmarks can be found in Gómez-Robles et al. (2008, 2011a, 2011b, 2015) and in SI. Variation corresponding to location, size, and orientation, which does not represent shape variation, was removed through Generalized Procrustes Analysis (GPA, Rohlf & Slice, 1990). A relative warps analysis (Bookstein, 1991) was carried out for each tooth. Discriminant analysis was used to evaluate the probability of each tooth to be assigned to either Neandertals or modern humans (Gómez-Robles et al., 2007, 2008, 2011a, 2012; Skinner, Gunz, Wood & Hublin, 2008a; Bermúdez de Castro et al., 2011). Percentages of correct assignment for both species were tested using a leave-one-out cross validation (see details Supporting Information B - Detailed methods and Fig. B.1).

Finally, the size of the root of the URI1 was characterized by its surface area and volume measurements following Le Cabec et al. (2013).

Results

Crown dimensions of LF upper teeth as well as non-metric traits at the outer enamel surface for all the LF specimens are provided in Tables 1 and 2, respectively. Root dimensions for UI1 are presented in Table 3. Non-metric traits at the enamel dentine junction (EDJ) are provided in Table 4. Finally, non-metric traits at the outer enamel surface of LF lower teeth

are listed in Tables 5. More detailed information and descriptions are available in Supporting Information B for all the teeth.

LF9 – Upper right central incisor

LF9 has a partly damaged crown (a large portion of enamel is missing at the *cervix*) and an almost intact root (Figure 1). The root is formed, the crown is moderately worn (stage 4) with small mesial and distal interproximal facets, showing that the tooth had been functional for some years.

Its MD diameter falls within the range of variation of all our comparative samples, close to their means, while BL diameter is not measurable (Table 1). The flat labial surface of LF9 (ASUDAS grade 1) corresponds to the dominant pattern of modern humans and contrasts with the marked labial convexity of Neandertals (Figure 3 and Table 2). The lack of marked shoveling on LF9 (ASUDAS grade 1) aligns it with modern humans (grade ≤ 3, AAEMH/UPMH: 76.5%, RMH: 94.6%) whereas shoveling is well marked on Neandertals (grade ≥ 3; 90.4%). The *tuberculum dentale* can only be observed at the EDJ, where it forms a moderate basal eminence produced by two thin V-shaped ridges without a free apex.

The root of LF9 is short (10.9 mm) and falls at the lowest limit of the Neandertal range and outside the RMH variation (Table 3). Its cervical surface area and root volume are closer to RMH and UPMH means than to the Neandertal mean. The ratio labio-lingual crown diameter/ root length (0.61) is also closer to UPMH (0.57, n = 6) and RMH mean values (0.56, n = 24) than to the Neandertal mean value (see details in Supporting Information B, Table B.8).

In sum, the set of non-metric traits both at the OES and EDJ (weak labial convexity, lack of marked shovel shape) as well as, to a lesser extent, root size, indicate that LF9 was likely a modern human.

LF11 – Upper left canine

This tooth retains a large part of the crown (post-mortem breakage removed its mesial quarter) and most of the root (Figure 1). The crown is heavily worn (stage 6), with a

secondary dentine patch, and the root is completely formed, although the apex was damaged after the excavations (small fragments were found in the tooth box).

The BL crown diameter of LF11 falls within the range of variation of all groups, closer to the Neandertal mean (Figure 3 and Table 1). The OES and the EDJ exhibit a well-developed *tuberculum dentale* with a free apex (Martinón-Torres et al., 2012, grade 5) (Figures 1 and 4, Table 2), a pattern systematically found in Neandertals (grade ≥ 3, 100%) and less common in modern humans (AAEMH/UPMH: 40%, RMH: 8.9%). The crown certainly exhibited some level of shoveling but the preserved part is too small to assess its grade. The EDJ exhibits the base of a distal accessory crest and the trace of an additional accessory crest, which are not observed at the OES due to the wear. These features at the OES are present in both Neandertals and modern humans (Table 2).

Although incomplete, the LF11 root length (≥ 19.9 mm on the lingual side) falls well within the Neandertal range (n=12, 17.69–25.16) and exceeds the range of variation of recent modern humans (n=12, 13.53–18.71 mm) (Le Cabec et al., 2013).

In sum, the features observed in LF11 (in particular its strong *tuberculum dentale* and long root) align this tooth with Neandertals.

LF7 – Upper right fourth premolar

LF7 consists of a complete, moderately worn crown (grade 3), damaged by several cracks, with a partially preserved single-root (absence of one third of the buccal root) (Figure 1). Although broken, it is likely that the root was formed, and interproximal wear facets show that the tooth had been functional for years.

LF7 has a large crown (MD: 7.4 mm; BL: 10.4 mm), both diameters are close to the Neandertal and AAEMH means (Figure 3 and Table 1). Due to the moderate wear, the OES only shows two main cusps, with a lingual cusp mesially displaced, an anterior fovea and an arched sagittal fissure. At the EDJ, LF7 exhibits a bifurcated lingual essential crest (grade 2) and a distal accessory cusp (grade 1), two features only found in Neandertals (Figure 3 and Table 4, see details in Supporting Information B, Table B.10). The presence of a continuous transverse crest (grade 2) (not visible at the OES due to wear) also corresponds to the Neandertal pattern (Table 4). At the EDJ, LF7 lacks accessory ridges and a mesial accessory

cusp (grade 0), but such a pattern can be found in all groups, although Neandertals rarely lack a mesial accessory ridge. As regards geometric morphometrics, the occlusal polygon and outline of LF7 correspond clearly to the Neandertal pattern (99.5% of probability). This classification is based on the asymmetrical shape, the lingual expansion and the high interfoveal distance of LF7, as it is observed in Neandertals (Figure 5; see details in Supporting Information B, Figure B.2).

In sum, the combination of the non-metric traits observed at the EDJ, as well as the occlusal polygon and outline shape, strongly support the classification of LF7 as a Neandertal premolar.

LF12 – Lower right third premolar

This very well-preserved premolar has intact and completely formed crown and root (Figure 1). The crown is slightly worn (stage 2).

The crown of LF12 is small (MD: 7.6 mm; BL: 8.4 mm) and falls in the lower half of the Neandertal and AAEMH ranges of variation (Figure 3 and Table 1). OES and EDJ exhibit only one lingual cusp (ASUDAS grade 1), which is the most frequent pattern observed in UPMH (grade 1: 36.8%) and RMH (grade ≤ 1: 64.7%) while lingual cusps are more developed or numerous in Neandertals (grade ≥ 2: 80.4%) (Figure 3 and Table 5). This tooth shows a continuous but weakly developed transverse crest (grade 1), which can be found in all groups at moderate frequency (Table 5). LF12 shows a distal accessory crest at the OES and EDJ, a trait that is frequent among Pleistocene hominins (90% of the Neandertals, 46.7% of the UPMH), but rare in RMH (9.7%). Geometric morphometric analysis shows that LF12 has a reduced and lingually located occlusal polygon (like Neandertals) but an almost totally symmetric general shape (like modern humans) (Figure 5). This symmetric shape drives the classification of LF12 as a modern human premolar with a moderately high probability (83.5%).

LF12 shows an unusual combination of Neandertal and modern human traits. Indeed, the GMM analysis of LF12 indicates a modern human affinity on the basis of its symmetric shape. However, even if LP3 occlusal shape as described by 2D configurations of landmarks and semilandmarks can very clearly distinguish early from later *Homo,* it can be equivocal regarding the classification of Neandertals and modern humans (Gómez-Robles et al. 2008).

Some features of LF12, such as the reduced and lingually placed occlusal polygon (associated with a strong convexity of the buccal face) and the mesially compressed root, better support a Neandertal affinity for this individual. Based on these traits, together with a possible Aurignacian context (see below), the taxonomic affinity of LF12 remains unclear.

LFG1 – Lower right second molar

This tooth is well-preserved with crown and roots completely formed (Figure 1). The crown is moderately worn (small dentine patch exposed at the mesio-buccal cusp tip, stage 2 or 3).

The crown of LFG1 is small, falling in the lower half of the range of variation of all our comparative samples, but closer to the UPMH mean (Figure 3 and Table 1). Both OES and EDJ show only four cusps, that are separated by a cruciform (+) groove pattern, like the vast majority of modern humans (Figure 1 and Table 5). Moreover, LFG1 is classified as a modern human tooth (91.5%), based on typically modern human four-cusped configuration. Although this pattern can occasionally be found in Neandertals, it is substantially more frequent in modern humans than in any other taxa (Figure 5).

The crown of LFG1 exhibits a distal trigonid crest that is discontinuous at the OES (ASUDAS grade 1) but continuous at the EDJ. A middle trigonid crest is absent at both surfaces. This overall trigonid crests pattern at the OES (type D; Martínez de Pinillos et al., 2014) is common in RMH (75%) but has not been observed in Neandertals. The small anterior fovea that is present at the OES of LFG1 (ASUDAS grade 1) is recorded on all groups at a similar frequency (Table 5), although the fovea is generally larger in Neandertals (grade 2, 72.7%) whereas it is often absent in modern humans (Table 5).

All together, the non-metric traits recorded at the OES/EDJ, its general size and the geometric morphometric analysis of its occlusal shape support the classification of LFG1 as a modern human molar.

LF10 – Lower right third molar

This tooth is complete but damaged due to a large break and several microfractures running through the crown and the roots (Figure 1). LF10 has fully developed roots and crown with

minimal occlusal wear (only slight enamel facets with no exposed dentine, stage 2) (Figure 1). The crown shows a linear enamel hypoplasia located 2 mm from the neck in buccal view.

The crown size of LF10 is small when compared to Neandertals and AAEMH (falling in the lower half of their range), but closer to UPMH (especially its MD diameter). However, this LM3 falls in the overlapping area of all groups on the bivariate plot (Figure 3 and Table 1). The crown has five cusps (the protoconid and metaconid are the largest) with a well developed hypoconulid (ASUDAS, grade 3), which can be found in all groups, although it is generally larger on Neandertals than on modern humans (Table 5). LF10 has a X groove pattern (ASUDAS grade 2), which is observed in the vast majority of modern humans (AAEMH/UPMH: 85.7%; RMH: 80.9%). At the OES, two discontinuous crests link both the mesial and distal regions of the protoconid and metaconid (middle trigonid crest, grade 1 after Martinón-Torres et al., 2012; distal trigonid crest, ASUDAS grade 1B). These crests are weak and continuous at the EDJ (type 12 after Martínez de Pinillos et al., 2014). This association of discontinuous middle and distal trigonid crests at the OES (type D of Martínez de Pinillos al., 2014) corresponds to a pattern more frequently recorded among RMH (2/4) than Neandertals (1/10). However, the configuration at the EDJ is the predominant pattern in Neandertals, including LM3s (73.9%, n = 21, after Bailey et al., 2011). Furthermore, a well-developed anterior fovea is present at the OES (ASUDAS grade 2), a pattern shared with most of the Neandertals (83.3%), whereas it is most often reduced on modern humans (see details in Supporting Information B - Table B.9). Finally, the geometric morphometric analysis of the occlusal shape of LF10, and especially the development of the talonid cusps, assigns this tooth to Neandertals with a high probability (98.6%), although correct classification percentages by groups are moderate: 69.2% for Neandertals and 80.6% for modern humans (Figure 5; see details in Supporting Information B, Figure B.2).

To summarize, some features at the OES (discontinuous middle and distal trigonid crests) correspond to a pattern more frequently recorded in modern humans than in Neandertals. By contrast, the well-developed C5, the large anterior fovea at the OES, the continuous mesial-mesial trigonid crest at the EDJ and the general occlusal morphology as described in our geometric morphometric analysis align this tooth with Neandertals. Although third molar anatomy does not unequivocally separate Neandertals from modern humans, there are more traits that support a Neandertal classification rather than a modern human one. Therefore, the most likely attribution for this specimen is to Neandertals.

Discussion and conclusion

In the present study, among the six teeth analyzed, three specimens are classified as Neandertals and two as modern humans (Table 6). The crown shape and EDJ non-metric traits of LF7 (URP4) strongly support its classification as a Neandertal. Given that both LF1 and LF2 retain their URP4, this tooth represents a third Neandertal adult individual. The crown morphology and root length of LF11 (ULC) also favor a Neandertal affiliation for this tooth. This tooth represents an adult individual distinct from LF1 (which retains all the upper teeth), and its size and wear stage are not compatible with the LF2 URC (Heim, 1976). Occlusal wear difference also precludes that it belongs to the same individual than LF7. Therefore, LF11 represents a fourth Neandertal adult individual found at the Grand Abri. Finally, the morphology of LF10 (LRM3) argues for its classification as a Neandertal. This is puzzling given that the tooth was assumed to be associated with faunal elements from the Gravettian ("Périgordien V") layer J, K or L from the Peyrony stratigraphy (Gambier, 1992). However we do not have any detailed information as regards its location or stratigraphic context. In the absence of direct dating and a complete taphonomic analysis of the site, we cannot completely rule out some mixing of the faunal remains at the excavation or at the museum, or the potential re-elaborated nature of this object during its pos-depositional history and before it was unearthed more than one century ago. Its attribution to a Neandertal undoubtedly questions its association with a Gravettian context unless it is a re-elaborated element coming from the erosion of older layers. Should its attribution to a Neandertal be confirmed by other lines of evidence, this would not increase the number of individuals as its individual attribution is not incompatible with LF7. In summary, there are currently a minimum of four adult and five immature Neandertal individuals represented in the LF collection coming from the "Grand Abri".

One other tooth analyzed here is attributed to modern humans. The morphology at both the OES and EDJ of LF9 (URI1) clearly aligns it with modern humans, as suggested by Gambier (1992). This tooth was found among faunal remains supposedly coming from an Early Aurignacian layer (Gambier, 1990). However, its association with this techno-complex is not demonstrated and would need to be validated because we lack any precise information about the provenience of the tooth. The taxonomical status of LRP3 (LF12) remains unclear based on dental traits. Additionally, it comes from a supposedly Aurignacian layer. Although the biological identity of the makers of the Aurignacian was challenged two decades ago (e.g. Gambier, 1990; Churchill & Smith, 2000; Conard et al., 2004; Henry-Gambier et al., 2004;

Teyssandier et al., 2010), several reassessments of human remains from secure Aurignacian contexts (including Early Aurignacian) have now shown that they are indisputably modern humans (Bailey & Hublin, 2006; Bailey et al., 2009; Verna et al., 2012). In this context, due to the overlapping between Neandertals and modern humans in some of the dental features of LF12, we have preferred to leave this tooth unassigned. In any case, the cultural attribution of the layer where it was found should be revisited. The non-metric traits and crown shape of LFG1 (LRM2), which may come from an Aurignacian layer of the "Grotte", assign it to an adult modern human. As this tooth was discovered in a different site in the LF complex than LF9 ("Grand Abri"), it belongs to a second modern human adult individual and the first one from la "Grotte". As a result, there are currently a minimum of two adult modern human individuals represented in the LF collection coming from both "Grand Abri" and "Grotte".

The lack of detailed information about the stratigraphic context of the Capitan/Peyrony excavations and particularly of the specimens found through the reassessment fauna collected during these excavations (Gambier et al., 1990; Gambier, 1992) prevents a reliable cultural attribution of the two teeth assigned to modern humans (LFG1 and LF9). Finally, one element that can be attributed to Neandertals, LF7, was found in a layer containing Châtelperronian tools. However, the technological and typological examination of the lithic elements found in the layer L2bj in Square 1 of the H. Delporte excavation was done for this study. It confirms that this layer contains a mix of Châtelperronian and Mousterian objects. Levallois debitage, scrapers, laminar and lamellar products, and pieces of Levallois knives or points were identified. A preliminary analysis of the of the tools shows two groups, one showing smooth edges and striation resulting from friction, which indicates that post-depositional events are at the origin of this mixing. As a result, the association of this Neandertal tooth with Châtelperronian tools cannot be confirmed at this point and it does not bring any new or more reliable evidence to the debate.

It is noteworthy that the spatial distribution of the recovered Neandertal remains is not restricted to the area where the LF1-LF6 and LF 8 were found but now covers the full extension of the excavated area (Figure 2). Moreover, while both Neandertal and modern human occupations have yielded isolated human remains, the partial-to-complete skeletons only belong to Neandertals (Laville, 2007). For this matter, La Ferrassie does not deviate from other sites with Aurignacian occupations, for which human remains are scarce and usually made of isolated bone fragments and teeth (e.g. La Quina-Aval, Brassempouy, Chez les Rois; Henry-Gambier et al., 2004, 2006; Bailey & Hublin, 2005; Verna et al., 2012). Besides some

possible taphonomic factors, this scarcity of human remains and lack of burials in the Early Upper Paleolithic layers at La Ferrassie - and more broadly in the western Eurasian UP fossil record - may result from distinct funerary practices as already proposed by some authors (Henry-Gambier & White, 2006).

Acknowledgments

We would like to thank C. Schwab (MAN), J.J. Cleyet-Merle (MNP), A. Froment and P. Mennecier (MNHN) for the permission to study the materials under their care. Thanks to V. Laborde, A. Fort, L. Huet (MNHN) and M.-S. Larguèze (MAN) for technical assistance. We thank the AST-RX platform (Accès Scientifique à la Tomographie à Rayons X), UMS 2700 « Outils et méthodes de la systématique intégrative », CNRS-MNHN, Paris, France, for the micro-CT scanning procedures. We would like to thank J. Braga and J. Dumoncel (AMIS laboratory, UMR 5288, Toulouse) to have provide technical support for 3D data treatment. J.J. Hublin (MPI-EVA), the NESPOS society, the ESRF Paleontological Database, H. and M.A. de Lumley and the EPCC-CERP de Tautavel gave access to material used in this study. Financial support was given by the UMR 7194 CNRS-HNHP/UPVD. A.G.-O. was supported by a Marie Curie Intra-European Fellowship during part of this work. The study was supported by the Spanish *Ministerio de Ciencia y Tecnología* (CGL2012-38434-C03-01 and CGL2015-65387-C3-2-P -MINECO/FEDER-) and by the Gobierno Vasco/Eusko Jaurlaritza (Research Group IT834-13 and IT1044-16).

References

Bailey, S. (2002). *Neandertal dental morphology: Implications for modern human origins* (Unpublished doctoral dissertation). Arizona State University, Tempe.

Bailey, S.E., & Hublin, J.-J. (2005). Who made the Early Aurignacian? A reconsideration of the Brassempouy dental remains. *Bulletins et Mémoires de la Société d'Anthropologie de Paris,* 17, 115-121.

Bailey, S. (2006). Beyond shovel-shaped incisors: Neandertal dental morphology in a comparative context. *Periodicum Biologorum*, 8, 253–267.

Bailey, S.E., & Hublin, J. (2006). Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). *Journal of Human Evolution*, 50, 485–508.

Bailey, S.E., Weaver, T.D., & Hublin, J.-J. (2009). Who made the Aurignacian and other early Upper Paleolithic industries? *Journal of Human Evolution*, 57, 11-26.

Bermúdez de Castro, J.M., Martinón-Torres, M., Gómez-Roblez, A., Prado-Simón, L., Martín-Francés, L., Lapresa, M., Olejniczack, A., & Carbonell, E. (2011). Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): A comparative morphological study. *Journal of Human Evolution*, 61, 12–25.

Bookstein, F.L. (1991). Thin-plate splines and the atlas problem for biomedical images. *Information Processing in Medical Imaging*, 551, 326-342.

Bräuer, G. (1988). Osteometrie. In R. Knussmann (Ed.), *Anthropologie. Handbuch der vergleichenden Biologie des Menschen* (pp. 160–232). Gustav Fischer, Stuttgart.

Churchill, S.E., & Smith, F.H. (2000). Makers of the early Aurignacian of Europe. *Yearbook of Physical Anthropology*, 43, 61–115.

Conard, N., Grootes, P.M., & Smith, F.H. (2004). Unexpected recent dates for human remains from Vogelherd. *Nature*, 430, 198–201.

Delporte, H. (1984). Situation et historique. In H. Delporte (Ed.), *Le grand abri de la Ferrassie* (pp. 13–21). Paris, France: Éditions du Laboratoire de Paléontologie Humaine et de Préhistoire.

Gambier, D., Hoüet, F., & Tillier, A.M. (1990). Dents de Font-de-Gaume (Chatelperronien et Aurignacien) et de La Ferrassie (Aurignacien ancien) en Dordogne. *Paléo*, 2, 143–152.

Gambier, D. (1992). Vestiges humains du Paléolithique supérieur. Inventaire et description préliminaire de spécimens inédits des collections du Musée national de Préhistoire (Les Eyzies-de-Tayac). *Paléo*, 4, 91–100.

Gómez-Olivencia, A., Crevecoeur, I., Balzeau, A. (2015). La Ferrassie 8 Neandertal child reloaded: new remains and re-assessment of the original collection. *Journal of Human Evolution,* , 82, 107–128.

Gómez-Olivencia, A., Quam, R., Sala, N., Bardey, M., Ohman, J.C., & Balzeau, A. (2018). La Ferrassie 1: New perspectives on a "classic" Neandertal. *Journal of Human Evolution*, 117, 13-32.

Gómez-Robles, A., Martinón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A., Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., & Martínez, L.M. (2007). A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution*, 53, 272–285.

Gómez-Robles, A., Martinón-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*. *Journal of Human Evolution*, 55, 627–638.

Gómez-Robles, A., Olejniczack, A.J., Martinón-Torres, M., Prado-Simón L., & Bermúdez de Castro, J.M. (2011a). Evolutionary novelties and losses in geometric morphometric: a practical approach through hominin molar morphology. *Journal of Human Evolution*, 65, 1772–1790.

Gómez-Robles, A., Martinón-Torres, M., Bermúdez de Castro, J.M., Prado-Simón, L., & Arsuaga, J.L. (2011b). A geometric morphetric analysis of hominin upper premolars. Shape variation and morphological integration. *Journal of Human Evolution*, 61, 688–702.

Gómez-Robles, A., Bermúdez de Castro, J.M., Martinón-Torres, M., Prado-Simón L., & Arsuaga, J.L. (2012). A geometric morphometric analysis of hominin upper second and third molars, with particular emphasis on European Pleistocene population. *Journal of Human Evolution*, 63, 512–526.

Gómez-Robles, A., Bermúdez de Castro, Martinón-Torres, M., J.M., Prado-Simón, L., & Arsuaga, J.L. (2015). A geometric morphometric analysis of hominin lower molars:

Evolutionary implication and overview of postcanine dental variation. *Journal of Human Evolution*, 82, 34–50.

Guérin, G., Frouin, M., Talamo, S., Aldeias, V., Bruxelles, L., Chiotti, L., Dibble, H. L., Goldberg, P., Hublin, J.-J., Jain, M., Lahaye, C., Madelaine, S., Maureille, B, McPherron, S. P., Mercier, N., Murray, A. S., Sandgathe, D., Steele, T. E., Thomsen, K. J., Turq, A. (2015). A multi-method luminescence dating of the Palaeolithic sequence of La Ferrassie based on new excavations adjacent to the La Ferrassie 1 and 2 skeletons. *Journal of Archeological Science*, 58, 147-166.

Heim, J.-L. (1976). *Les Hommes fossiles de la Ferrassie. I. Le gisement. Les squelettes adultes (crâne et squelette du tronc)*. Paris: Masson.

Heim, J.-L. (1982a). *Les enfants néandertaliens de la Ferrassie. Étude anthropologique et analyse ontogénique des hommes de Néandertal*. Paris: Masson.

Heim, J.-L. (1982b). *Les hommes fossiles de La Ferrassie. II. Les squelettes d'adultes: squelettes des membres*. Paris: Masson.

Henry-Gambier, D., Maureille, B., & White, R. (2004). Vestiges humains des niveaux de l'Aurignacien ancien du site de Brassempouy (Landes). *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, 6, 49–87.

Henry-Gambier, D., & White, R. (2006). Modifications artificielles des vestiges humains de l'Aurignacien ancien de la Grotte des Hyènes (Brassempouy, Landes). Quelle signification? In V. Cabrera Valdés, F. Bernaldo de Quirós, J.M. Maíllo (Eds.), *En el Centenario de la Cueva de El Castillo: El ocaso de los Neandertales* (pp 73–88). Centro Asociado a la Universidad Nacional de Educación a Distancia en Cantabria, Santander.

Laville, D. (2007). *La Ferrassie : taphonomie d'un site sépulcral moustérien* (Master's thesis) Université de Liège, Belgique.

Laville, H., & Tuffreau, A. (1984). Les dépôts du grand abri de la Ferrassie : stratigraphie, signification climatique et chronologie. In: H. Delporte (Ed.), *Le grand abri de la Ferrassie* (pp. 25–50). Paris , France: Éditions du Laboratoire de Paléontologie Humaine et de Préhistoire.

Le Cabec, A., Gunz, P., Kupczik, K,. Braga, J., & Hublin, J.J. (2013). Anterior tooth root morphology and size in Neandertals: Taxonomic and functional implications. *Journal of Human Evolution*, 64, 169–193.

Martínez de Pinillos, M., Martinón-Torres, M., Skinner, M.M., Arsuaga, J.L., Gracia-Téllez, A., Martínez, I., Martín-Francés, L., & Bermúdez de Castro, J.M. (2014). Trigonid crests expression in Atapuerca-Sima de los Huesos lower molars: Internal and external morphological expression and evolutionary inferences. *Comptes Rendus Palevol*, 13, 205–211.

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Prado-Simón, L., & Arsuaga, J.L. (2012). Morphological description and comparison of the dental remains from Atapuerca-Sima de los Huesos site (Spain). *Journal of Human Evolution,* 62, 7–58.

Maureille, B., Rougier, H., Houët, H., & Vandermeersch, B. (2001). Les dents inférieures du néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne): analyses métriques et comparatives. *Paleo*, 13, 183–200.

Molnar, S. (1971). Human tooth wear, tooth function and cultural variability. *American Journal of Physical Anthropology*, 34, 175–190.

Rohlf, F.J., & Slice, D. (1990). Extensions of the Procrustes Method for the Optimal Superimposition of Landmarks. *Systematic Biology*, 39, 40-59.

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

Skinner, M.M., Gunz, P., Wood, B., & Hublin, J.J. (2008a). Enamel-dentine junction (EDJ) morphology distinguishes the lower molars of *Australopithecus africanus* and *Paranthropus robustus*. *Journal of Human Evolution*, 55, 979–988.

Teyssandier, N., Bon, F., & Bordes, J.-G. (2010). Within projectile range. Some thoughts on the appearance of the Aurignacian in Europe. *Journal Anthropological Research*, 66, 209–229.

Turner, C.G., Nichol, C.R., & Scott, G.R. (1991). Scoring procedures for keymorphological traits of the permanent dentition: the Arizona State University Dental Anthropology System. In M. Kelley, C. Larsen (Eds.), *Advances in Dental Anthropology* (pp.13–31). New York, USA: Wiley Liss.

Turq, A., Dibble, H., Goldberg, P., McPherron, S.J.P., Sandgathe, D., Mercier, N., Bruxelles, L., Laville, D., & Madelaine, S. (2012) Reprise des fouilles dans la partie ouest du gisement de La Ferrassie, Savignac-de-Miremont, Dordogne : problématique et premiers résultats. In P.

Bertran, A. Lenoble (Eds.), *Quaternaire continental d'Aquitaine: un point sur les travaux récents* (pp. 78-87). France: Association des Sédimentologistes Français.

Verna, C., Dujardin, V., & Trinkaus, E. (2012)**.** The Aurignacian human remains from La Quina-Aval (France). *Journal of Human Evolution*, 62, 605–617.

Tables

Table 1. Comparison of external crown metric data between La Ferrassie teeth and Neandertals (NEA), African and Asian early modern humans (AAEMH) and upper Paleolithic modern humans (UPMH).

Tooth		LF	NEA				AAEMH				UPMH			
			n	m	Sd	Azs	*n*	m	sd	Azs	*n*	m	sd	Azs
URI1	MD	9.7	37	9.5	0.80	0.10	8	9.9	0.82	-0.11	29	9.1	1.02	0.29
	BL	>7.6	41	8.3	0.62		7	8.2	0.51		28	7.5	0.40	
	CBA		36	79.9	11.85		7	79.9	10.49		25	68.1	7.88	
ULC	MD	>8	36	8.5	0.85		9	8.6	0.54		24	8.0	0.49	
	BL	9.9	40	9.8	0.76	0.03	9	9.2	0.77	0.39	23	9.0	0.87	0.48
	CBA		36	83.6	13.25		9	78.7	9.77		23	72.0	10.75	
URP4	MD	7.4	37	7.3	0.72	0.03	9	7.5	0.97	-0.05	28	6.9	0.63	0.36
	BL	10.4	36	10.3	0.63	0.05	9	10.4	0.98	0.00	30	9.7	0.60	0.53
	CBA	76.1	36	75.3	11.46	0.04	8	79.4	16.18	-0.09	29	67.6	10.07	0.41
LRP3	MD	7.6	47	7.7	0.57	-0.15	8	8.0	0.53	-0.39	26	7.1	0.48	0.42
	BL	8.4	46	9.0	0.69	-0.45	9	8.9	0.57	-0.41	27	8.4	0.44	-0.04
	CBA	63.2	46	69.6	9.23	-0.34	8	72.9	6.31	-0.65	24	60.6	6.43	0.19
LRM2	MD	10.9	60	11.9	0.83	-0.59	11	11.8	1.27	-0.31	47	11.2	0.85	-0.20
	BL	10.6	61	11.1	0.74	-0.31	12	11.6	0.77	-0.56	48	10.9	0.76	-0.18
	CBA	115.6	60	131.7	16.27	-0.49	11	137.1	23.37	-0.41	46	122.6	16.30	-0.21
LRM3	MD	11.3	52	11.8	0.68	-0.33	13	12.0	0.99	-0.32	25	11.1	1.15	0.07
	BL	10.3	52	11.0	0.79	-0.46	13	11.0	0.93	-0.36	26	10.7	0.92	-0.22
	CBA	116.3	51	129.7	13.45	-0.50	13	132.9	21.01	-0.36	25	119.9	21.91	-0.08

MD: Mesio-distal diameter, in mm; BL: Bucco-lingual diameter, in mm. CBA: Crown base area, in mm²; m: Mean; sd: Standard-deviation; Azs: Adjusted Z-score; URI1: Upper right central incisor; ULC: Upper left canine; URP4: Upper right fourth premolar; LRP3: Lower right third premolar; LRM2: Lower right second molar; LRM3: Lower right third molar.

Table 2. Comparison of non-metric traits at the outer enamel surface (OES) between upper teeth from La Ferrassie and Neandertals (NEA), African and Asian early modern humans/upper Paleolithic modern humans (AAEMH/UPMH) and recent modern humans (RMH).

Upper	Nonmetric traits	Grade	Grade for	NEA		AAEMH/UPMH		RMH	
tooth	at the OES		LF tooth	n	%	n	%	n	%
URI1	Labial convexity	≤ 2	1	0/21	0	12/17	70.6	85/91	93.5
		≥ 3		21/21	100	5/17	29.4	6/91	6.6
	Shovel shape	≤ 3	1	7/21	33.3	13/17	76.5	86/91	94.6
		≥ 4		14/21	66.7	4/17	23.5	5/91	5.4
ULC	*Tuberculum dentale*	≤ 2		0/21	0	6/10	60.0	103/113	91.1
		≥ 3	5	21/21	100	4/10	40.0	10/113	8.9
	Distal accessory ridge	0*		9/16	56.2	2/7	28.6	61/90	67.8
		≥ 1**	1 or 2	7/16	43.8	5/7	71.4	30/90	32.2
URP4	Buccal essential crest	0*		0/15	0	0/11	0	1/106	0.9
		≥ 1**	1 or 2	15/15	100	11/11	100	95/106	99.1
	Lingual essential crest	0*		0/14	0	0/11	0	0/108	0
		≥ 1**	1 or 2	14/14	100	11/11	100	108/108	100
	Transverse crest	0		14/16	87.5	9/11	81.8	113/113	100
		≥ 1**	1 or 2	2/16	12.5	2/11	18.2	0/113	0

Morphological traits frequencies for NEA, AAEMH/UPMH and RMH are from Martinón-Torres et al. (2012). The different grades have been combined to better discriminate Neandertals from modern humans. n= number of occurrences over the total sample size. URI1: upper right central incisor; ULC: upper left canine; URP4: upper right fourth premolar; * and ** stand for absence and presence of the trait, respectively. See details in Supporting Information B, Tables B.7 and B.9.

Table 3. Comparative descriptive statistics for the root of the upper central incisor between LF9 (URI1) and Neandertals (NEA), African and Asian early modern humans (AAEMH), upper Paleolithic modern humans (UPMH) and recent modern humans (RMH).

Taxa	Statistic	RL	CA	RV	CrLL/RL
		(mm)	(mm^2)	(mm^3)	(-)
URI1 (LF9)		10.87	37.59	229.01	0.61
NEA	m (CV)	17.23 (2.4)	41.88 (8)	452 (123.52)	0.5 (0.08)
n = 17	range	10.54 - 19.79	33.15 - 59.07	195.84 - 693.61	0.42 - 0.77
AAEMH	m (CV)	16.61 (3.55)	36.75 (9.3)	346.74 (180.86)	0.47 (0.05)
n = 2/3	range	14.1 - 19.12	29.99 - 47.35	218.85 - 474.63	0.43 - 0.5
UPMH	m (CV)	13.5 (2.09)	36.04 (3.85)	274.95 (65.65)	0.57 (0.08)
n = 6	range	10.61 - 15.8	29.54 - 41.32	197.44 - 388.04	0.48 - 0.68
RMH	m (CV)	12.94 (1.39)	29.93 (3.48)	225.6 (46.6)	0.56
n = 24	range	11.08 - 16.32	23.93 - 36.26	147.75 - 333.03	0.46 - 0.67

The data for the groups of NEA, AAEMH, UPMH and RMH are from Le Cabec et al. (2013). URI1: Upper right central incisor; RL: Root length; CA: Cervical area; RV: Root volume CrLL: maximum labio-lingual crown diameter; RL: root length; m: Mean; CV: Coefficient of variation.

Table 4. Comparison of nonmetric traits at the enamel-dentine junction (EDJ) between LF7 (URP4) and Neandertals (NEA), African and Asian early modern humans (AAEMH), Upper Paleolithic modern humans (UPMH) and recent modern humans (RMH).

Upper	Nonmetric traits	Grade for	NEA		AAEMH		UPMH		RMH	
tooth	at the EDJ	La Ferrassie	n	%	n	%	n	%	n	%
URP4	Buccal essential crest	2 (bifurcated)	7/12	58.3	1/2	50.0	0/1	0	4/20	20.0
	Lingual essential crest	2 (bifurcated)	11/12	91.7	0/2	0	0/1	0	0/20	0
	Distal accessory ridge	0 (absent)	7/12	58.3	2/2	100	0/1	0	8/20	40.0
	Mesial accessory ridge	0 (absent)	1/12	8.3	0/2	0	1/1	100	8/20	40.0
	Mesial accessory Cusp	0 (absent)	12/12	100	2/2	100	1/1	100	20/20	100
	Distal accessory Cusp	1 (present)	2/12	16.7	0/2	0	0/1	0	0/20	0
	Transverse crest	2 (continuous)	8/12	66.7	2/2	100	0/1	0	2/14	14.3

URP4: Upper right fourth premolar. See details in Supporting Information B, Table B.10.

Table 5. Comparison of nonmetric traits at the outer enamel surface (OES) between lower teeth from La Ferrassie and Neandertals (NEA), African and Asian early modern humans/upper Paleolithic modern humans (AAEMH/UPMH) and recent modern humans (RMH).

Lower	Nonmetric traits	Grade	Grade for	NEA		AAEMH/UPMH		RMH	
tooth	at the OES		LF tooth	*n*	%	*n*	%	*n*	%
LRP3	Lingual cusps	≤ 1	1	5/27	18.5	8/19	42.1	97/150	64.7
		≥ 2		22/27	81.5	11/19	57.9	53/150	35.3
	Transverse crest	0		4/26	15.4	3/18	16.7	105/157	66.9
		1	1	8/26	30.8	3/18	16.7	32/157	20.4
		2		14/26	53.8	12/18	66.6	20/157	12.7
	Distal accessory ridge	0*		2/20	10.0	8/15	53.3	121/134	90.3
		1**	1	18/20	90.0	7/15	46.7	13/134	9.7
	Mesial accessory ridge	0*	0	20/21	95.2	11/12	91.7	119/135	88.1
		1**		1/21	4.8	1/12	8.3	16/135	11.9
LRM2	Anterior fovea	0		1/22	4.5	12/22	54.6	100/156	64.1
		1	1	5/22	22.7	5/22	22.7	47/156	30.1
		2		16/22	72.7	5/22	22.7	9/156	5.8
	Mid-trigonid crest	0	0	0/23	0	17/23	73.9	126/153	82.4
		1		6/23	26.1	6/23	26.1	26/153	17.0
		2		17/23	73.9	0/23	0	1/153	0.6
	Distal trigonid crest	0		9/22	40.9	18/24	75.0	134/151	88.7
		1	1	11/22	50.0	5/24	20.8	8/151	5.3
		2		2/22	9.1	1/24	4.2	9/151	6.0
	Hypoconulid size	0*	0	2/24	14.2	16/25	64.0	117/157	74.5
		≥ 1**		22/24	91.6	9/25	36.0	40/157	25.5
	C6 size	0*	0	11/24	45.8	19/24	79.2	143/151	94.7
		≥ 1**		13/24	54.2	5/24	20.8	8/151	5.3
	C7 size	0*	0	7/23	30.4	19/25	76.0	139/155	89.7
		≥ 1**		16/23	69.6	6/25	24.0	16/155	10.3
	Groove pattern	1		17/24	70.8	9/26	34.6	41/155	26.5
		2	2	7/24	29.2	17/26	65.4	114/155	73.5
LRM3	Anterior fovea	≤ 1		3/18	16.7	12/17	70.6	104/122	85.2
		2	2	15/18	83.3	5/17	29.4	18/122	14.8
	Middle trigonid crest	0		1/17	5.9	14/15	93.3	107/119	55.7
		1	1	4/17	23.5	1/15	6.7	12/119	29.5
		2		12/17	70.6	0/15	0	0/119	14.8
	Distal trigonid crest	0		10/16	62.5	10/16	62.5	90/120	75.0
		1	1	3/16	18.8	4/16	25.0	21/120	17.5
		2		3/16	18.8	2/16	12.5	9/120	7.5
	Hypoconulid size	≤ 2		3/16	18.8	9/18	50.0	80/126	63.5
		≥ 3	3	13/16	81.2	9/18	50.0	46/126	36.5

C6 size	0*	0	5/15	33.3	12/18	66.7	94/121	77.7
	≥ 1**		10/15	66.7	6/18	33.3	27/121	22.3
C7 size	0*	0	8/15	53.5	13/17	76.5	98/124	79.0
	≥ 1**		7/15	46.7	4/17	23.5	26/124	21.0
Groove pattern	1		9/15	60.0	2/14	14.3	21/110	19.1
	2	2	6/15	40.0	12/14	85.7	89/121	80.9

The frequencies of the degrees of expression of the main morphological traits for the groups of NEA, AAEMH/UPMH and RMH are from Martinón-Torres et al. (2012). The different grades have been combined to better discriminate Neandertals from modern humans. LRP3: lower right third premolar; LRM2: lower right second molar; LRM3: lower right third molar; * and ** stand for absence and presence of the trait, respectively. See details in Supporting information B, Table B.9.

Table 6. Summary of the new hominin remains from La Ferrassie: specimen, anatomical, original label, techno-complex and taxonomic attributions.

Specimen	Tooth	Original label	Level, cultural context (Reference)	Taxonomic affinity
LF11	Upper left canine	73.60.M2e 136	Level M2. Mousterian (Delporte, 1984)	Neandertal
LF7	Upper right fourth premolar	70.1.L2bJ.168	Level L2bJ. Mixed Mousterian and Châtelperronian tools (Delporte, 1984)	Neandertal
LF12	Lower right third premolar	tamisage L2 carré 13	Level L2. Aurignacian (Delporte, 1984)	Indeterminate
LF9	Upper right central incisor	MNP 1934-4-1-1	Level E ("Aurignacien ancien")* (Gambier et al., 1990; Gambier, 1992)	Modern Human
LFG1	Lower right second molar	MNP 1934-4-1-2	"Aurignacien I level" * (Gambier, 1992)	Modern Human
LF10	Lower right third molar	MNP 1934-4-1-3	Level J, K or L from Peyrony's excavations ("Périgordien V"). Gravettian?* (Gambier, 1992)	Neandertal

*Given that these remains were found many decades ago, the association with these techno-complexes should be regarded as questionable, particularly for LF10, which is classified as a Neandertal.

Figure 1. The new teeth from La Ferrassie in mesial, lingual, distal, buccal and occlusal views. (a) LF9 (URI1); (b) LF11 (ULC); (c) LF7 (URP4); (d) LF12 (LRP3); (e) LFG1 (LRM2); (f) LF10 (LRM3). Scales = 1cm.

199x109mm (300 x 300 DPI)

Figure 2. West-East and South-North sections in "Grand Abri" at La Ferrassie at the end of the 1968-1973 excavations (A) and map of the site showing the position of the isolated hominin remains (LF7, LF11 and LF12) relative to the Neandertal skeletons. The gray lines on the map show the position of the walls that were built after the end of the excavations to protect the site. The precise position of LF9 and LF10 within the site is unknown.

199x57mm (300 x 300 DPI)

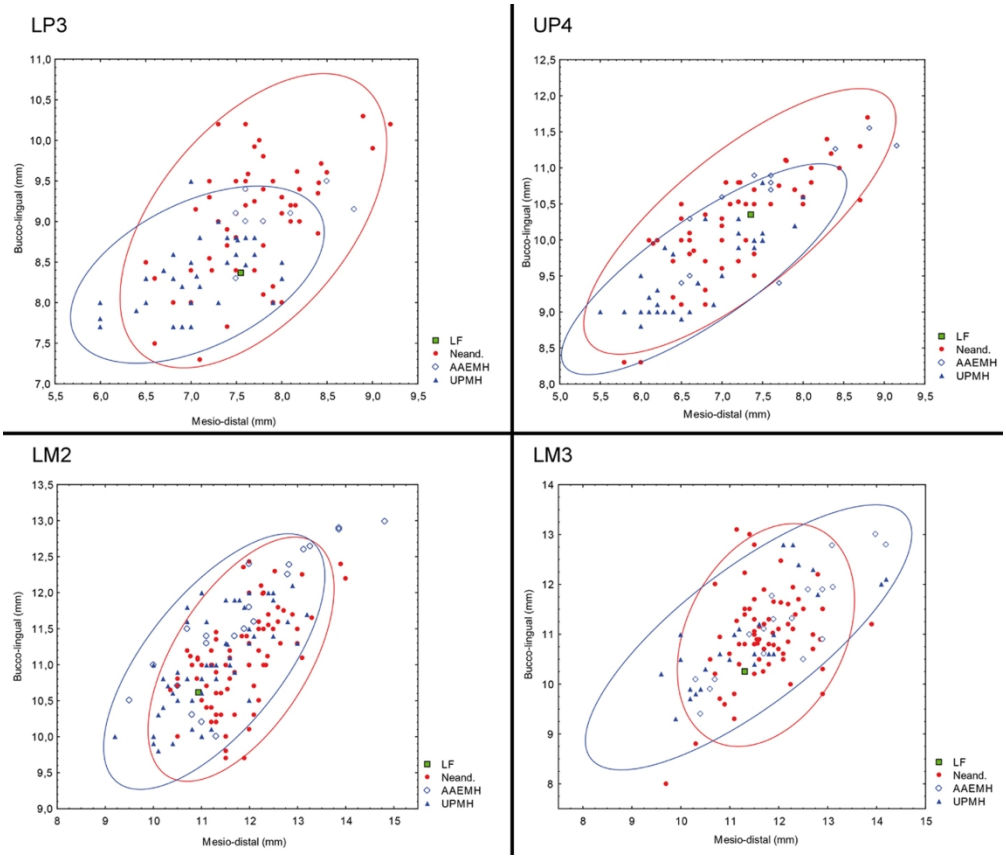

Figure 3. Biplots of the mesio-distal and bucco-lingual crown diameters of the LP3, UP4, LM2 and LM3 from La Ferrassie (Neandertals and fossil modern humans). LF: La Ferrassie teeth; Neand: Neandertals; AAEMH: Asian and African Early Modern Humans; UPMH: Upper Paleolithic modern humans.

170x144mm (300 x 300 DPI)

Figure 4. Three-dimensional topography at the enamel-dentine junction (EDJ) of the teeth from La Ferrassie, in occlusal view. (a) LF9 (URI1); (b) LF11 (ULC); (c) LF7 (URP4); (d) LF12 (LRP3); (e) LFG1 (LRM2); (f) LF10 (LRM3). Scale = 1cm.

199x54mm (300 x 300 DPI)

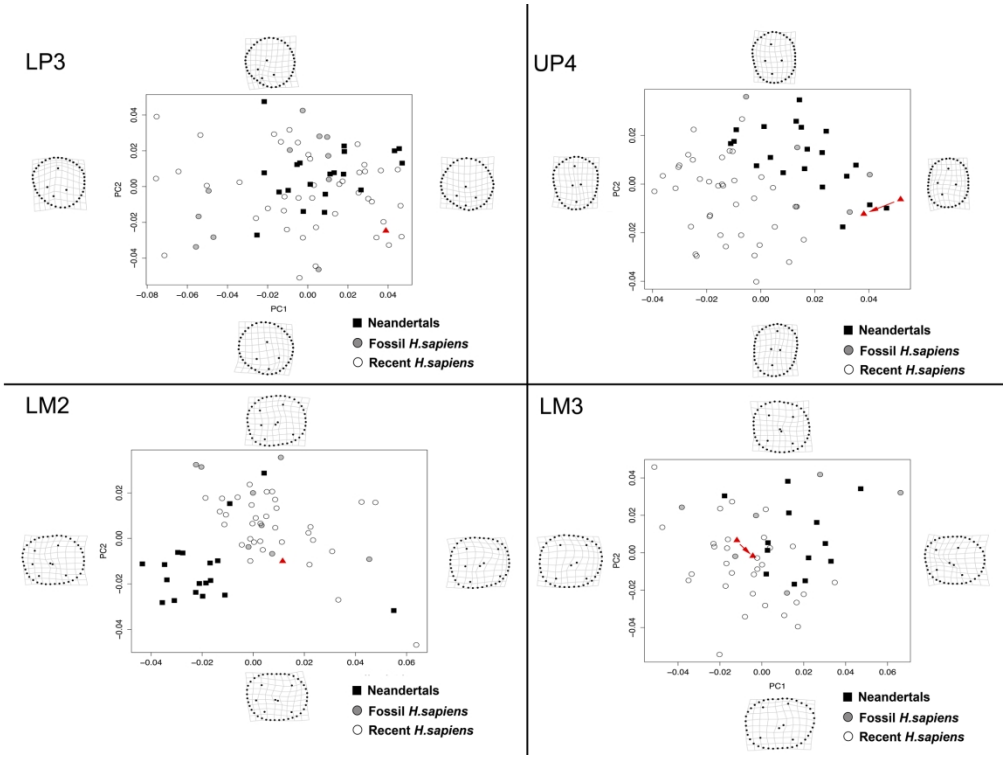

Figure 5. Principal components analyses of shape variation in LP3, UP4, LM2 and LM3. Teeth from La Ferrassie are represented as red triangles.

199x150mm (300 x 300 DPI)