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A Neanderthal partial femoral diaphysis from the "grotte de la Tour", La Chaise-de-Vouthon (Charente, France): Outer morphology and endostructural organization

La diaphyse fémorale néandertalienne de la « grotte de la Tour », La Chaise-de-Vouthon (Charente, France) : morphologie externe et organisation endostructurale

Laurent Puymerail[a,*,b], Virginie Volpato[c], André Debénath[b], Arnaud Mazurier[d], Jean-François Tournepiche[e,f], Roberto Macchiarelli[b,g]

[a] *Unité d'Anthropologie bio-culturelle, Droit, Éthique et Santé (ADÉS), UMR 7268, Université d'Aix-Marseille-EFS-CNRS, boulevard Pierre-Dramard, 13344 Marseille, France*
[b] *Département de Préhistoire, Muséum national d'Histoire naturelle, UMR 7194, 75005 Paris, France*
[c] *Paleoanthropology and Messel Research, Senckenberg Research Institute, 60325 Frankfurt am Main, Germany*
[d] *Société Études Recherches Matériaux, 86000 Poitiers, France*
[e] *Musée d'Angoulême, 16000 Angoulême, France*
[f] *IPGQ-UMR 5199, université Bordeaux-1, 33405 Talence, France*
[g] *Département Géosciences, Université de Poitiers, 86022 Poitiers, France*

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ABSTRACT

We describe a human partial femoral shaft discovered during speleological exploration of the "grotte de la Tour", near the prehistoric site of La Chaise-de-Vouthon (Charente, France). The context of discovery is compatible with a hyena den deposit; the associated mammal assemblage suggests a preliminary chronological attribution to MIS 3. Combined information from its outer morphology, cross-sectional geometric properties, and from the high-resolution 3D imaging and quantitative analysis of its inner structural organization shows that this specimen (CDV-Tour 1) is from an adult Neanderthal individual, more likely a male.

RÉSUMÉ

Nous décrivons une portion de diaphyse fémorale humaine découverte lors de l'exploration spéléologique de la « grotte de la Tour », près du site préhistorique de La Chaise-de-Vouthon (Charente, France). Le contexte de découverte est compatible avec un dépôt de tanière de hyène ; l'assemblage des restes mammifères associés suggère une attribution chronologique au MIS 3. La morphologie externe, les propriétés géométriques des

* Corresponding author.
E-mail address: puymerail@mnhn.fr (L. Puymerail).

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sections et l'analyse quantitative tridimensionnelle à haute résolution de la structure interne montrent que ce spécimen (CDV-Tour 1) appartient à un individu néandertalien adulte, vraisemblablement de sexe masculin.

1. Introduction

The "grotte de la Tour" is a new cavity of paleoanthropological interest discovered near the prehistoric site of La Chaise-de-Vouthon, in the department of Charente (Poitou-Charentes region, western France). This famous Middle to Late Pleistocene site complex, in a Middle Jurassic (Bajocian-Bathonian) limestone plateau, consists of a network of NW-oriented karstic caves whose opening is ~10 m above the Tardoire river (Debénath, 2006).

Discovered in 1850 and extensively excavated between 1930 and 1963 (by P. David) and between 1967 and 1983 (by A.D.), La Chaise-de-Vouthon comprises two major rock shelters/caves, both having provided Neanderthal remains: the Abri Suard, whose deposits were originally referred to a period ranging from Riss II to Riss-Würm, and the Abri Bourgeois-Delaunay, covering a period from Riss III to Würm III (Blackwell et al., 1983, 1992; Debénath, 1974, 1977, 2006; Schwarcz and Debénath, 1979). According to a new set of $^{230}Th/^{234}U$ speleothem dates (Couchoud, 2006; Vieillevigne et al., 2008), the human remains from the Abri Suard, all from MIS 6 and associated to a typically cold mammal fauna (Griggo, 1995), are younger than 163 kyr, while the age of those from Bourgeois-Delaunay (MIS 5e, Eemian), associated to a temperate fauna (Armand, 1998), is between 127 and 116 kyr (Debénath, 2006).

To date, La Chaise has provided a human fossil sample consisting of 75 subadult and adult Neanderthal remains (52 from Suard and 23 from Bourgeois-Delaunay), including a number of isolated teeth (Condemi, 2001; Debénath, 2006; Genet-Varcin, 1974, 1975a, b, 1976; Legoux, 1976; Macchiarelli et al., 2006; Piveteau, 1953, 1955, 1970a, b; Piveteau et al., 1982; Teilhol, 2001, 2003; Tillier and Genet-Varcin, 1980). Among the adult postcranial remains, a rather slender partial right femoral shaft of 239.5 mm, BD 5, was recovered at the Abri Bourgeois-Delaunay (Condemi, 2001: pp. 137–152).

The human femoral shaft reported in this study was collected in 2006 by D. Augier during speleological exploration of a cavity named "grotte de la Tour" (Tour of La Chaise cave), whose entrance is at ~130 m W of Abri Suard (0°26′48″ E, 45°40′13″ N) (Fig. 1). The specimen, CDV-Tour 1, was found on surface associated to a bovid long bone fragment among the soil *déblais*, likely accumulated by a badger near the entrance of a narrow duct leading to a larger inner cavity. About 10 m from this spot, a concentration of faunal remains showing the characteristics of a hyena den deposit, with bones broken or etched from digestion, has been discovered inside the duct. A preliminary surface survey of the cavity revealed no archaeological evidence of human activity, which supports the interpretation of a carnivore den, similar to the contexts ascertained for the cave sites of Rochelot (Tournepiche et al., 1996) and Rochers-de-Villeneuve (Beauval et al., 2005), from the same region, both having provided Neanderthal remains.

The faunal remains from Tour of La Chaise collected so far represent *Equus* sp. cf. *germanicus*, *E. hydruntinus*, *Sus scrofa*, Bovinae (*Bos* and *Bison*), *Cervus elaphus*, *Capreolus capreolus*, *Megaloceros* sp., *Crocuta crocuta spelaea*, *Canis lupus*, *Panthera spelaea*, *P. pardus*, *Ursus spelaeus*, *Vulpes vulpes*. As a whole, this Late Pleistocene mammal assemblage, suggesting a rather temperate climate, overlaps those reported for the nearby site of La Chauverie (El Albani et al., 2011) and from Rochers-de-Villeneuve, in the neighbouring department of Vienne (Beauval et al., 2005), both dated to MIS 3. Nonetheless, this preliminary chronological setting deserves confirmation and, based on the available information, it should be only considered as the most likely.

CDV-Tour 1 (Fig. 2) represents a shaft portion from a left femur whose diaphyseal dimensions and proportions, subperiosteal contour, and inner structural morphology globally differ from the conditions seen in fossil and extant modern humans and allow its attribution to an adult Neanderthal.

2. Methods of analysis

CDV-Tour 1 has been imaged in 2008 by X-ray microtomography (μCT) at the Centre de Microtomographie of the University of Poitiers. Two acquisitions have been run to scan the entire shaft and the records have been merged after volume reconstruction. Scans were realized by a X8050-16 Viscom AG (image intensifier with a 1004 × 1004 12 bit camera and a pixel size of 147 μm) according to the following parameters: 120 kV voltage, 560 μA current, 32 integrations/projection, and 1200 projections (each 0.30°). The final volume was reconstructed using DigiCT v.2.4.2 (Digisens) in 8-bit format, with an isotropic voxel size of 107.8 μm.

Because of globally good outer and inner bone preservation quality and the lack of any sedimentary infill of the medullary cavity, a semi-automatic threshold-based segmentation with manual corrections has been successfully carried out following the Half-Maximum Height method (HMH; Spoor et al., 1993) and the region of interest thresholding protocol (ROI-Tb; Fajardo et al., 2002) and by taking repeated measurements on different slices of the virtual stack (Coleman and Colbert, 2007) by Avizo v.6.2. (Visualization Sciences Group Inc.) and ImageJ v.1.46a (Rasband, 2010).

To orient the specimen anatomically, we used the position of the *linea aspera*. The approximate position of the midshaft was confidently defined on comparative ground through the morphology of the *linea aspera* and the shaft outline in medial and lateral views. The 50% cross-section precise location is usually less clearly indicated in fossil human femora displaying subcircular diaphyses and lacking a true pilaster, such as CDV-Tour 1; however, this region shows little longitudinal changes in morphology along several centimetres, making modest errors in the location

Fig. 1. Location of « grotte de la Tour » (La Chaise-de-Vouthon, Charente, France) and plan of the site: 1: place of discovery of the human femoral shaft near the entrance of the duct; 2: the hyena den deposit. Survey: P. Vauvilliers; drawing: J.-F. Tournepiche.

Fig. 1. Localisation de la « grotte de la Tour » (La Chaise-de-Vouthon, Charente, France) et plan du site : 1 : emplacement de la découverte de la diaphyse fémorale humaine près de l'entrée de la galerie ; 2 : le dépôt de la tanière d'hyène. Relevé : P. Vauvilliers ; dessin : J.-F. Tournepiche.

of these sections not critical for the structural characterization of the specimen (Sládek et al., 2010; Trinkaus and Ruff, 2012).

Cross-sectional geometric (CSG) properties of CDV-Tour 1 were measured on four selected virtual sections (A to D) respectively corresponding to: the uppermost (A, 62.4 mm above the midshaft) and the lowermost (D, 33.4 mm below the midshaft) complete sections found along the shaft in proximo-distal direction; the midshaft (C); the mid-distance between the uppermost and the midshaft sections (B) (Fig. 3). As CDV-Tour 1 misses both articular ends, we could not directly measure its biomechanical length. However, if the average value of ~407 mm obtained for a sample of eight European Neanderthals (La Chapelle-aux-Saints 1, Feldhofer 1, La Ferrassie 1 and 2, Fond-de-Forêt 1, Palomas 92 and 96, Spy 2; in Trinkaus and Ruff, 2012, table A1) is used as a proxy for estimating the biomechanical length of CDV-Tour 1, the segment A-D (95.8 mm) should approximately correspond to the shaft portion comprised between 42% (distal) and 65% (proximal) of its biomechanical length, the section B corresponding to ~57.5%.

In addition to the anteroposterior (a-m) and mediolateral (m-l) outer diameters (in millimeter, both measured directly on the original shaft by a dial-equipped vernier caliper to the nearest 0.1 mm, and also on the virtually reconstructed specimen), the following CSG parameters have been considered by using a custom routine developed in R v.2.11.1 (R Development Core Team, 2011): total area (TA, in mm^2); cortical area (CA, in mm^2); percent of cortical area (%CA); second moments of area about the m-l and a-p axes (Ix, Iy, in mm^4); polar second moment of area (*J*, in mm^4); section modulus about the m-l and a-p axes (Zx, Zy, in mm^3); polar section modulus (Zp, in mm^3); maximal and minimal second moments of area (Imax, Imin, in mm^4) (Ruff, 2008).

In order to place CDV-Tour 1 within the pattern of variation reported for the European Late Pleistocene fossil record, comparative data for %CA and the Ix/Iy ratio measured at 50% and 65% cross-sectional level were obtained for a number of Neanderthal (Neand.) and Upper Paleolithic (EUPH) human femora from the database recently published by Trinkaus and Ruff (2012), integrated by fresh evidence on a Neanderthal femoral shaft from the MIS 4 French site of Les Pradelles (Mussini et al., 2012) (Table 1). For the comparative assessment of the pilastric index (diameter a-p/m-l × 100), we used the same samples detailed in Table 1 integrated by data from the following specimens: Santa Croce 1 and Stadelhöhle 1, among the Neanderthals, and Barma Grande 6, Caviglione 1, and Předmostí 3, 4, 9, 10 and 14, for the Upper Paleolithic sample (Trinkaus and Ruff, 2012, table A13).

By using an original (μ)CT record, we also comparatively detailed cortical bone thickness variation at eight specific sites (anticlockwise: posterior, postero-lateral, lateral, antero-lateral, anterior, antero-medial, medial, postero-medial) of the 50% and 65% cross-sections in

Fig. 2. CDV-Tour 1 (left femoral shaft) in anterior (a), posterior (b), medial (c), and lateral (d) views (proximal is upper). Scale bar: 1.5 cm.
Fig. 2. CDV-Tour 1 (diaphyse fémorale gauche) en vues antérieure (a), postérieure (b), médiale (c) et latérale (d) (proximale vers le haut). Échelle : 1,5 cm.

CDV-Tour 1, La Ferrassie 1 (left), Rochers-de-Villeneuve 1 (50%), Spy 8 (Volpato et al., 2012b), Cro-Magnon 1 (left; Puymerail, 2011; Puymerail and Macchiarelli, 2009), and in the Magdalenian skeleton from Chancelade (right femur; Bondioli et al., 2010; Puymerail, 2011; Puymerail and Macchiarelli, 2009), as well as in an extant human reference sample.

In our study, the extant human condition is illustrated by 20 femora measured from medical CT records performed at spatial resolutions ranging from 350 to 791 μm (Puymerail, 2011; Puymerail et al., 2012). This sample (EH) pools adults of both sexes from 19th century France and the Imperial Roman graveyard of Velia, Italy, stored at the Musée de l'Homme of Paris, the University of Poitiers, and the Museo Nazionale Preistorico Etnografico "L. Pigorini" of Rome.

Three-dimensional cortical thickness topographic distribution in CDV-Tour 1 for the whole portion A-D has been virtually rendered for each anatomical projection by a chromatic scale increasing from dark blue (thin) to red (thick), where bone thickness is defined for each point on the periosteal surface as the distance to the closest point on the endosteal surface (Bayle et al., 2011; Bondioli et al., 2010; Mazurier et al., 2010; Puymerail et al., 2012; Volpato et al., 2011, 2012a, b).

Technical advances in the qualitative and quantitative structural characterization through functional imaging of the femoral diaphyseal organization have made possible the realization of morphometric maps suitable for synthetic visual appreciation and comparison (Bondioli et al., 2010; Puymerail, 2011; Puymerail et al., 2012). Accordingly, the A-D periosteal surface portion of CDV-Tour 1 has been mapped onto a cylinder, whose diameter corresponds to the maximum width of the original surface of the shaft, virtually unzipped along a predefined vertical line along the anterior aspect, and then unrolled into a plane. Thickness values have been standardized between 0 and 1 (methodological details in Bondioli et al., 2010). For the specific purposes of the present study, we directly compared the structural signature characterizing CDV-Tour 1 to the morphometric maps obtained for the 42–65% shaft portion of their respective biomechanical lengths for the Neanderthal femora La Ferrassie 1 (left) and Spy 8 and the Gravettian Cro-Magnon 1 (left). With this respect, we also provided comments about the μCT-based morphometric map already generated for the Chancelade 1 femur (Bayle et al., 2011, fig. 6; Bondioli et al., 2010, fig. 3; Puymerail and Macchiarelli, 2009). Finally, since it is possible to perform generalized additive models (GAM) of interpolation to obtain consensus maps by merging individual morphometric maps into a single dataset (Wood, 2006),

Table 1
The Late Pleistocene European Neanderthal (Neand.) and European Upper Paleolithic (EUPH) specimens used in the comparative analysis for %CA and the Ix/Iy ratio measured at 50% and 65% cross-sectional level of the femoral diaphysis. Original data selected from Trinkaus and Ruff (2012, tables A4 and A5) (see also Mussini et al., 2012).
Tableau 1
Les spécimens néandertaliens européens du Pléistocène supérieur (Neand.) et les spécimens du Paléolithique supérieur (EUPH) utilisés dans l'analyse comparative du %CA et du ratio Ix/Iy mesurés à 50 % et à 65 % de la diaphyse fémorale. Données extraites de Trinkaus et Ruff (2012, tableaux A4 et A5) (voir aussi Mussini et al., 2012).

Sample	Cross-sectional level	Specimens
Neand.	50% and 65%	Feldhofer 1, La Ferrassie 1 and 2, Fond-de-Forêt 1, Spy 2
	50% only	La Chapelle-aux-Saints 1, Palomas 96, La Quina 5, Rochers-de-Villeneuve 1, Saint-Césaire 1, Les Pradelles
	65% only	Krapina 257.32 and 257.33, Palomas 52 and 92, La Quina 38
EUPH	50% and 65%	Cro-Magnon 1, 4322 and 4324, Dolní Věstonice 3, 13, 14 and 16, Paviland 1, Pavlov 1, Sunghir 1 and 4, Willendorf 1
	50% only	Arene Candide 1, Barma Grande 2 (50%), Dolní Věstonice 35, Grotte des Enfants 4, Mladeč 27, Paglicci 25, Rochette 2, Veneri 1 and 2,
	65% only	Dolní Věstonice 41, Mladeč 28,

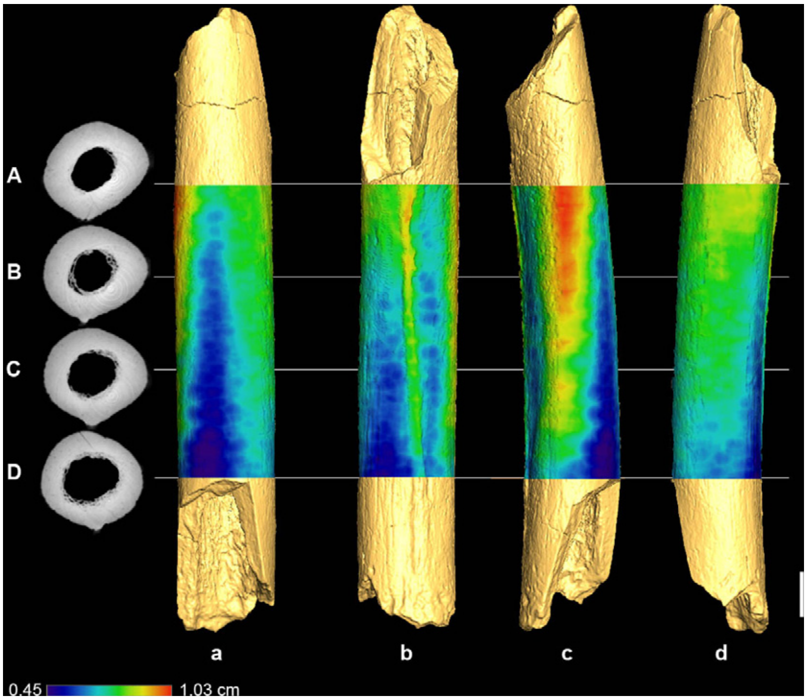

Fig. 3. CDV-Tour 1. Microtomographic-based reconstruction of the femoral shaft in anterior (a), posterior (b), medial (c), and lateral (d) views and topographic distribution of the cortical thickness for the portion approximately comprised between 42% (distal, level D) and 65% (proximal, level A) of its biomechanical length virtually rendered by means of a 10-stepped chromatic scale (dark blue is thin, red is thick). The cross-sectional outlines (posterior is below, medial is to the right) are provided at four levels (A to D), where C corresponds to the midshaft and B is intermediate between A and C. Scale bar: 1.5 cm.

Fig. 3. CDV-Tour 1. Reconstruction sur base microtomographique de la diaphyse fémorale en vues antérieure (a), postérieure (b), médiale (c) et latérale (d) et variations d'épaisseur de l'os cortical de la portion comprise entre 42 % (distal, niveau D) et 65 % (proximal, niveau A) de sa longueur biomécanique représentées selon une échelle chromatique (en bleu les valeurs les plus fines, en rouge les plus épaisses). Les sections transversales virtuelles (côté postérieur vers le bas, médial à gauche) représentent quatre niveaux (A à D), où C correspond à la mi-diaphyse et où B est équidistant de A et C. Échelle : 1,5 cm.

we also included in the comparative analysis the consensus map summarizing the whole variation expressed by our recent comparative sample (EH; Puymerail, 2011; Puymerail et al., 2012). To generate the maps, we used the pattern of relative thickness repartition (local morphometric properties) obtained by a custom routine developed in Scilab v.4.1.2 (The Scilab Consortium) with the support of the R v.2.11.1 (R Development Core Team, 2011) packages mcgv (Wood, 2004, 2006, 2008), spatstat (Baddeley, 2008), and gstat (Pebesma, 2004).

3. The CDV-Tour 1 human femoral shaft

3.1. Outer morphology

3.1.1. Preservation and taphonomy

While lacking its metaphyseal ends, the femoral diaphysis from Tour of La Chaise is from a fully mature individual because of its high cross-sectional diameter values, dense and smooth subperiosteal surface, and thick cortical bone (Fig. 2). Maximum length of the specimen is 204.7 mm; the full circumference is preserved for 95.8 mm (47%). The midshaft is estimated at 121 mm from the proximal fractured end.

All free fractured margins of CDV-Tour 1 are not fresh and show the same patina at the subperiosteal surface. The slightly spiral-shaped breaks, very likely originally produced on the fresh bone, show relatively clean edges at the distal end of the anterior aspect and, to a minor extent, at the proximal end (postero-lateral aspect). The oblique break opening along the postero-lateral aspect of the upper end is 58.7 mm long and 27.3 mm wide; on the anterior aspect, maximum length and breadth of the distal break are 50.5 mm and 33.31 mm, respectively.

The surface texture, lacking distinct indications of weathering (Behrensmeyer and Hook, 1992), does not suggest significant displacement of the specimen. However, some multidirectional cracks resulting from compression and locally affecting the entire cortical thickness to the endosteal surface are found towards the proximal end, notably on its postero-medial aspect, as well as on the anterior and lateral sides. Some superficial and faint longitudinal striae, discontinuously extended to about 35 mm, also occur along the distal part of the medial aspect and, around the midshaft, on the lateral side.

No evident cortical thickness loss is found along the shaft or at the upper margins. Only towards the very distal edge of the specimen, the bone shows moderate thinning posteriorly in association to the presence of multiple carnivore tooth-marks. Other isolated shallow punctuations are also present towards the proximal end of CDV-Tour 1, near the *linea aspera*. However, the nature of these latter features is not clear, due to their proximity to the local roughness of the *linea* and, mostly, to a broad and porous area occurring towards the proximal half of the medial/postero-medial aspect of the specimen. This diffuse porosity, which mimics a modest periosteal reaction, more likely relates to chemical dissolution, a phenomenon also observed on a number of the faunal remains from the same den cavity and common in similar contexts (Tournepiche et al., 1996). No macroscopic pathological lesions/changes or anthropic marks are present on this partial femoral diaphysis.

3.1.2. External morphology

The CDV-Tour 1 midshaft region shows a cross-sectional morphology from slightly transversally expanded to sub-circular. The antero-posterior and medio-lateral diameters at midshaft correspond to 31.6 mm and 33.7 mm, respectively (Table 2), with a pilastric index of 93.8. Based on its cross-sectional values, which fall near the upper range of the Neanderthal variation (Table 2), we estimate that this globally robust shaft is more likely from a male individual.

As a whole, CDV-Tour 1 is only modestly bowed anteroposteriorly (Fig. 2). Compared to the corresponding portions of the femora from the Feldhofer cave, La Ferrassie 1, and Spy II, it is also poorly bowed latero-medially. With this respect, it is somewhat intermediate between the almost straight (poor mesial convexity) partial femur BD 5 from La Chaise Bourgeois-Delaunay (Condemi, 2001) and the right femur Spy 8, from Spy II (Volpato et al., 2012b).

While in CDV-Tour 1 a pilaster is missing, the *linea aspera* is present, even if modestly salient and rather smooth along its preserved portion, with no adjacent flattening. Proximally, it extends to the base of the gluteal buttress. Similarly to the condition described for the RdV 1 Neanderthal shaft from the likely penecontemporaneous site of Rochers-de-Villeneuve (Beauval et al., 2005), as well as directly observed on La Ferrassie 1, its two lips coalesce into a single relief locally forming a smooth crest. The maximum breadth of this relief, encountered at medium-distal level, reaches 5.5 mm (vs. 4.0 mm measured at a distance of about 25 mm above the midshaft). Distally, the *linea* tends to disappear without really splitting into a medial and a lateral supracondylar components, both present but very poorly expressed in CDV-Tour 1. This condition slightly differs from that observed on La Ferrassie 1 and La Chapelle-aux-Saints 1, where the lateral supracondylar line is more salient and the medial one hardly discernible.

The portion above the midshaft, where the *linea* gently turns laterally, shows more wrinkled and slightly sharper margins. At about one third of the distance between the midshaft and the distal end, a small nutrient foramen is present within a shallow and narrow gutter leaning against the medial side of the *linea*. Just above, a 5–6 mm wide shallow groove corresponding to the imprint of the *adductor longus* slightly obliquely runs for 25–30 mm. Its position fits that of similar imprints present on Feldhofer 1, where it appears more vertically oriented, and in Spy 8, similarly oriented but slightly more medially displaced. A homologous feature is also present on La Ferrassie 1 (right: 5 × 35 mm) and La Chapelle-aux-Saints 1 (left: 3–4 × 45 mm). Another shallow imprint, likely left by the *adductor brevis*, is found on CDV-Tour 1 immediately medial to the *linea aspera*, about 25–30 mm above the midshaft. This feature is apparent on both femora from La Chapelle-aux-Saints 1, as well as on the right femur of La Ferrassie 1.

Antero-medially, the corpus shows an oval-shaped area of faint flattening around the midshaft. Similar to La Ferrassie 1 and La Chapelle-aux-Saints 1, a moderately developed buttress, running slightly obliquely proximo-distally, is also present medially.

3.2. Cross-sectional geometry and inner structure

The unstandardized values of the cross-sectional geometric properties of CDV-Tour 1 measured (in proximo-distal direction) at ∼65% (section A), ∼57.5% (B), at midshaft (C) and at ∼42% (D) of its estimated biomechanical length are shown in Table 2. The cross-sectional outlines of the specimen at the same sites are shown in Fig. 3.

Percent cortical area (%CA) decreases distally, but the lower value measured at 42% could reflect the moderate thinning observed on the posterior outer surface in association with some carnivore tooth-marks. At any rate, a slight periosteal expansion is observed along the ∼31 mm between section B and A. As revealed by the second moment of area about the antero-posterior axis (Iy) and the polar section modulus (Zp), a similar pattern is shown in medio-lateral bending rigidity and torsional strength, both increasing proximally in CDV-Tour 1 in association with a slight but constant trend towards a more oval shaft (the Imax/Imin ratio shifting from 1.17, at D, to 1.43, at A, the values at C and B are 1.22 and 1.29, respectively). At midshaft, the Zx/Zy ratio, which reflects antero-posterior to medio-lateral bending strength of the diaphysis, is 0.81. CDV-Tour 1 shows the typical Neanderthal condition of medio-lateral strengthening (Trinkaus and Ruff, 2012; Volpato et al., 2012b).

At midshaft, site-specific cortical bone thickness follows the decreasing pattern:

posterior (9.3 mm)
≥ lateral (9.1 mm)
> postero-lateral (8.1 mm)
> medial (7.7 mm)
≥ antero-medial (7.4 mm)
> anterior (6.9 mm)
≥ postero-medial (6.8 mm)
> antero-lateral (6.0 mm).

The average thickness at this level corresponding to 7.7 mm. At ∼65% cross-sectional level, where mean cortical bone is thicker (8.7 mm), site-specific distribution shows the following model:

lateral (10.4 mm)
> medial (9.2 mm)
≥ posterior (9.1 mm)
> antero-lateral (8.5 mm)
≥ antero-medial (8.3 mm)
≥ postero-medial (8.2 mm)
> postero-lateral (7.4 mm).

In a three-dimensional perspective, bone topographic variation in CDV-Tour 1 along the portion A-D is rendered in pseudo-colours in Fig. 3, distinctly for each anatomical

Table 2
Comparative values of the outer antero-posterior (a-p) and medio-lateral (m-l) diameters of the femoral diaphysis and unstandardized cross-sectional geometric properties measured at four sections (A to D; Fig. 3 for localization) in CDV-Tour 1 and (when available) in three samples representing Late Pleistocene European Neanderthals (Neand.; $n = 17$), European Upper Paleolithic (EUPH; $n = 44$) and extant humans (EH; $n = 20$). In italics, the standard deviation. Neand. and EUPH data from Trinkaus and Ruff (2012, table A13) (see also Mussini et al., 2012). See the text (Methods of analysis) for the meaning of the variables.
Tableau 2
Mesures comparatives des diamètres externes antéropostérieur (a-p) et médio-latéral (m-l) de la diaphyse fémorale et valeurs brutes des paramètres de section mesurés au niveau des quatre sections (A à D ; Fig. 3 pour la localisation) pour CDV-Tour 1 et (si disponible) pour trois échantillons de Néandertaliens européens du Pléistocène supérieur (Neand., $n = 17$), d'Européens du Paléolithique supérieur (EUPH, $n = 44$) et d'humains modernes (EH ; $n = 20$). Les valeurs d'écart-type sont en italique. Les valeurs des Neand. et EUPH sont extraites de Trinkaus et Ruff (2012, tableau A13) (voir aussi Mussini et al., 2012). Voir le texte (Méthodes) pour la signification des variables.

Section	Spec./sample	a-p	m-l	TA	CA	%CA	Ix	Iy	Ix/Iy	*J*	Zx	Zy	Zx/Zy	Zp	Imax	Imin
~65% (A)	CDV-Tour 1	31.6	33.7	745	600	80.5	39 294	48 004	0.81	87 298	2486	2846	0.87	5344	51 387	35 883
	Neand.			603	504	84.0	26 193	32 994	0.84	59 188					34 981	24 206
				108	*84*	*6.4*	*8087*	*11 779*	*0.22*	*18 730*					*11 483*	*8037*
	EUPH			596	481	80.6	29 520	27 481	1.01	57 002					32 590	24 411
				110	*100*	*5.3*	*12 579*	*9781*	*0.23*	*21 331*					*12 477*	*9133*
	MH	28.4	28.2	594	461	77.9	27 798	28 026	1.01	55 824	1922	1945	0.99	3871	30 419	25 405
		2.3	*2.6*	*99*	*77*	*7.5*	*8686*	*9187*	*0.14*	*17 327*	*453*	*476*	*0.08*	*910*	*9192*	*8311*
~57.5% (B)	CDV-Tour 1	31.2	33.5	741	563	76.0	36 847	47 239	0.78	84 087	2364	2818	0.84	5199	47 354	36 706
	MH	29.1	27.6	578	445	77.0	28 242	25 569	1.11	53 812	1907	1818	1.05	3730	30 061	23 755
		2.4	*2.4*	*93*	*73*	*5.0*	*8925*	*8253*	*0.12*	*16 952*	*453*	*432*	*0.06*	*879*	*8811*	*8279*
50% (C)	CDV-Tour 1	31.2	33.3	744	566	76.2	37 844	46 344	0.81	84 188	2414	2799	0.86	5224	46 327	37 839
	Neand.	29.2	29.4	656	525	79.6	32 755	34 934	0.94	67 613	2052	2192	0.94	3924	38 882	28 807
		2.2	*1.9*	*85*	*87*	*5.3*	*8420*	*8406*	*0.14*	*15 917*	*426*	*449*	*0.13*	*748*	*10 123*	*6540*
	EUPH	32.1	27.6	607	456	74.9	35 513	24 358	1.45	59 872	1949	1659	1.17	3377	36 503	23 365
		4.2	*2.4*	*101*	*93*	*6.7*	*14 126*	*8171*	*0.23*	*21 748*	*567*	*397*	*0.14*	*878*	*14 347*	*7672*
	MH	29.7	27.6	581	428	73.8	29 150	24 713	1.18	53 863	1928	1762	1.09	3699	30 428	23 437
		2.5	*2.5*	*91*	*67*	*5.5*	*8896*	*7660*	*0.13*	*16 283*	*442*	*395*	*0.07*	*829*	*8712*	*7727*
~42% (D)	CDV-Tour 1	31.5	32.6	760	510	67.2	39 011	43 618	0.89	82 630	2474	2672	0.92	5150	44 702	37 969
	MH	29.6	28.2	599	394	65.9	28 249	25 466	1.12	53 715	1882	1762	1.06	3655	29 156	24 540
		2.2	*2.6*	*92*	*60*	*5.6*	*7960*	*7854*	*0.13*	*15 541*	*416*	*395*	*0.06*	*808*	*8002*	*7732*

view. Cortical thickness varies from a minimum of 4.5 mm, measured along the antero-medial aspect of the distal portion towards section D, up to 10.3 mm, along the proximal medial portion of the shaft (portion A-B), the median value corresponding to 7.6 mm. While the area of distinct reinforcement characterizing the medial aspect of CDV-Tour 1 is relatively wide and extended vertically (Fig. 3c), the posterior thickening is confined to a narrow and short strip along the *linea aspera* (Fig. 3b).

As a whole, cortical bone within the shaft portion A-C, notably the trait A-B, is thicker than within the segment C-D. More specifically, relative cortical bone volume (cortical bone volume on total volume percent ratio) increases disto-proximally from 68.6%, in C-D, through 73.9%, in B-C, up to 78.3%, in A-B, a trend paralleled by a proportional reduction of the medullary cavity (from 31.4% to 21.7%).

4. Discussion

Although the femoral shaft portion CDV-Tour 1 represents only approximately 50% of its estimated original biomechanical length (204.7 mm of ~407 mm), it preserves enough morphological and structural information to allow its characterization and reliable attribution to an adult Neanderthal individual, more likely a male. Besides its general outer morphology (notably, the absence of a pilaster and its general robusticity), this is suggested by the comparison of the antero-posterior and medio-lateral diameters at midshaft (Table 2, Fig. 4a) and the pilastric index (Fig. 4b) of CDV-Tour 1 to figures of the Late Pleistocene European Neanderthals (Mussini et al., 2012; Trinkaus and Ruff, 2012), and European Upper Paleolithic (Trinkaus and Ruff, 2012) and recent humans (Puymerail, 2011; Puymerail et al., 2012). However, in this respect, the range of variation displayed by the European Upper Paleolithic femoral sample is noteworthy: it mainly reflects a positive allometric effect in which a-p rigidity increases faster than m-l rigidity (slopes greater than 1.0; Trinkaus and Ruff, 2012). For these parameters, CDV-Tour 1's closest fits are the femora known as La Ferrassie 1 and 2, La Quina 5, and Saint-Césaire 1 (in Trinkaus and Ruff, 2012). Conversely, it shows no overlap for the pilastric index exists with the reference sample used in the present study, nor for the outer diameters, which were measured at 65% of the estimated biomechanical length, where CDV-Tour 1 largely exceeds our extant figures (Table 2).

The strong similarity of CDV-Tour 1 to the Neanderthal estimates and its difference with respect to both Upper Paleolithic and recent samples are revealed by the cross-sectional geometric (CSG) parameters summarized in Table 2.

In particular, for the anteroposterior (Ix) and medio-lateral (Iy) second moments of area (Fig. 5a), CDV-Tour 1 approximates the lowest Neanderthal values at both 50% and 65% cross-sections (greater resistance to medio-lateral bending charges), and clearly is set apart from the fossil and extant modern human estimates, systematically showing higher ratios (Trinkaus and Ruff, 1989, 1999, 2012; Trinkaus et al., 1998; Volpato et al., 2012b). At 50%, the difference for the Ix/Iy ratio between CDV-Tour 1 and the Neanderthal median equals 0.11, whereas those from the

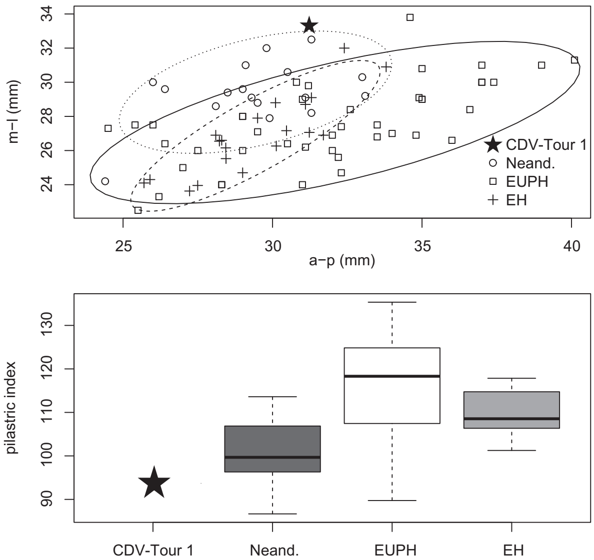

Fig. 4. Comparative values of the antero-posterior (a-p) vs. medio-lateral (m-d) diameters at midshaft (a) and of the pilastric index (b) in CDV-Tour 1 (black star) and in three samples representing Late Pleistocene European Neanderthals (Neand.; $n = 17$; dotted line in a), European Upper Paleolithic (EUPH; $n = 44$; continuous line in a) and extant humans (EH; $n = 20$; dashed line in a). Neand. and EUPH data calculated from Trinkaus and Ruff (2012, table A13) (see also Mussini et al., 2012). Besides the specimens listed in Table 1, this comparative analysis has also considered: Santa Croce 1 and Stadelhöhle 1, among the Neand., and Barma Grande 6, Caviglione 1, and Předmostí 3, 4, 9, 10 and 14, for the EUPH samples.

Fig. 4. Mesures comparatives du diamètre antéro-postérieur (a-p) vs. le diamètre médio-latéral (m-l) à mi-diaphyse (a) et de l'indice pilastrique (b) pour CDV-Tour 1 (étoile noire) et pour trois échantillons de Néandertaliens européens du Pléistocène supérieur (Neand., $n = 17$; ligne pointillée en a), d'Européens du Paléolithique supérieur (EUPH, $n = 44$; ligne continue en a) et d'humains modernes (EH ; $n = 20$; ligne discontinue en a). Les valeurs des Neand. et EUPH sont extraites de Trinkaus et Ruff (2012, tableau A13) (voir aussi Mussini et al., 2012). En plus des spécimens listés dans le Tableau 1, cette analyse comparative considère également : Santa Croce 1 et Stadelhöhle 1, parmi les Neand., et Barma Grande 6, Caviglione 1, et Předmostí 3, 4, 9, 10 et 14 pour les EUPH.

Upper Paleolithic and the extant samples correspond to 0.65 and 0.35, respectively. A similar pattern is found also at 65%, the differences in this case corresponding to 0.01, 0.24, and 0.17, respectively.

Following a recent reassessment of femoral diaphyseal properties through Pleistocene *Homo*, it is likely that changes in cross-sectional shape recorded in the middle portion of the diaphysis during the Late Pleistocene, expressed by a relative antero-posterior vs. medio-lateral reinforcement, reinforcement, more closely reflect shifts in pelvic shape and proximal femoral proportions rather than differential ranging (Trinkaus and Ruff, 2012; contra Beauval et al., 2005; Trinkaus et al., 1998).

Compared to other CSG parameters, the same time-related trend analysis (Trinkaus and Ruff, 2012) suggests a modest informative value in terms of biomechanics provided by the relative cortical area (%CA), an indicator that shows significant intra- and inter-group variation and no evident evolutionary pattern from Middle to Late Pleistocene humans (Trinkaus and Ruff, 2012; for *H. erectus*, see

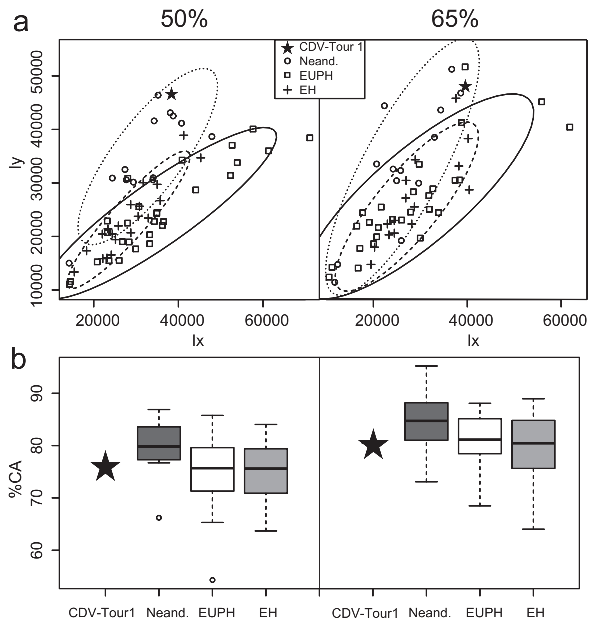

Fig. 5. Comparative values of the second moments of area about the m-l (Ix) vs. the a-p (Iy) axes (a) and percent cortical area (%CA, b) measured at 50% (midshaft) and 65% (proximal) of the estimated biomechanical length in CDV-Tour 1 (black star) and in three samples representing Late Pleistocene European Neanderthals (Neand.; n 50% = 13, n 65% = 13; dotted line in a), European Upper Paleolithic (EUPH; n 50% = 28, n 65% = 22; continuous line in a) and extant humans (EH; n = 20; dashed line in a). Neand. and EUPH data calculated from Trinkaus and Ruff (2012, tables A4 and A5) (see also Mussini et al., 2012). See Table 1 for the list of the specimens included in the Neand. and EUPH comparative samples.

Fig. 5. Mesures comparatives du second moment de l'aire selon l'axe m-l (Ix) vs. l'axe a-p (Iy) (a) et du pourcentage d'aire corticale (%CA, b) mesurée à 50 % (mi-diaphyse) et 65 % (proximale) de la longueur biomécanique pour CDV-Tour 1 (étoile noire) et pour trois échantillons de Néandertaliens européens du Pléistocène supérieur (Neand. ; n 50 % = 13, n 65 % = 13 ; ligne pointillée en a), d'Européens du Paléolithique supérieur (EUPH ; n 50 % = 28, n 65 % = 22 ; ligne continue en a) et d'humains modernes (EH ; n = 20 ; ligne discontinue en a). Les valeurs des Neand. et EUPH sont extraites de Trinkaus et Ruff (2012, tableaux A4 et A5) (voir aussi Mussini et al., 2012). Voir Tableau 1 pour la liste des spécimens inclus dans les échantillons comparatifs de Neand. et EUPH.

also Puymerail et al., 2012). The cortical area provides a measure of resistance to axial loads (Ruff et al., 1993), and the combination of cortical and total area reflects the differential subperiosteal deposition and endosteal resorption of bone, principally during development (Ruff and Hayes, 1983; Ruff et al., 1994). Accordingly, as also suggested by the %CA comparative plots at 50% and 65% cross-sectional level shown in Fig. 5b (Table 2), percent cortical area should mostly represent a measure of differential developmental and aging processes, not a subtle mechanical indicator (Trinkaus and Ruff, 2012).

For the shaft portion 50–65%, we compared the amount of cortical bone volume in CDV-Tour 1 (34.8 cm^3, i.e., 76% of the total volume) to the estimates obtained for the Neanderthal femora known as La Ferrassie 1 (left: 38.5 cm^3 = 81%) and Spy 8 (right: 27.4 cm^3 = 79%; Volpato et al., 2012b), to the Upper Paleolithic specimens Cro-Magnon 1 (left: 43.3 cm^3 = 85%) and Chancelade (right: 30.7 cm^3 = 84%), and to the figures from our reference sample (average: 28.0 cm^3 ± 5.5 = 77% ± 5.7). However, this approach did not reveal any possible Neanderthal vs. modern (fossil and/or extant) pattern.

In order to tentatively identify at specific cross-sectional levels a recurrent model in bone topographic distribution characterizing the Neanderthals and/or the morphologically modern humans considered in this study, we also used our (μ)CT record to measure linear cortical thickness at eight sites along the 50% and 65% sections in CDV-Tour 1, La Ferrassie 1, Rochers-de-Villeneuve 1 (50% only), Spy 8, Cro-Magnon 1, and Chancelade (Bondioli et al., 2010; Puymerail, 2011; Puymerail and Macchiarelli, 2009), and in the recent human sample. The results are summarized in Table 3. At midshaft, cortical bone is thicker posteriorly in virtually all investigated cases, including among the recent humans, but the sequences of relative bone distribution at the remaining sites are quite variable among the fossil specimens as well as within the comparative reference sample (model based on the site-specific average values), with no apparent recurrent model. Interestingly, while measured at only six sites (i.e., excluding the posterior and the anterior cortices), a decreasing pattern in cortical bone thickness at midshaft close to that displayed by CDV-Tour 1 (Table 3) has been established for the left femur of the 2.5–3 years old Neanderthal child from Roc de Marsal (lateral > postero-lateral > medial = postero-medial > antero-lateral > antero-medial; Macchiarelli et al., 2007, fig. 4). However, it has been noted that in this case also, the structural model shown by this Neanderthal immature does not clearly differ from the condition found in samples of recent human femora from individuals < 6 years (Cowgill, 2010; Macchiarelli et al., 2007; Volpato et al., 2007).

In our series, the average cortex measured at ∼65% of the biomechanical length is universally thicker than at midshaft (Table 3), the highest value being displayed by the left femur Cro-Magnon 1 (10.0 mm), the same specimen that at midshaft shows the thinnest average cortex (6.7 mm) among the six fossil femora considered in the present study. In terms of relative bone distribution and decreasing patterns, also at this cross-sectional level no distinction is possible between Neanderthal and modern figures.

As a whole, when combined, these specific volumetric and punctual linear measurements support the suggestion that variation in the relative distribution of cortical bone within the femoral shaft is primarily affected by age- (and likely sex-) related differential endosteal resorption and subperiosteal deposition dynamics (Gosman et al., 2011; Macchiarelli, 1988; Ruff and Hayes, 1983; Ruff et al., 1994, 2006a, b; Trinkaus and Ruff, 2012; Trinkaus et al., 1994). However, the extremely limited number of fossil specimens examined so far does not allow any conclusive statement on this matter, and only extensive future research can test the present findings.

Preliminary functional imaging of the inner organization of the femoral diaphysis through the planar representation of its structural pattern has revealed some differences in local morphometric properties between Neanderthals and fossil and extant humans (Bondioli et al., 2010; Puymerail, 2011; Puymerail and Macchiarelli, 2009).

Table 3
Comparative patterns of linear variation (in decreasing order) of the cortical bone thickness measured at eight sites (1 to 8) of the 50% and 65% cross-sections of the femoral diaphysis in CDV-Tour 1, in other Neanderthal (Neand.) specimens, in European Upper Paleolithic (EUPH) specimens, and in a sample of extant humans (EH; $n = 20$).

Tableau 3
Patrons comparatifs de variation des mesures linéaires d'épaisseur de l'os cortical (par ordre décroissant) relevées en huit points (1 à 8) à 50 % et à 65 % de la diaphyse fémorale pour CDV-Tour 1, pour les spécimens néandertaliens (Neand.) et du Paléolithique supérieur (EUPH) et pour l'échantillon humain moderne (EH ; $n = 20$).

Sample/specimens	av. thick.(mm)	Pattern at 50%
Neand.		
CDV-Tour 1 (l)	7.7	1 ≥ 3 > 2 > 7 ≥ 6 > 5 ≥ 8 > 4
La Ferrassie 1 (l)	7.6	1 > 8 > 4 ≥ 3 > 7 ≥ 2 ≥ 5 > 6
Spy 8 (r)	7.4	1 ≥ 8 > 7 > 4 ≥ 5 ≥ 6 > 2 ≥ 3
RdV 1 (l)	7.6	1 > 8 > 2 > 6 ≥ 5 ≥ 4 ≥ 7 ≥ 3
EUPH		
Cro-Magnon 1 (l)	6.7	1 > 7 ≥ 3 ≥ 4 ≥ 6 > 2 ≥ 5 > 8
Chancelade (r)	7.4	1 > 7 ≥ 3 = 8 ≥ 6 ≥ 4 > 5 ≥ 2
EH[a]	6.5 ± 1.7	1 > 3 ≥ 7 ≥ 4 > 8 > 6 > 2 > 5
		Pattern at ∼65%
Neand.		
CDV-Tour 1 (l)	8.7	3 > 7 ≥ 1 > 4 ≥ 6 ≥ 5 = 8 > 2
La Ferrassie 1 (l)	8.5	3 ≥ 2 > 1 = 6 ≥ 7 ≥ 8 > 4 > 5
Spy 8 (r)	7.8	1 = 3 > 2 ≥ 8 ≥ 4 = 6 ≥ 5 ≥ 7
EUPH		
Cro-Magnon 1 (l)	10.0	1 > 3 = 8 ≥ 2 ≥ 7 > 5 > 4 > 6
Chancelade (r)	7.8	4 > 3 ≥ 8 ≥ 1 > 5 > 2 = 6 ≥ 7
EH[a]	7.3 ± 1.5	1 = 3 > 7 ≥ 8 ≥ 4 ≥ 2 > 6 > 5

1: posterior; 2: postero-lateral; 3: lateral; 4: antero-lateral; 5: anterior; 6: antero-medial; 7: medial; 8: postero-medial; l: left; r: right.
[a] Average values.

In order to ascertain its structural signature, in Fig. 6, we compared the standardized morphometric map of cortical bone thickness variation in CDV-Tour 1 (portion 42–65%) to the maps obtained for La Ferrassie 1, Spy 8 (Volpato et al., 2012b) and Cro-Magnon 1 (Puymerail, 2011; Puymerail and Macchiarelli, 2009), which were generated through the virtually unzipped and then unrolled projection of the same portion. The variation expressed by our recent reference sample is also summarized into a single consensus map (EH; Puymerail et al., 2012). In all cases, the plots

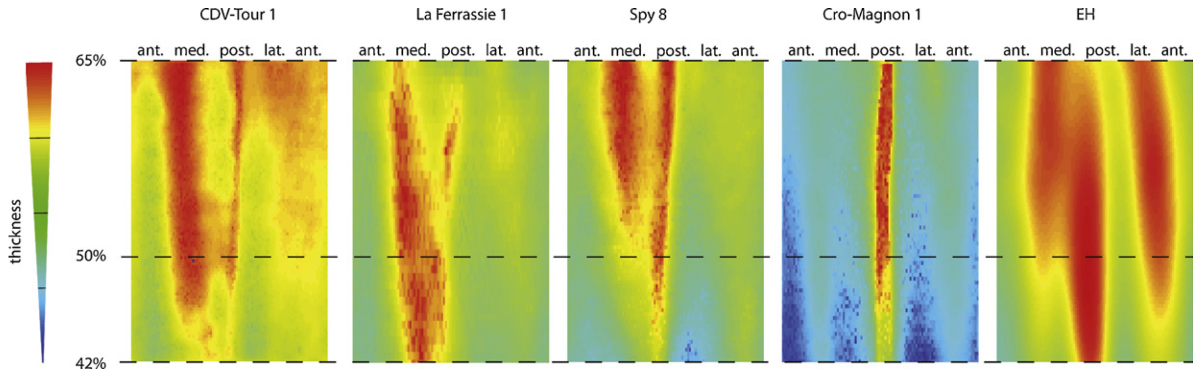

Fig. 6. Standardized morphometric map of cortical bone thickness variation in CDV-Tour 1 (∼42–65% portion) compared to the CT-based maps obtained for the same portion in the Neanderthal femora La Ferrassie 1 (left) and Spy 8 (right), the Upper Paleolithic specimen Cro-Magnon 1 (left), and to the consensus map modelling the extant human adult condition (EH; $n = 20$). The original femora have been virtually unzipped vertically along the middle of their anterior aspect and then unrolled. Independently from their original side, all specimens are virtually rendered as left; imaging perspective is systematically from the inner to the outer surface (medial is to the left). Each map is set within a grid of 100 columns (x) and 200 rows (y). ant.: anterior; lat.: lateral; med.: medial; post.: posterior. Thickness rendered by a chromatic scale increasing from dark blue (0) to red (1).

Fig. 6. Cartographie des variations topographiques standardisées de l'épaisseur de l'os cortical pour CDV-Tour 1 (portion ∼42–65 %) comparée aux cartographies obtenues à partir de relevés CT pour la même portion pour les fémurs néandertaliens de La Ferrassie 1 (gauche) et Spy 8 (droit), pour le spécimen du Paléolithique supérieur Cro-Magnon 1 (gauche) et pour le consensus de l'échantillon humain moderne (EH ; $n = 20$). Chaque fémur a été virtuellement découpé verticalement le long de la face antérieure puis déroulé. Indépendamment de leur latéralité, tous les spécimens sont virtuellement représentés comme gauche ; le point de vue est systématiquement de l'intérieur vers l'extérieur (côté médial à gauche). Chaque cartographie est représentée à l'aide d'une grille de 100 colonnes (x) par 200 lignes (y). ant. : antérieur ; lat. : latéral ; med. : médial ; post. : postérieur. Épaisseur représentée selon une échelle chromatique croissante variant du bleu foncé (0) au rouge (1).

represent the relative thickness of the cortex at different levels of the shaft.

The structural signature of CDV-Tour 1, displaying a slightly oblique distinct reinforcement concentrated along the medial aspect of the mid-proximal shaft portion associated with a narrow bony thickening along the *linea aspera*, closely resembles those of the two Neanderthal specimens considered in the present analysis (Volpato et al., 2012b). This pattern, which expresses the Neanderthal condition of medio-lateral strengthening of the proximal femoral shaft (Trinkaus and Ruff, 2012), contrasts with that found in Cro-Magnon 1, where the thickest values are concentrated along the posterior aspect in relation to a fully developed pilaster, and both medial and lateral aspects show only moderately thick bone. It is noteworthy that a similar signature to that of Cro-Magnon 1, also expressing a greater resistance to axial bending and torsional loads, characterizes the femoral diaphysis of the Magdalenian adult skeleton from Chancelade (Bondioli et al., 2010, fig. 3; Puymerail and Macchiarelli, 2009). In contrast, the structural condition provided by the consensus map of the recent sample features three extended major reinforcements, respectively corresponding to the posterior pilaster (where, as in Cro-Magnon 1 and Chancelade, the thickest bone is found around the midshaft), to the proximal medial and the proximal lateral aspects of the shaft (Puymerail et al., 2012). However, whereas the first two features are systematically found in recent human femora, the degree of expression of the lateral thickening is quite variable. Within this comparative context, the Gravettian Cro-Magnon 1 displays a distinct signature from both Neanderthals and recent humans.

5. Concluding remarks

The accidental discovery of the CDV-Tour 1 partial human femoral shaft and associated faunal remains during speleological exploration of "grotte de la Tour", one of the numerous cavities forming the site complex of La Chaise-de-Vouthon, in Charente (Debénath, 2006), confirms the fossiliferous richness of the Middle to Late Pleistocene sedimentary deposits partially filling the karstic network opening along the Tardoire river, and points to their value for future prehistoric and paleoanthropological investigation. Similar to other contexts reported from the same region (e.g., Beauval et al., 2005; El Albani et al., 2011; Tournepiche et al., 1996; for a review, see Discamps, 2011), the currently available record supports the preliminary interpretation of a carnivore den for this cavity, and the mammal assemblage recovered so far is compatible with a chronological attribution to the MIS 3. The multiple toothmarks left on the femoral shaft confirm a close interaction in the region between human groups and large carnivores, especially in the use of natural shelters (Beauval et al., 2005).

Despite the incompleteness of the specimen, our analytical and comparative analysis of CDV-Tour 1, integrating information from classical morphology, cross-sectional geometric properties, and the microtomographic-based 2-3D quantification of its inner structural organization, including the functional signature revealed by its morphometric map of cortical bone topographic variation, convincingly shows that this partial femoral shaft is from an adult Neanderthal individual. Of course, only future research at the "grotte de la Tour" under controlled conditions will confirm the reliability of our assessment concerning its chronological and taphonomic context and allow the identification of additional human remains possibly still preserved in this promising cavity.

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