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Introduction

1 Compared to modern human femurs, the external morphology of the adult Neanderthal femur displays a subcircular periosteal contour at midshaft, the variable development of a medial buttress, a relatively thin linea aspera and the absence of a pilaster (Heim 1976, 1982; Trinkaus 1976; Trinkaus and Ruff 1999; Condemi 2001; Beauval et al. 2005).

The Neanderthal femur is associated with a comparable degree of sexual dimorphism to that found in recent human populations (Trinkaus 1980; Walker et al. 2011), but also presents generalized shaft robustness. This aspect is compatible with greater biomechanical loads and a higher resistance to medio lateral strain, as well as greater axial resistance to torsional stress. Globally, these characteristics represent adaptations linked to the specific pelvic morphology and body proportions of Neanderthals (Weaver 2003, 2009; Walker et al. 2011; Trinkaus and Ruff 2012). The morphometric characteristics of the external part of the Neanderthal femoral shaft are well documented today (cf. overview by Mussini et al. 2012). However, the organization of the internal structure remains to be explored in functional terms, particularly for the cortical bone. The analysis of the topographic variability of the cortical shaft thicknesses of Neanderthal femurs from different periods and geographical zones can thus provide pertinent biomechanical information (Churchill 1998; Trinkaus et al. 1998; Trinkaus and Ruff 1999; Mussini et al. 2012; Puymerail et al. 2012a).

2 In association with the genetic models pointing to the existence of several sub-groups within the continental European Neanderthal population (Fabre et al. 2009; Hodgson, Bergey, Disotell 2010; Degioanni, Fabre, Condemi 2011; Dalen et al. 2012), diachronic variations in the morphology of the skeleton have also been shown throughout the Upper Pleistocene (rev. in Degioanni, Fabre, Condemi 2011; Di Vicenzo, Churchill, Manzi 2012; Stewart and Stringer 2012). In this context, as well as their external morphology, we virtually extracted, analyzed and compared the internal characteristics of two Neanderthal femoral shafts from the same site, specimens BD 5 and CDV-Tour 1 from La Chaise-de-Vouthon, in Charente, chronologically separated by about 80,000 years (Condemi 2001; Puymerail et al. 2012a). Even though the two specimens are incomplete (particularly the specimen from Tour Cave) and are both from specimens of different sex, through the descriptions of new parameters describing the functional variations in the organization of the cortical bone, this preliminary study aims to identify the existence of possible endostructural differences between femoral shafts from Neanderthals ranging from isotopic stage (MIS) 5 to MIS 3.

Material and methods

3 The site of La Chaise-de-Vouthon is located on the left bank of the Tardoire, an affluent of the Charente, on a platform of Bathonian/Bajocian limestone characterized by intense erosion resulting in the formation of a series of rock shelters and the opening of several karstic cavities. The galleries extend over several tens of metres and open out through three main porches, called shelters Duport, Bourgeois- Delaunay and Suard (Debénath 1974, 1977, 2006).

4 The femoral shaft BD 5 comes from the Bourgeois-Delaunay (BD) shelter. This rock shelter was excavated by the abbots Bourgeois and Delaunay in 1865, but it is only towards the end of the 1930s that P. David began systematic excavations that continued until 1963. At J. Piveteau's request, A. Debénath then took over research at the site between 1967 and 1983 (Debénath 2006). Broadly speaking, this site spans the period from the Riss III to the Würm III (Debénath 1974, 1977, 2006; Schwarcz and Debénath 1979; Blackwell et al.1983, 1992; Armand 1998). Direct speleothem dating by 230Th/234U yielded ages between 127 and 116 ka (Couchoud 2006; Vieillevigne et al. 2008), which corresponds to MIS 5e. The specimen BD 5, extracted from a stalagmitic block

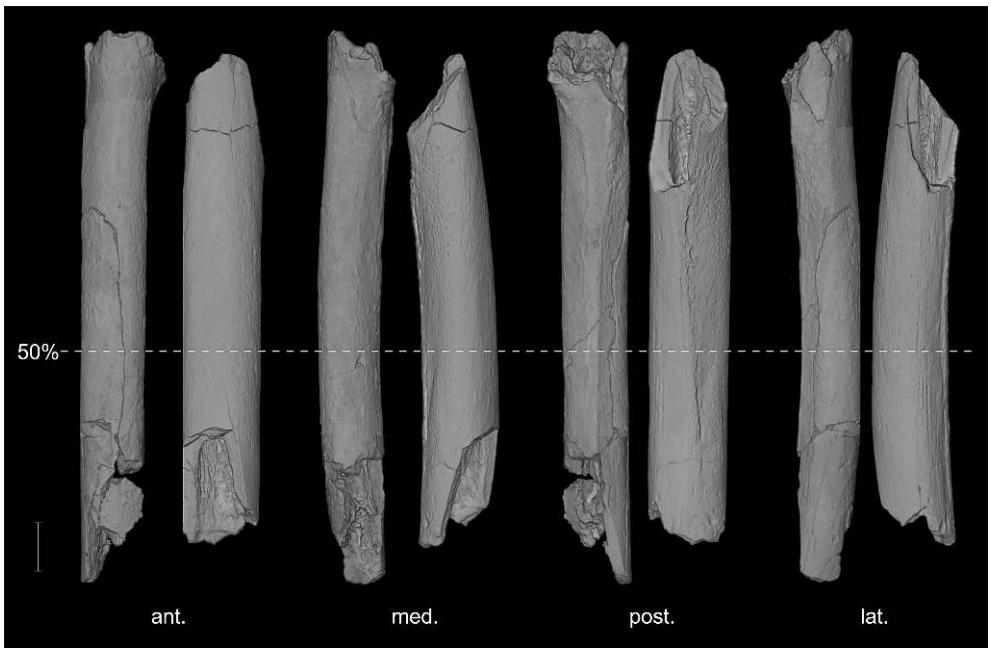
containing other cranial pieces in 1968, represents one of the 23 Neanderthal remains from adults and young individuals, comprising mainly isolated teeth, discovered during the course of the most recent excavations over a surface of about 4 m² (rev. in Condemi 2001; Debénath 2006; Macchiarelli et al. 2006). The specimen represents a right femoral portion of a young adult, which appears to be a female, given the slight robustness, with a preserved length of 239.5 mm, from the base of the lesser trochanter (trochanter minor) until below midshaft (Condemi 2001).

5 The specimen CDV-Tour 1 was discovered during potholing exploration in Tour cave, the entrance of which is located about 130 m west of the Suard rock shelter. The discovery context is compatible with a hyena den deposit and compared to the regional record from other systematically excavated sites, the associated assemblage of mammal remains suggests a chronological attribution to MIS 3 (Puymerail et al. 2012a). This fossil corresponds to a left femoral shaft portion from what appears to be an adult male, given the robustness of the bone, with a preserved length of 204.7 mm and a total preserved contour of 95.8 mm (Puymerail et al. 2012a).

6 The external morphology of these two fossils, curated with the collections of the Angoulême Museum, is presented in figure 1.

7 Microtomography (CT) was carried out on BD 5 and CDV-Tour 1 in 2008 at the Centre of Microtomography at the University of Poitiers. In order to provide details for the whole specimens, three acquisition stages were necessary for BD 5 and two for CDV-Tour 1.

Figure 1 - Microtomographic-based virtual reconstruction of the specimens BD 5 (to the left) and CDV-Tour 1 (right) in anterior, medial, posterior and lateral views. The midshaft level is indicated. Scale bar: 2 cm.



8 The acquisitions were carried out with X8050-16 multi-scale Viscom A G equipment (camera 1.004 × 1.004 of 12 bits with a pixel size of 147 m), with 1,200 projections (every 0.30°) and 32 integrations/projection. For BD 5, an energy of 100 kV and an intensity of 580 µA were applied, while the same parameters correspond to 120 kV and 560 A for CDV-Tour 1. The final volume of images was reconstructed with the software DigiCT v.

1.15 (DIGISENS), at an isometric voxel size of 86.3 µm for BD 5 and 107.8 m for CDV-Tour 1.

9 Due to the good state of preservation of the periosteal and endosteal contours of the shafts, both associated with the absence of sedimentary infilling of the medullar cavity, it was possible to apply the global thresholding method (Spoor, Zonneveld, Macho 1993), by measuring the average of the bone/air interface in about twenty sections out of the series of images (Fajardo, Ryan, Kapelman 2002; Coleman and Colbert 2007). The semi-automatic segmentation with manual corrections was conducted with the Avizo v. 7.0.0 (Visualization Sciences Group Inc.) and ImageJ v.1.46a (Rasband 2010). The result of the segmentation is a triangular meshing of the periosteal and endosteal surfaces made up of 3D coordinates linked by lines that generate triangular sides after smoothing. The smoothing (marching cube) was conducted with the program Avizo v. 7.0.0 (unconstrained smoothing option), without influencing the sensitivity of the analyses and results.

10 The specimens were anatomically oriented based on the position of the linea aspera, which was significant in both specimens. We then situated the section at about 50 %, based on the morphology and the course of this line examined in medial and lateral projection. Compared to modern humans, the exact location of the midshaft is generally less clear in Neanderthal femurs with a sub-circular contour and with no pilaster. On the other hand, this shaft region only presents slight morpho-structural changes over several centimetres, rendering the errors of localization and the associated analyses marginal (Beauval et al. 2005; Sládek et al. 2010; Puymerail et al. 2012a, b; Trinkaus and Ruff 2012).

11 In order to gauge the biomechanical length of BD 5, we identified the position of the section on the CT record at 1 cm from the base of the lesser trochanter, which by definition corresponds to 80 % of the biomechanical length (Ruff et al. 1999). Then, by taking into account the position of the midshaft, we determined the distal section, the contour of which is preserved at about 37 % of the biomechanical length. The protocol applied for measuring the specimen CDV-Tour 1, which positioned the proximal section at 65 % and the distal section at ca. 42 % of the biomechanical length, was recently described in detail in Puymerail et al. (2012a).

12 Using a routine developed in terminology R v.2.11.1 (R Development Core Team 2011), the following geometry cross-section parameters were measured/calculated every 1 % along the two Neanderthal shafts: total area (TA, in mm2); cortical area (CA, in mm2); percentage of cortical area (% CA); second moment of the area according to the medio-lateral axes (m-l) and antero-posterior axes (a-p) (Ix, Iy, in mm4); second polar area moment (J, n mm4); second moment of maximum and minimum area (Imax, Imin, in mm4) (for methodological details, see Ruff 2008).

13 In order to place the two specimens from La Chaise in a context of chrono-geographical variations, in addition to the shaft diameters a-p and m-l (M6, M7, M9, M10; Martin and Saller 1956-1962) and the pilastric (at 50 %) and platymeric indexes (at 80 %), we compared the geometric properties of their sections measured at 50 % and at 65 % (for both specimens) and at 80 % (only for BD5) to the available fossil record for 22 adult Neanderthal femurs from central-western Europe with no sexual distinction ranging from MIS 5 to MIS 3 (tab. 1). Most of these comparative data are from a recently published overview by Trinkaus and Ruff (2012) and from the study of the French Pradelles specimen (Mussini et al. 2012). Modern humans are represented here by a

wide sample of 102 femurs measured from a medical tomographic record (CT) with a resolution varying between 350 and 976 m (cf. Puymerail 2011; Puymerail et al. 2012c). This sample is made up of adults of both sexes from 19th century French osteological collections, from the Roman archaeological site of Velia (Italy) and from the PACS system of l'Assistance Publique des Hôpitaux de Marseille.

14 From a functional perspective, methodological advances in the domain of 3D imagery now allow for the virtual analysis of the external shaft surface and its projection using morphometric mapping representing the topographic variations of the thickness of the cortical tissue across and along the observed bone portion (Bondioli et al. 2010; Puymerail et al. 2012a, b). First of all, the thickness is defined for each point of the periosteal surface as the distance in relation to the nearest point on the internal surface (Mazurier, Nakatsukasa, Macchiarelli 2010; Bayle et al. 2011; Volpato et al. 2011, 2012, 2013; Puymerail et al. 2012a, b). The mapping of the thicknesses is then projected onto the surface of a cylinder, the width of which corresponds to the maximum diameter of the shaft, which is virtually unrolled along an axis passing through the centre of the anterior side of the bone (Bondioli et al. 2010). In a comparative aim, in this study, we took into consideration the morphometric mapping of the Neanderthal femurs from La Ferrassie 2 (right) and Spy II (right) (in Puymerail et al. 2012a), respectively attributed to MIS 5 (Jaubert et al. 2010; but see also Blackwell et al. 2007; Bertran et al. 2008) and MIS 3 (Semal et al. 2009). In order to generate a single and consensual mapping of our sample of 102 modern humans, we used geostatistical kriging and GAM (generalized additive model). For this, with mgcv (Wood 2006), spatstat (Baddeley 2008) and gstat (Pebesma 2004), we used the distribution model of relative thicknesses obtained with a routine developed using Scilab v.4.1.2 (Consortium Scilab) and R v.2.11.1 (R Development Core Team 2011).

15 As shown by similar studies on the 3D modelization of long bones using different imagery systems (Bondioli et al. 2010; Mazurier et al. 2010; Bayle et al. 2011; Volpato et al. 2011, 2012, 2013; Puymerail et al. 2012a, b), a certain number of inter and intra-observational comparisons revealed differences inferior to or equal to 5 %.

Results and Discussions

External Morphology

16 The femoral shaft BD 5 is quite slender, with no midshaft narrowing and presents slight medial convexity associated with a clearer anterior convexity. In association with the absence of pilaster, the periosteal contour is subcircular. The proximal end is incomplete but the presence of a clearly defined lesser trochanter indicates the strong insertion of the psoas iliac muscle. The linea aspera is also well defined and presents a thick and blunt upper portion but is not divided by a groove (Condemi 2001). In spite of obvious size differences between the two fossils (which attain about 52 % for the total area of the midshaft section and 46 % at 65 %), these morphological characteristics are also present on CDV-Tour 1. This MIS 3 specimen presents slight anterior and medial curves. The contour of its midshaft region varies between a slight extension along the m1 axis and a subcircular section. The linea aspera shows two lips merging to form a relatively smooth crest on the proximal end (Puymerail et al. 2012a).

17 The comparative values of the a-p and m-l diameters are presented in table 2, whereas the variation of the pilastric and platymeric indexes is illustrated in figure 2. The decomposition of these two indexes in diameter ratios demonstrates the effects of allometry. The pilastric index values of 96.5 and 93.7, for BD 5 and CDV-Tour 1 respectively, thus fit into the upper and lower limits of the Neanderthal cloud diagram, which is clearly different to that of modern humans (fig. 2a). BD 5 is characterized by relatively low a-p (M6) and m-l (M7) diameter values and is thus closer to specimens considered to be female, such as Palomas 96 (Walker et al. 2011) and La Ferrassie 2 (Heim 1976, 1982). Conversely, due to a very high m-l diameter, CDV-Tour 1 is more similar to the Saint-Césaire 1 (Trinkaus et al. 1998) and La Ferrassie 1 (Heim 1976, 1982) specimens. As for the chronological differences between the samples, overall, compared to the 10 MIS 3 specimens, the femurs attributed to MIS 5 show quite low a-p diameter values, associated with rather high m-1 diameter values. In this study, MIS 4 is only represented by two specimens which appear to be very close for their high a-p diameter values (fig. 2a). Only the sub-trochanter section (80 %) from BD 5 can be compared, as this portion is missing from CDV-Tour 1. Once again, in this respect, the a-p and m-l diameter values place the specimen from the Bourgeois-Delaunay shelter among the more slender Neanderthal femurs, such as Krapina 214 and Tabun 1 (Trinkaus and Ruff 2012). At this shaft level, there do not appear to be any differences between the samples from MIS 5 and 3, whereas those from MIS 4 display the highest absolute a-p diameter values.

18 This biometric variability is well summarized by the pilastric and platymeric index variations presented in figure 2b.

Figure 2 - Comparative measures of the m-l and a-p diameters at 50% and 80% (a), and pilastric and platymeric index values (b) for BD 5 (black triangle), CDV-Tour 1 (black star), three Neanderthal samples from MIS 5, 4, 3, and the extant human sample (EH) (cf. table 2).

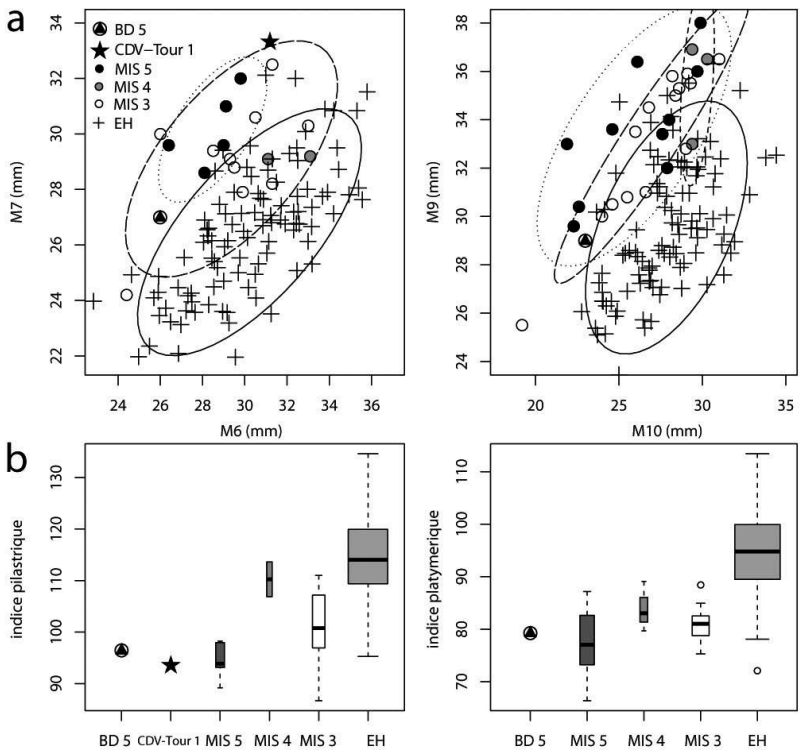


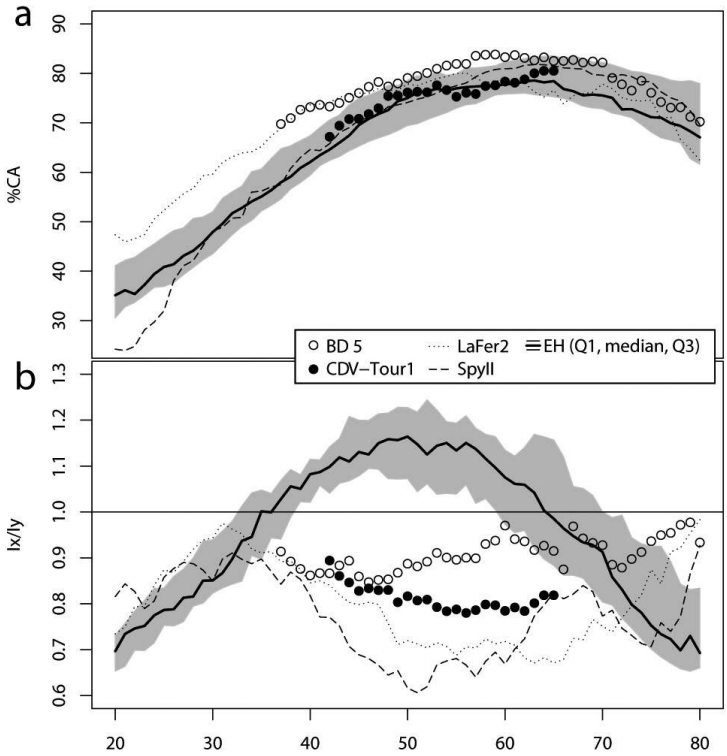
Table 1 - Chronological distribution (MIS 5-3) of the Neanderthal specimens used in the comparative analysis of the m-l and a-p diameters measured at midshaft level (*) and at 80% (#) of the biomechanical length; the cross-sectional geometry parameters measured at 50 % (!), at 65 % (§) and at 80 % (¤) of the femoral shaft. Data from Trinkaus and Ruff (2012, tables A4, A5, A6 and A13; see also Mussini et al. 2012).

MIS	spécimens
5	Ferrassie 1*#!§¤, Ferrassie 2*#!§¤, Krapina 213#, Krapina 214#, Krapina 257.32#¤, Krapina 257.33#¤, Stadelhole 1*#
4	Les Pradelles*!, Chapelle-aux-Saints 1*#!
3	Feldhofer 1*#!§¤, Fond de Foret 1*!§, Hortus 34#, Palomas 52#¤, Palomas 92§, Palomas 96*!§, Quina 5*#!, Quina 38#§, Rochers-de-V. 1*!, Saint-Césaire 1*#!¤, Santa Croce 1*#, Spy 2*#!§¤, Zafarraya 1#

Internal Morphology

19 The values of the geometric properties of the sections of the two specimens from La Chaise-de-Vouthon and the comparative samples are given in table 2. It is to be noted that no value is available for the MIS 4 Neanderthal sample at 35 % of the biomechanical femoral length. For the Neanderthal specimens BD 5, CDV-Tour 1, La Ferrassie 2 and Spy II and for the modern human sample used in this study (for which we have individual 3D data from the [micro]tomographic record), figure 3 shows the variations of the %CA and Ix/Iy ratio parameters measured every 1 % along the shaft. For %CA, all the fossil and modern specimens present a more robust shaft in the proximal portion (particularly in the 65-70% region) compared to the distal half of the femur (fig. 3a). In this context, CDV-Tour 1 is within the range of modern variability, whereas BD 5 presents higher robustness values all along the preserved portion, apart from the most proximal part. We also note that this femur presents a variation profile similar to the La Ferrassie 2 specimen, also from MIS 5 and considered to be female, and that considerable homogeneity exists between CDV-Tour 1 and Spy II, both from MIS 3.

Figure 3 - Percentage of cortical area (a) and Ix/Iy ratio (b) measured at regular intervals each 1 % along the femoral shaft (20-80 % portion of the biomechanical length) of BD 5, CDV-Tour 1, La Ferrassie 2, Spy II and in the extant human sample (EH).



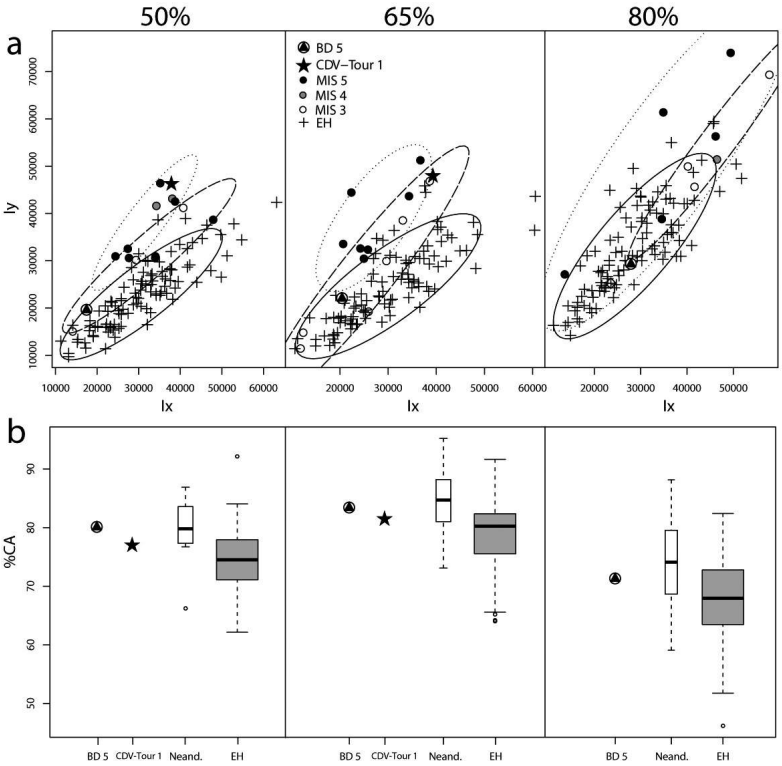
20 The Ix/Iy ratio values, which denote resistance to bending compared to the antero-posterior and medio-lateral axes (a-p/ m-l), are presented in figure 3b. For this parameter, the values greater than 1 indicate major resistance along the a-p axis, whereas those less than 1 indicate major resistance along the m-l axis. In this case, the Neanderthal endostructural signature is clearly distinct from that of modern humans. In effect, the femoral shaft of modern humans is characterized by strong resistance to strain along the m-l axis at the most distal and proximal sections, whereas the characteristic presence of a pilaster entails a greater resistance to strain along the a-p axis at midshaft. In relation to this structural schema, with no obvious chronological difference, the four Neanderthals analyzed here all present Ix/Iy ratio values of less than 1 for the 35-65 portion (fig. 3b).

21 We also studied the comparative distribution of the second moment of the area along the a-p axis (Ix) and the m-l axis (Iy) at 50 %, 65 % and 80 % of the estimated biomechanical length (tab. 2 and fig. 4). As described for the a-p and m-l diameters at midshaft (fig. 2a), at 50 % and 65 %, BD 5 is clustered with Palomas 96 (Walker et al. 2011) at the lower limit of Neanderthal distribution, while CDV-Tour 1 is among the most robust specimens, with La Ferrassie 1 (Heim 1976, 1982) and Fond-de-Forêt (Trinkaus and Ruff 1989). At these two sections, the Neanderthals attributed to MIS 5 present relatively high Iy values. At 80 % (value not available for CDV-Tour 1), the femur from the Bourgeois-Delaunay rock shelter again presents traits showing that it is not very robust compared to the Neanderthal average and is once again similar to Krapina 214 (Trinkaus and Ruff 2012). Given this context, as already indicated for other Neanderthal specimens (Trinkaus 1980), the slender morphology of BD 5 and the biomechanical robustness of CDV-Tour 1 are due to sexual dimorphism.

Table 2 - Comparative measures of the m-l and a-p diameters and gross values of the nine cross-sectional geometry parameters measured at 50 %, 65 % and 80 % of the biomechanical length for BD 5 and CDV-Tour 1 from La Chaise-de-Vouthon and in three Neanderthal samples from MIS 5, 4, 3. The extant human condition is represented by the EH sample. For each sample, the mean and standard deviation (in italics) are presented. The number of observations (n) is systematically listed for both the shaft diameter (Ø) and the cross- sectional geometry (PGS). Data from Trinkaus and Ruff (2012, tables A4, A5, A6 and A13; see also Mussini et al. 2012).

section	spéc./échant.	a-p	m-l	TA	CA	%CA	Ix	Iy	Ix/Iy	J	Imax	Imin
80%	BD 5	23	29	572	401	70,2	23553	25230	0,93	48784	29441	19352
	MIS 5 nØ:10; nPGS: 5	25,9 *2,9*	33,3 *2,8*	741 *156*	561 *107*	76,7 *10,3*	35721 *14021*	51521 *18601*	0,69 *0,16*	87241 *31530*	54312 *19321*	32930 *12743*
	MIS 4 nØ:3; nPGS:1	29,7 *0,5*	35,4 *2,1*	797 *NA*	634 *NA*	79,5 *NA*	46481 *NA*	51455 *NA*	0,90 *NA*	97936 *NA*	51467 *NA*	46469 *NA*
	MIS 3 nØ:14; nPGS:3	26,9 *2,9*	33,2 *3,1*	777 *142*	565 *82*	73,9 *10,1*	39773 *13070*	52815 *15703*	0,75 *0,15*	92587 *27636*	55076 *15930*	37511 *12826*
	EH nØ:102; nPGS:102	27,9 *2,5*	29,5 *2,7*	639 *99*	432 *67*	67,8 *7,1*	28385 *8809*	32876 *9936*	0,87 *0,14*	61261 *17853*	34751 *10254*	26512 *8067*
65%	BD 5	25,8	27,1	510	425	83,2	20096	21693	0,91	41790	23694	18086
	CDV-Tour 1	31,6	33,7	745	600	80,5	39294	48004	0,81	87298	51387	35883
	MIS 5 nPGS:7			596 *120*	499 *94*	84,1 *6,5*	25258 *8776*	32768 *13276*	0,82 *0,22*	58026 *21152*	34316 *12855*	23710 *8942*
	MIS 3 nPGS:6			603 *111*	504 *87*	84,0 *6,0*	26193 *8359*	32995 *12258*	0,84 *0,21*	59188 *19668*	34982 *11851*	24206 *8519*
	EH nØ:102; nPGS:102	*29,3* *2,6*	*26,4* *2,3*	*582* *91*	*458* *73*	*78,9* *5,8*	*30002* *9828*	*24602* *7830*	*1,23* *0,22*	*54605* *16812*	*31191* *9935*	*23409* *7311*
50%	BD 5	26	27	488	385	79,1	17456	19676	0,88	37133	19714	17395
	CDV-Tour 1	31,2	33,3	744	566	76,2	37844	46344	0,81	84188	46327	37839
	MIS 5 nØ:5; nPGS:4	28,5 *1,3*	30,1 *1,3*	669 *65*	522 *60*	77,9 *1,4*	31426 *6673*	38085 *7553*	0,82 *0,06*	69511 *13882*	41419 *8888*	28092 *5469*
	MIS 4 nØ:2; nPGS:2	32,1 *NA*	29,1 *NA*	713 *NA*	591 *NA*	82,9 *NA*	36172 *NA*	42350 *NA*	0,85 *NA*	78023 *NA*	44379 *NA*	34143 *NA*
	MIS 3 nØ:10; nPGS:7	29,4 *2,5*	29,1 *2,7*	645 *89*	513 *90*	79,0 *5,5*	32134 *9032*	33585 *8466*	0,95 *0,14*	65720 *16625*	37883 *107550*	27837 *6448*
	EH nØ:102; nPGS:102	*30,2* *2,7*	*26,4* *2,3*	*577* *90*	*427* *70*	*74,2* *5,3*	*30618* *9960*	*22916* *7093*	*1,34* *0,21*	*53535* *16476*	*31216* *9935*	*22319* *6954*

Figure 4 - Comparative measures of the second moment of area Ix vs. Iy (a) and the percentage of cortical area (b) at 50 %, 65 % and 80 % of the biomechanical length for BD 5 (black triangle), CDV-Tour 1 (black star), three Neanderthal samples from MIS 5, 4, 3, and the extant human sample (EH) (cf. table 2).



22 At 50 %, like at 65 % of the biomechanical length, our Neanderthal sample shows clearly identifiable traits compared to the structural properties characterizing the modern sample. In Neanderthals, the stress along the m-l axis is systematically superior to that of the a-p axis. However, this template shows higher variability in the proximal section, particularly in relation to the high m-l constraints (fig. 4a), which appears to reflect the direct influence of the specific Neanderthal pelvic morphology (Ponce de León et al. 2008; Weaver and Hublin 2009; Meyer et al. 2011; Trinkaus 2011; Trinkaus and Ruff 2012). As for the percentage of the cortical area (%CA), at 50 % (79.1 vs. 76.2) and at 65 % (83.2 vs. 80.5) BD 5 is slightly more robust than CDV- Tour 1 (fig. 4b). On the other hand, at 80 % the %CA values of BD 5 cannot be distinguished from Neanderthal and modern samples.

23 Like for other Neanderthal femurs, the BD 5 and CDV-Tour 1 shafts are characterized by considerable stress resistance along the m-l axis, which results in the presence of a clear midshaft medial reinforcement in both specimens (fig. 5). The (micro)tomographic record shows the virtual unrolling of the shaft and the mapping of the topographic variations of the cortical bone leads to a more detailed morpho-functional characterization of this Neanderthal trait (fig. 6). Here, we compared the morphometric mapping of femurs BD 5 (portion ~37-80 %) and CDV-Tour 1 (portion ~42-65 %) to those obtained for the specimens La Ferrassie 2 and Spy II (Puymerail et al. 2012a; Volpato et al. 2013), generated for the portion between 20 % and 80 % of the biomechanical length.

24 In our analysis, modern humans are represented by a single consensual mapping resuming all the endostructural information from our large reference collection of 102

adult femurs. This methodological approach, where each morphometric mapping represents the relative variations in the topographic distribution of the cortical tissue, describes distribution schemas rather than the thicknesses themselves (Puymerail et al. 2012a). In this comparative context (fig. 6), BD 5 presents an oblique structural strengthening along the medial side, associated with a fine reinforcement along the posterior side corresponding to the shape of the linea aspera. The greatest thicknesses are measured on the proximal level of the lateral side and correspond to the insertion of the gluteal muscles (Mariotti and Belcastro 2011; Puymerail et al. 2012a).

25 The preserved portion from CDV-Tour 1 is much less extensive. Nonetheless, we also observe the oblique medial reinforcement present on BD 5, similarly associated with a posterior strengthening. These endostructural features, which characterize the Neanderthal model in relation to modern humans, are also present in the other fossil specimens used in our analysis, without any visible difference related to the chronological context or sexual dimorphism.

26 A medio-lateral shaft strengthening was revealed by cross-section geometry and the morphometric mapping of this zone provided further information on the medial contribution of this buttress. As mentioned above, BD 5 appears to be from a young female adult (Condemi 2001), whereas CDV-Tour 1 is from a robust male specimen (Puymerail et al. 2012a). Nonetheless, unlike the cross-section shaft measurements (diameters, areas), the analysis of the topographic distribution of the cortical tissue does not reveal any differences attributable to sexual dimorphism.

Figure 5 - Virtual reconstruction of the specimens BD 5 (to the left) and CDV-Tour 1 (right) in anterior, medial, posterior and lateral views. Topographic distribution of the cortical thickness for the portion approximately comprised between 37 % and 80 % of the biomechanical length for BD 5 and between 42 % and 65 % for CDV-Tour 1 virtually rendered by means of a increasing chromatic scale (dark blue is thin, red is thick). The midshaft level is indicated. Scale bar: 2 cm.

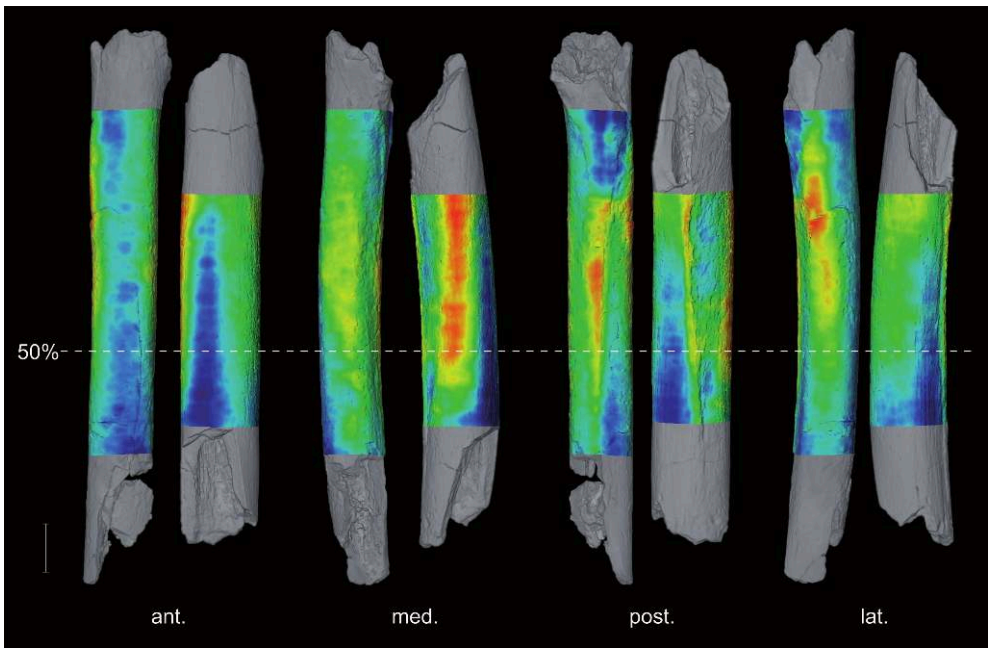
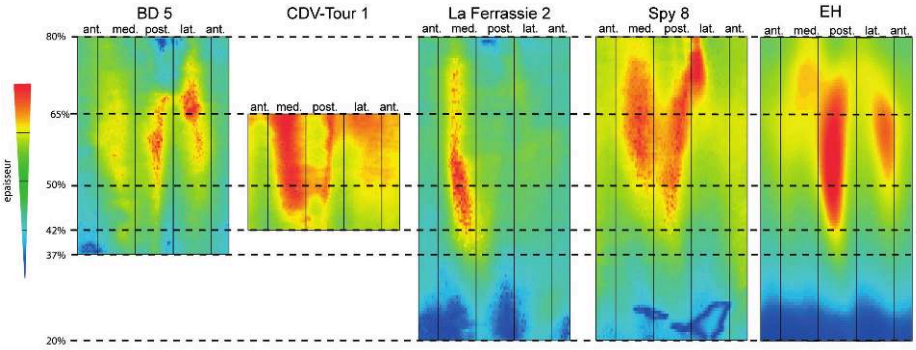


Figure 6 - Standardized morphometric map of cortical bone thickness variation in BD 5 (~37-80 % portion) and CDV-Tour 1 (~42–65 %) compared to the maps obtained in La Ferrassie 2 (right) and Spy II (right) and to the to the consensus map modelling the extant human adult condition (EH; n = 102). The original femora have been virtually cut open vertically along the middle of their anterior aspect and then unrolled. Independently of their original side, all specimens are virtually rendered as left; imaging perspective is systematically from the inner to the outer surface (the medial side is on 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).



Conclusions

27 The comparative analysis of the external and internal structural organization of the Neanderthal femoral shafts BD 5 and CDV-Tour 1, from the site of La Chaise-de-Vouthon, in Charente, but chronologically separated by about 80,000 years, brought to light several similar features in these two adult specimens. In particular, in spite of dimensional differences reflecting sexual dimorphism, both fossils display a subcircular periosteal contour at midshaft, a medial buttress (cf. Mussini et al. 2012), a relatively thin linea aspera associated with the absence of pilaster. As shown by the results of the analysis of the properties of cross-section geometry, in both cases, the proximal part of the shaft is structurally well reinforced. Furthermore, the comparison of the morphometric mapping generated by the virtual unrolling of the specimens indicates the presence of a medial thickening of the cortical tissue in both samples.

28 Thus, like other Neanderthal femurs, the femoral shafts from La Chaise present greater resistance to medio-laterally oriented bending stress, which suggests a more lateral position of the body above the vertical support (Trinkaus 1976, 2007), as well as the influence on the distribution and dissipation of biomechanical loads on the pelvic morphology and limb proportions (Ruff 1995; Weaver et al. 2003; Trinkaus 2011; Trinkaus and Ruff 2012). In spite of significant differences in the external dimensions of the femoral shaft (e.g. Trinkaus 1980), the topographic distribution of the cortical tissue revealed by morphometric mapping does not bring to light any evidence of features linked to sexual dimorphism in the fossils from La Chaise. Finally, in relation to the sample analyzed in this paper and the quantitative parameters measured, we do not observe any evolutionary tendency indicating clear changes in the endostructural organization and the biomechanical properties of the Neanderthal femoral shaft. However, it is important to note here the small size of the currently available MIS 4 sample and, especially, the necessity of future analyses to provide details on the variations of cortical bone along the whole shaft (every 1 %), using many high resolution digital records.

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ABSTRACTS

Neanderthal femoral shaft of BD 5 (MIS 5e), representing a young adult female, and CDV-Tour 1 (MIS 3), an adult male, are both from the site of La Chaise-de-Vouthon, Charente, but are separated by about 80,000 years. In order to identify possible evolutionary morpho-structural changes during this time span, we present a comparative analysis of their internal and external structure. In addition to the morphological characteristics and changes in their external diameters at midshaft and subtrochanteric levels, we quantified, from their microtomographic record (µCT), the cross-sectional geometric properties of these specimens at 50 %, 65 % and 80 % of the biomechanical femoral length and analyzed the morphometric maps of the topographical distribution of cortical bone. Despite differences likely related to sexual dimorphism, both shaft of La Chaise share among themselves but also with all European Neanderthals femurs considered in this study, the typical structural features of this taxon. Indeed, at least compared to the quantitative parameters measured and specimens available for this type of analysis, during the time period MIS 5-3 we did not notice any obvious changes in the endostructural arrangement and in the biomechanical properties of the Neanderthal femoral shaft.

Les diaphyses fémorales néandertaliennes BD 5 (MIS 5e), représentant un jeune adulte de sexe féminin, et CDV-Tour 1 (MIS 3), un sujet adulte de sexe masculin, proviennent tous les deux du site de La Chaise-de-Vouthon, en Charente, mais sont séparées d'environ 80 000 ans. Dans le but de mettre en évidence d'éventuels changements évolutifs de nature morpho-structurelle au cours de ce laps de temps, nous présentons ici l'analyse comparative de leur structure externe et interne. En plus des caractéristiques morphologiques et des variations des diamètres externes au niveau mi-diaphysaire et de la section sous-trochantérienne, nous avons quantifié, à partir de leur registre microtomographique (µCT), les propriétés géométriques de sections de ces spécimens à 50 %, 65 % et 80 % de la longueur biomécanique et réalisé la cartographie morphométrique de la distribution topographique du tissu cortical. Malgré des différences vraisemblablement liées au dimorphisme sexuel, les deux diaphyses de La Chaise partagent, entre elles, mais aussi avec l'ensemble des fémurs néandertaliens européens considérés dans cette étude, les caractéristiques structurales typiques de ce taxon. En effet, au moins par rapport aux paramètres quantitatifs mesurés et aux spécimens disponibles à ce jour pour ce type d'analyses, au cours de la période chronologique MIS 5-3 nous n'avons pas remarqué de changements évidents dans l'agencement endostructural et dans les propriétés biomécaniques de la diaphyse fémorale néandertalienne.

INDEX

Mots-clés: La Chaise-de-Vouthon, fémurs néandertaliens, endostructure, biomécanique
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