

Diaphyseal cross-sectional morphology and biomechanics of the Fond-de-Forêt 1 femur and the Spy 2 femur and tibia

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INTRODUCTION

In human paleontology there has long been concern with the quantification of morphology observed in the fossil record and the comparison of that morphology within and between samples. Since such quantitative comparison has been one of the primary concerns of Prof. André Leguebe, in whose honor this volume is dedicated, it is appropriate that we should present the methodology and preliminary results of new quantitative analyses of the lower limb remains of two important Neandertal specimens from Belgium, Fond-de-Forêt 1 and Spy 2.

THE FOSSIL SPECIMENS

The paleontological specimens of concern here include one femur and the tibia attributed to Spy 2 and the femur which comprises Fond-de-Forêt 1 (fig. 1). The former specimens are part of the remains from several partial skeletons discovered in Middle Paleolithic association in 1886 at the Grotte de Betche-aux-Rotches (or Bec-aux-Roches) near Spy by M. Lohest and M. De Puydt (De Puydt and Lohest, 1887; Fraipont and Lohest, 1887). They include an essentially complete right femur lacking only the superior greater trochanter (specimen N°8) and a complete left tibia (specimen N°9). They derive from one individual and are usually associated with the Spy 2 cranial remains. The Fond-de-Forêt 1 left femur was discovered in the Grotte du Bay-Bonnet at Fond-de-Forêt in 1895 by J. Tihon in association with Middle Paleolithic artifacts (Tihon, 1898; Twiesselmann, 1961). It consists of a complete diaphysis from the region of the lesser trochanter to the condyles. The Spy 2 remains, by their morphology and association with the Spy cranial material, and the Fond-de-Forêt 1 femur, on the basis of its morphology and Middle Paleolithic context, are included within the Neandertal late archaic human sample.

The Spy 2 femora and tibia, given their completeness and early discovery and publication, have figured significantly in most discussions of Neandertal lower limb morphology (e.g., Boule, 1911-13;

Mc Cown and Keith, 1939; Twiesselmann, 1961; Endo and Kimura, 1970; Trinkaus, 1976, 1983; Lovejoy and Trinkaus, 1980). The less complete Fond-de-Forêt 1 specimen, since its description by F. Twiesselmann (1961), has similarly become an important element in the Neandertal femora sample. From these discussions, it has become evident that these femora and tibia are similar to those of other Neandertals in having large diaphyseal diameters relative to length, with the femora being non-pilastric, meso-meric and anteriorly bowed while the tibia is retroverted and meso-cnemic with an amygdaloid diaphyseal cross-section. However, these studies have investigated these remains largely through external contours and metrics, only minimally exploiting the potential information in their internal, as well as external, architecture. In addition, the linear measurements employed in traditional osteometric analyses do not take into account the total areal distribution of bone within sections, a factor which is critical in assessing the biomechanical properties of diaphyses.

In light of this, we have undertaken an investigation of fossil hominid femora and tibiae using the cross-sectional geometry of specified diaphyseal locations to provide more detailed information on the diaphyseal biomechanics, and hence locomotor behavior, of these extinct hominids. Our presentation here is intended to detail the methodology involved and preliminary results concerning the Spy and Fond-de-Forêt remains.

MATERIALS AND METHODS

The goal of the study was to compute cross-sectional geometric properties for these and other fossil femora and tibiae, so that mechanically significant aspects of them could be quantitatively compared between specimens and across samples. The relevant geometric properties are cortical area (CA), medullary area (MA), total subperiosteal area (TA), maximum and minimum second moments of area (area moments of inertia; I_{max} and I_{min}), second moments of area



Fig. 1 : Posterior views of, from left to right, the Fond-de-Forêt 1 left femur, the Spy 2 right femur, and the Spy 2 left tibia.

about the x (M-L) and y (A-P) axes (I_x and I_y respectively), the polar second moment of area (J), and the angle between the M-L axis and the direction of greatest bending rigidity (θ). These properties for these fossils, other fossil specimens and recent human comparative samples have been computed by one of us (C.B.Ruff) using a semi-automated method employing a digitizer and interactive computer software from cross sections which accurately depict the external (subperiosteal) and internal (endosteal) contours of the bones.

To provide an accurate characterization of diaphyseal morphology in which the computed geometric properties are directly comparable between specimens, reference planes and diaphyseal lengths ('length') have been defined (Ruff, 1981; Ruff and Hayes, 1983). For the femur, the coronal and sagittal planes include the subtrochanteric and supracondylar diaphyseal midpoints, and the coronal plane is defined as parallel to the dorsal condylar tangent line; length' extends from the mean of the distal condylar tangent planes to the most proximal point of the defined diaphyseal axis (usually on the medial border of the greater trochanter). For the tibia, the coronal and sagittal planes include the talar trochlear articulation midpoint and the midpoint between the tibial condyle midpoints, and the coronal plane includes both condylar midpoints; length' is the average of the direct measurements between the talar trochlear surface midpoint and the midpoints of each tibial condyle. These length' dimensions were used, rather than maximum length or some other length

measurement, to avoid the effects of differences in femoral neck angulation and the degree of development of proximal femoral and tibial and distal tibial articular processes. The cross-sections are defined as perpendicular to these axes and occurring at, distal to proximal, 20 %, 35 %, 50 %, 65 % and 80 % of length' (fig. 2).

To determine non-invasively the appropriate cross-sections of fossil diaphyses, the following steps were taken by ET. The locations of the sections were marked on the diaphyses, using thin tape so as not to mark the original specimens. Horizontally and sagittally oriented silicone putty (Optosil, Unitek Corp.) contour molds were made of each cross-sectional subperiosteal contour, which were subsequently transcribed onto graph paper, with the x and y axes oriented according to the coronal and sagittal planes of the bone. Coronal and sagittal radiographs of each bone were taken with the source approximately 1m from the specimen and the location of the 50 % section marked on the film. A, P, M and L cortical thicknesses were measured from the x-rays, correcting for parallax using the long bone length and subperiosteal diameters. The endosteal contours were drawn between the resultant four points, following the subperiosteal contours as a further guide to the shape of the endosteal contour. It is estimated that the resultant cross-sectional contours (fig. 3) are within 5 % of the original bones. Alternative techniques are either destructive of the specimen (e.g., sawing) and hence

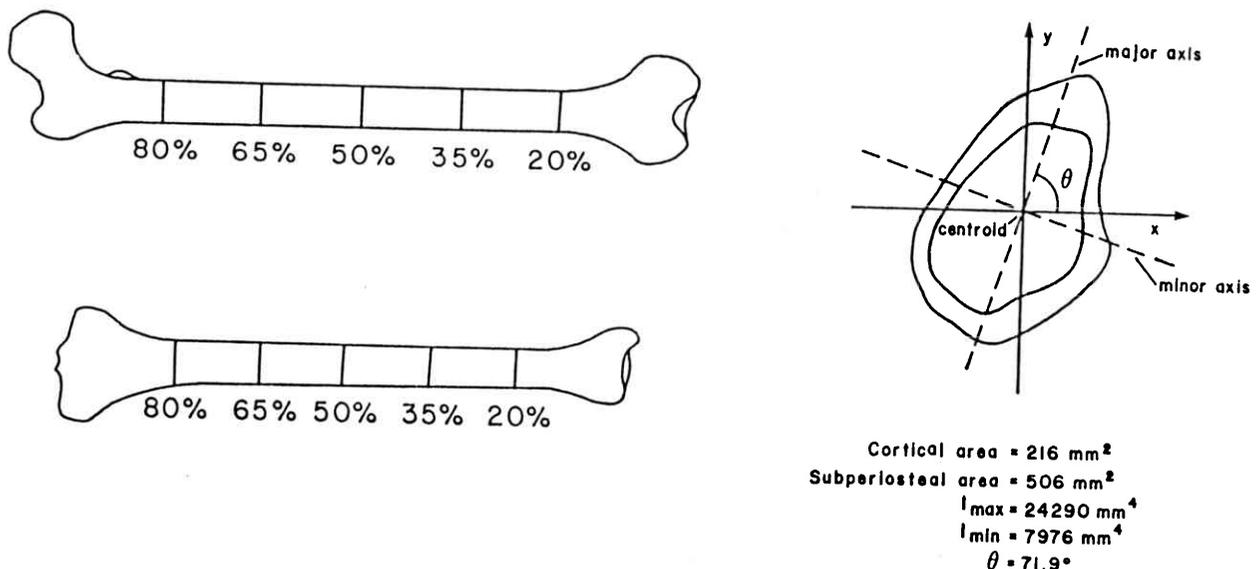


Fig. 2 : Diagrammatic representation of the locations of the sections on a modern human femur and tibia (left) and a tracing of a modern human cross-section (a 65 % section of an Amerindian [Pecos Pueblo] tibia) showing the x, y, major and minor axes, θ , and a listing of some of its cross-sectional parameters. Partly adapted from Ruff and Hayes (1983).

inapplicable here or, as in computed tomography (CT), have built in errors and require a level of calibration seldom available (Ruff and Leo, 1986). This technique, therefore, provides reasonably accurate cross-sections with no damage to the fossil specimens.

The section tracings were then photographed, processed as transparencies, and rear-projected onto a digitizer screen interfaced with a microcomputer. *x* and *y* point coordinates at 1mm intervals on the subperiosteal and endosteal contours were input to program SLICE (Nagurka and Hayes, 1980), which calculates section properties. The method is replicable to within 2% (Ruff, 1981; Ruff and Hayes, 1983).

The section properties used here to investigate femoral and tibial strength and rigidity assume that long bone diaphyses can be modeled as engineering beams, which has been shown to be a reasonable assumption (Huiskes, 1982). In a beam model, cross-sectional area (CA) is proportional to axial compressive and tensile rigidity, while second moments of area are proportional to bending (*I*_{max}, *I*_{min}, *I*_x, *I*_y) and torsional (*J*) rigidity (Lovejoy *et al.*, 1976; Ruff and Hayes, 1983). Areas are expressed in linear units to the second power, while second moments of area are expressed in linear units to the fourth power. Since *J* is also equal to *I*_{max} + *I*_{min} or *I*_x + *I*_y, it can also be used as an index of average bending rigidity in all planes of a section. To simplify comparisons in the following analyses, overall rigidity (or strength) is evaluated using *J*. To evaluate the relative distribution of bone within sections and/or relative strength of diaphyseal sections in different orientations, some ratios between properties, i.e., *I*_{max}/*I*_{min}, *I*_x/*I*_y and CA/TA (%CA), were also calculated as cross-sectional "shape" indices.

It has been shown that, among modern humans, section properties of long bones are approximately isometric with bone length; that is, areas scale with length², while second moments of area scale with length⁴ (Ruff, 1984). Therefore, to enable comparisons between individuals of different size, section properties were divided by these powers of bone length (length³); the resulting values (CA-STD and *J*-STD) can be interpreted as size-standardized indices of relative robusticity. Some of these parameters, and in particular CA (since it is proportional to axial strength and rigidity), may well scale to body size. We have therefore compared femoral midshaft CA to femoral head size (as an indicator of body mass [Ruff, 1988]) by dividing the cube root of femoral head volume by the square root of CA (HD/CA).

Length', the diaphyseal axes and the planar orientations of the Spy 2 tibia were determined directly on the essentially complete bone; the resultant length' is 307 mm. The damage to the greater

trochanter of the right femur necessitated the use of the more complete greater trochanter on the left femur (specimen N°16) to estimate the position of the proximal end of the right femoral length' measurement. The resultant length' is 411 mm for the Spy 2 right femur. The Fond-de-Forêt 1 femur is sufficiently complete to determine its diaphyseal orientation; however, the absence of the proximal epiphyses required estimation of length'. This was done by assuming that the distance from the mid-gluteal buttress on the proximo-lateral diaphysis to the proximal greater trochanter was similar on Fond-de-Forêt 1 and Spy 2; most likely it was slightly larger on Fond-de-Forêt 1. The resultant length' of ca. 438 mm is nonetheless greater than the trochanteric length (Martin N°3; the most similar standard osteometric) estimate of ca. 417 mm provided by Twisselmann (1961:12). Yet, using the 438 mm estimate for length', the calculated positions for the sections fall where they would be expected to occur based on diaphyseal morphology (e.g., 50 % at midshaft, 80 % at the subtrochanteric level), giving confidence in the reconstructed length.

The comparative sample consists of the available European and Near Eastern Neandertal femoral and tibial cross-sections and two modern human reference samples, an Amerindian (Pecos Pueblo) sample (Ruff, 1981; Ruff and Hayes, 1983) and a Euroamerican cadaver sample (Ruff and Hayes, 1988). The Neandertal comparative sample employed here includes midshaft (50 %) sections from Amud 1 (Endo and Kimura, 1970), La Chapelle-aux-Saints 1 (Boule, 1911-13), La Ferrassie 1 and 2 (Heim, 1982), Neandertal 1 (Schwalbe, 1901), St Césaire 1 (Vandermeersch, 1984), Shanidar 4 and 6 (Trinkaus, 1983) and Tabun C1 (McCown and Keith, 1939) plus data from sequential 20 % to 80 % sections from La Chapelle-aux-Saints 1, La Ferrassie 1 and 2 and Neandertal 1. The majority of sections were reconstructed from contour molds and x-rays as were the 14 from Fond-de-Forêt and Spy 2; the remainder were from scaled photographs of natural diaphyseal breaks.

The Fond-de-Forêt 1 and Spy 2 remains do not include sexually diagnostic pelvic remains, but size considerations suggest that both represent males (Trinkaus, 1980). There are consistent sexual differences in lower limb diaphyseal geometry among modern humans and similar patterns of dimorphism are evident in Neandertal external diaphyseal diameters (Ruff, 1987). However, given the uncertainty of the sex attributions for Fond-de-Forêt 1 and Spy 2 and the bias toward males in the comparative Neandertal sample, the comparisons here will be only with the total fossil and the combined sex modern human samples.

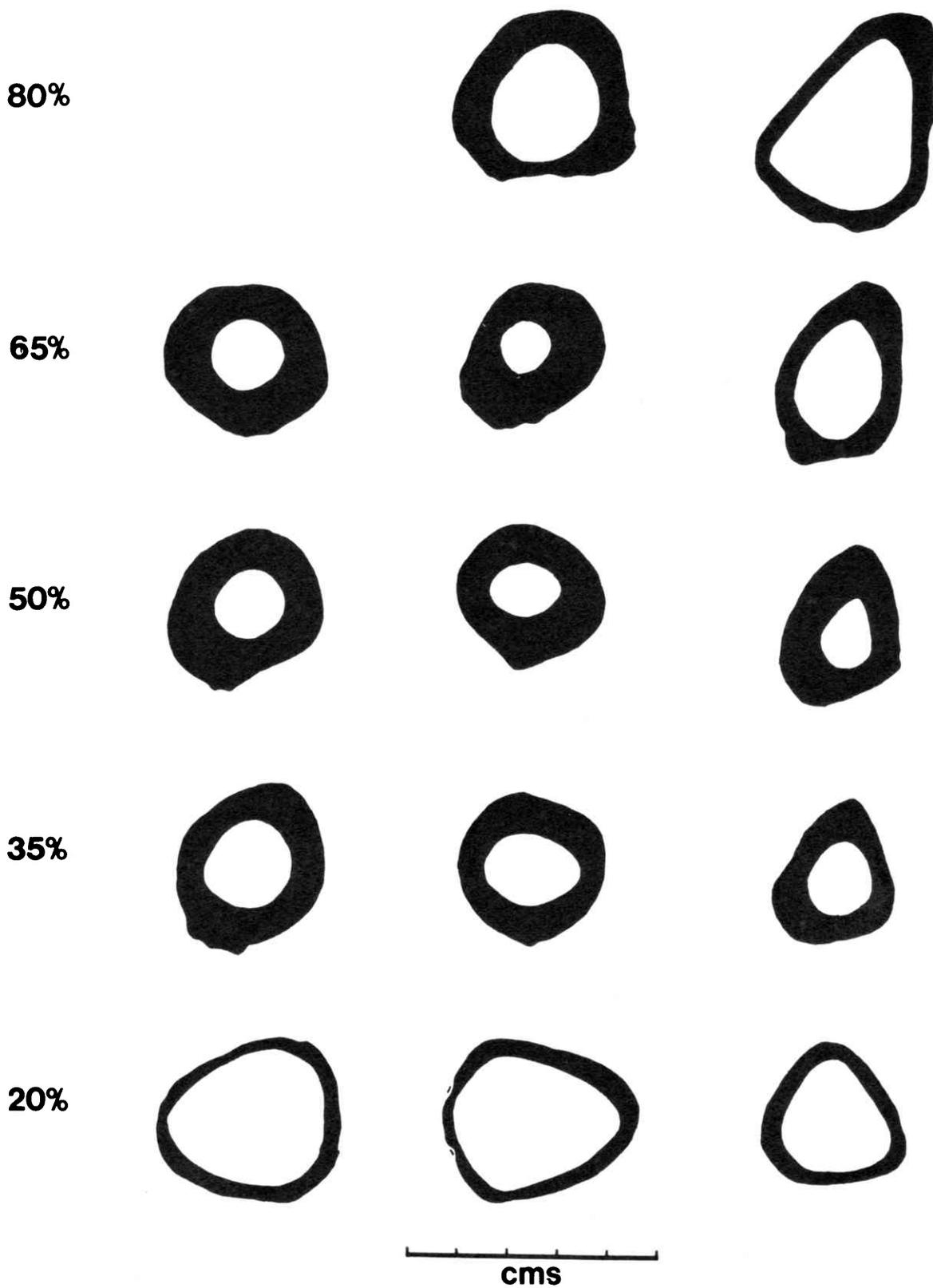


Fig. 3 : Tracings of the reconstructed diaphyseal cross-sections of the Fond-de-Forêt 1 left femur (left), the Spy 2 right femur (center) and the Spy 2 left tibia (right). The sections are drawn as though viewed from distal to proximal and the anterior margin is above in the drawings.

	Sect	Len'	CA	TA	Imax	Imin	Ix	Iy	J	θ
FF1 femur lt	20%	438	242	879	34689	24539	25914	33315	59228	22
	35%	438	492	726	47461	29740	42288	24912	77201	57
	50%	438	558	711	46970	31637	38811	39796	78607	43
	65%	438	591	756	49038	38249	39357	47929	87287	161
SP2 femur rt	20%	411	275	892	38035	27317	27322	38030	65352	-1
	35%	411	437	654	30438	29899	30436	29902	60337	94
	50%	411	491	614	31828	25954	27246	30536	57782	28
	65%	411	510	594	36238	20693	28236	28695	56931	136
	80%	411	564	959	68738	55068	55615	68192	123806	169
SP2 tibia lt	20%	307	218	567	16771	15477	15482	16766	32248	-3
	35%	307	318	467	20673	12371	19627	13418	33044	69
	50%	307	439	550	33024	16329	31003	18349	49353	70
	65%	307	382	698	48632	19707	44867	23472	68339	69
	80%	307	405	1065	83700	38088	72190	49598	121788	60

Table 1 : Cross-sectional geometric properties of the Fond-de-Forêt 1 (FF1) and Spy 2 (SP2) femora and tibia. See text for abbreviations.

RESULTS

The cross-sectional geometric properties of all of the preserved sections of the Fond-de-Forêt 1 and Spy 2 lower limb diaphyses are presented in table 1. Comparative data for the femoral and tibial 50 % sections, which are representative of the diaphyses generally, are presented in table 2. Graphic comparisons of sequential femoral %CA and θ and tibial Imax/Imin (for all individuals with at least four preserved sections) are presented in figures 4 to 6.

Robusticity

Neandertal femoral and tibial diaphyses have long been described as robust (e.g., Twisselmann, 1961; Trinkaus, 1976; Lovejoy and Trinkaus, 1980), and the data presented here support this observation. It is evident in both their CA and J values relative to size (length'). As is shown in table 2, in both the femoral and tibial midshafts, the Neandertals, including Fond-de-Forêt 1 and Spy 2, are quite separate from the recent human means with respect to CA standardized to length', slightly more so in the tibia than in the femur. The same pattern is evident in the comparisons of J standardized to length'. Again, the Neandertal values are largely distinct from the recent human samples. The Fond-de-Forêt 1 and Spy 2 femoral values and especially the Spy 2 tibial value fall well beyond two standard deviations from the modern means.

It should be kept in mind, however, that J sums Imax and Imin, in effect averaging the degrees of difference in each of these I values between the samples. Given the cross-sectional shape differences in middle

and distal femoral diaphyses between the Neandertals and the modern humans (see below), the J values may provide only a minimum estimate of the differences between the femora in the most biomechanically significant directions.

Interestingly, however, when CA is compared to body mass as represented by femoral head volume (HD/CA in table 2), there is no difference between the Neandertals and the recent human samples. Apparently CA and body mass are scaling together in the same manner among the Neandertals and modern humans, with the Neandertals having higher values for both relative to stature (as represented by femoral length).

Shape Considerations

In comparison to the recent human samples, the Neandertals show elevated %CA values (table 2), i.e., relatively thick cortices. This is evident in their tibial 50 % %CA values, in which the Neandertal mean is well above the recent human means and the Spy 2 value is toward the upper end of the Neandertal range of variation (table 2). It is also present in their femoral 50 % %CA values, although the difference there is less pronounced than in the tibial midshaft. For the five Neandertals with at least four femoral sections (fig. 4), %CA is clearly elevated for the 35 % and 50 % sections, more variable and slightly elevated on the average for the 65 % and 80 % sections, but similar to the recent human samples for the 20 % section. The degree of difference and amount of separation from the recent human means appears to follow the sequence of 50 %, 35 %, 65 %, 80 % and 20 %

from greatest to least. In this Fond-de-Forêt 1 and Spy 2 generally follow the Neandertal pattern, even though Fond-de-Forêt 1 has a low 65 % value and Spy 2 has a low 80 % value.

The Neandertal tibial 50 % I_{max}/I_{min} values fall largely between the means of the recent human samples, with Spy 2 having a relatively low value. The Neandertal tibiae with sequential sections (fig. 5) similarly have I_{max}/I_{min} values which fall near the recent human mean values (the higher values for the Amerindian sample 35 %, 50 % and 65 % sections reflect their greater A-P values and hence their platycnemia). Further support for this pattern is evident in the 50 % θ values of 70°, 81° and 67° for Spy 2, La Chapelle-aux-Saints 1 and La Ferrassie 2 respectively, all of which are insignificantly different from the recent human mean values.

In contrast, the Neandertal femoral midshafts show a clear shape difference relative to the modern human samples. Even though their I_{max}/I_{min} values are similar, their I_x/I_y values (reflecting A-P to M-L bending rigidity) are, on the average, below 1.00, with only 2 of the 9 specimens (Neandertal 1 and Shanidar 4) having I_x/I_y values above 1.00. Most of the modern humans, in contrast, have values well above 1.00 (table 2). Furthermore, most of the Neandertal θ values, including Spy 2 but not Fond-de-Forêt 1, are well below the modern human mean values. In the sequential θ graph (figure 6), it is apparent that the Neandertals tend to have relatively low (i.e., M-L oriented) values for the 35 % and 50 % sections compared to the Amerindian sample, even though the 20 %, 65 % and 80 % sections are similar to the recent humans.

		%CA	I _{max} /I _{min}	I _x /I _y	θ	CA-STD	J-STD	HD/CA
<i>Femur 50%</i>								
FF1		78.4	1.48	0.98	43.0	290.9	213.6	
SP2		80.0	1.23	0.89	28.0	290.7	202.5	1.963
Neand.	\bar{x}	76.4	1.37	0.85	21.4	306.6	246.7	1.826
	SE	4.3	0.07	0.06	9.3	28.7	26.1	0.075
	N	7	7	7	7	7	7	6
Amerind.	\bar{x}	71.6	1.38	1.10	51.6	215.6	136.6	1.827
	SE	0.7	0.02	0.02	2.1	2.5	2.1	0.013
	N	119	119	119	119	119	119	115
Euroam.	\bar{x}	69.1	1.28	1.21	78.0	204.2	130.5	1.896
	SE	1.0	0.03	0.04	4.3	4.5	4.9	0.024
	N	40	40	40	40	40	40	32
<i>Tibia 50%</i>								
SP2		79.8	1.69	2.02	70.0	465.8	555.6	
Neand.	\bar{x}	74.0	2.46	2.20	74.0	386.9	454.1	
	SE	2.5	0.19			14.1	28.1	
	N	7	7	2	2	7	7	
Amerind.	\bar{x}	62.7	2.93	1.88	64.7	234.6	227.6	
	SE	0.9	0.05	0.04	0.7	3.7	5.2	
	N	119	119	119	119	119	119	
Euroam.	\bar{x}	69.0	2.11	1.50	64.1	230.9	182.3	
	SE	0.9	0.07	0.04	1.7	6.3	9.5	
	N	37	37	37	37	37	37	

Table 2. Computed cross-sectional properties of the midshaft (50 %) sections of the Fond-de-Forêt 1 (FF1) and Spy 2 (SP2) femora and tibia, Neandertal combined sex samples and recent human combined sex samples. The Neandertal sample does not include the Fond-de-Forêt 1 and Spy 2 specimens. See text for abbreviations and methods of computation.

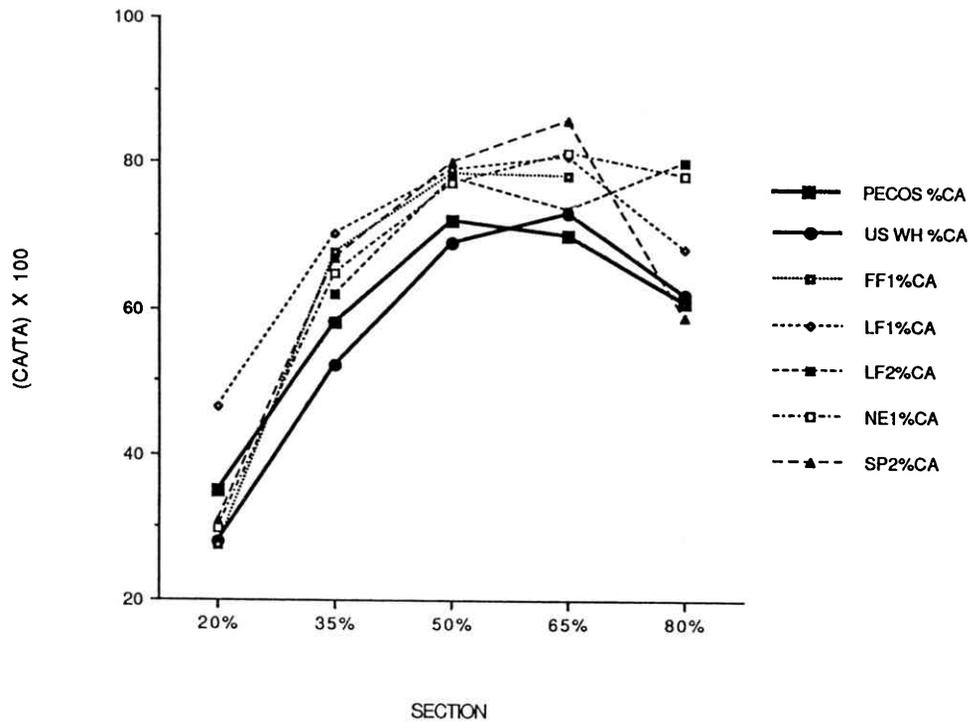


Fig. 4 : Femoral %CA for five Neandertals with sequential sections preserved (Fond-de-Forêt 1 : FF1, La Ferrassie 1 and 2 : LF1 and LF2, Neandertal 1 : NE1, Spy 2 : SP2) compared to the mean values for the modern Amerindian (PECOS) and Euroamerican (US WH) samples.

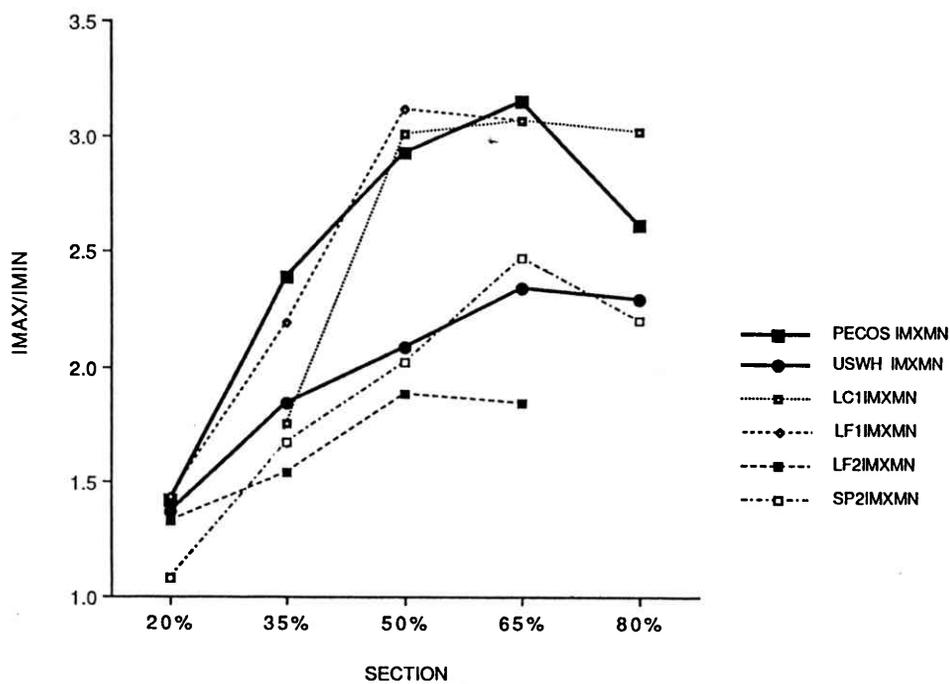


Fig. 5 : Tibial I_{max}/I_{min} values for four Neandertals with sequential sections compared to modern Amerindian and Euroamerican sample means. See figure 4 for abbreviations; LC1: La Chapelle-aux-Saints 1.

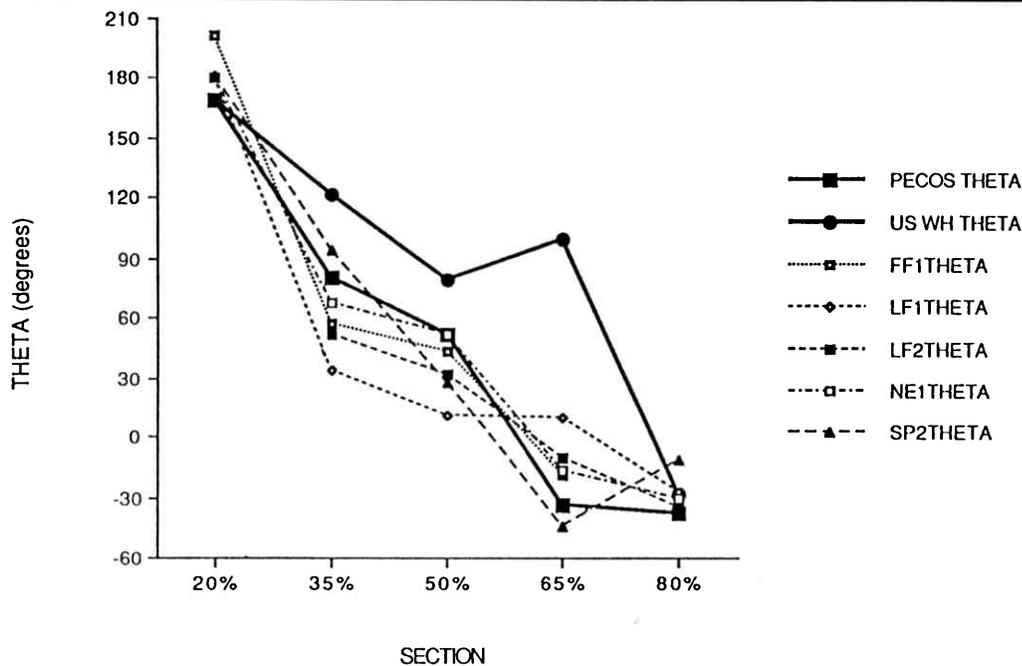


Fig. 6 : Femoral theta (θ) values for five Neandertals with sequential sections compared to modern Amerindian and Euroamerican sample means. See figure 4 for abbreviations.

DISCUSSION

From this preliminary comparison of these Neandertal and modern human data, several patterns emerge. Relative to long bone length, the relevant body size measure for considerations of bending and torsional strength and rigidity, the Neandertal femora and tibiae have average values well above those of the recent human means. Relative to body mass (as reflected by femoral head diameter), however, Neandertal femoral diaphyses appear similar in size to those of modern humans. In the tibia and proximal femur, the orientations of the implied elevated habitual bending stresses appear similar to those of recent humans, supporting the evidence from Neandertal lower limb articular morphology (Heim, 1982; Trinkaus, 1975, 1983) that the Neandertals habitually engaged in striding bipedal gaits essentially indistinguishable from those of modern humans.

Yet, in the mid and distal femur the implied bending stresses were apparently more medio-laterally oriented, suggesting a more lateral position of the body above the vertically supporting lower leg and foot. Interestingly, similarly elevated lateral stresses are implied by the relatively broad proximal pedal phalangeal diaphyses of the Neandertals (Trinkaus, 1975, 1983).

In all of these comparisons, the Spy 2 and Fond-de-Forêt 1 femora and tibia fall within the Neandertal range of variation. In some measures they are at the limits of the Neandertal range, but their overall pattern is indistinguishable from that of other Neandertals.

CONCLUSION

This presentation of the cross-sectional properties of the Fond-de-Forêt 1 and Spy 2 femora and tibia illustrates the methodology and preliminary results of such quantitative analyses of paleontological specimens, going beyond the simpler but less complete osteometrics traditionally used to quantify fossil morphology. Further analysis of these paleontological diaphyses should help us to comprehend more fully the locomotor anatomy and behavior of these extinct hominids.

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