PERIODICUM BIOLOGORUM
VOL. 114, No 1, 117–123, 2012

UDC 57:61
CODEN PDBIAD
ISSN 0031-5362

Original scientific paper

A new Neandertal femoral diaphysis from Les Pradelles (Marillac-le-Franc, Charente, France)

CÉLIMÈNE MUSSINI[1]
ISABELLE CREVECŒUR[1]
MARIA DOLORES GARRALDA[2,1]
ALAN MANN[3,1]
BRUNO MAUREILLE[1]

[1]UMR 5199 PACEA – Anthropologie des Populations Passées et Présentes, Université de Bordeaux, avenue des Facultés, 33405 Talence cedex, France

[2]U.D. de Antropología Física, Facultad de Biología, Universidad Complutense de Madrid, Espagne

[3]Department of Anthropology, Princeton University, Princeton, USA

Correspondence:
Célimène Mussini
UMR 5199-PACEA
Anthropologie des Populations Passées et Présentes, Université de Bordeaux
avenue des Facultés, bât. B8
33405 Talence cedex, France
E-mail: c.mussini@pacea.u-bordeaux1.fr

Received September 9, 2011.

Abstract

Background and purpose: *A femoral diaphysis of an adult Neandertal was discovered in 2010 at the site of Les Pradelles (Marillac-le-Franc, Charente, France) with occupation levels from MIS 4. We describe the Les Pradelles (LP) femoral diaphysis and discuss its morphometric characteristics in relation to Late Pleistocene diversity.*

Materials and methods: *The comparative sample for the LP femur consists of Neandertals, Middle Paleolithic modern humans and European Upper Palaeolithic modern humans. Classical measurements (diameters) and cross-sectional geometric properties were studied at mid-diaphysis. The pattern of thickness variations was also analyzed.*

Results: *Morphological aspects of this diaphysis clearly relate it to those of the Neandertals (anterior curvature, lack of pilaster, medial buttress). Exostoses near and on the linea aspera may be the consequence of a pathological bone reaction, with unknown cause. Cross-sectional geometric properties place the LP femur within the range of Neandertal variation. It presents, among other features, a greater amount of cortical bone in comparison to modern human variability. The 3D modeling highlights a medial side with an important cortical thickness corresponding to the medial buttress.*

Conclusions: *The LP femur provides additional data to our knowledge of MIS4 Neandertal variability, less well documented than those assigned to MIS5 and MIS3.*

INTRODUCTION

The site of Les Pradelles, also known as Marillac *(1, 2)*, is located in the village of Marillac-le-Franc (Charente, Southwest France). Excavations have revealed a number of archaeologically rich layers, all associated with a Quina type Mousterian industry *(3, 4)*. More than 20,000 animal bones have been recovered, about 90% reindeer, the remainder horse, bison and several carnivore species. Although the site has been disturbed by fluvial action, no evidence of habitation or fire: no traces of charcoal been found and no bones show signs of burning. The introduction of finished tools made on non-local flint and the butchering activities, mainly on Reindeers, indicating the processing of eatable portions for transport to another settlement *(5, 6)* suggest the hypothesis that the Neandertals used the site as a hunting camp *(4, 5, 6, 7)*.

A fragment of Neandertal mandible was discovered in 1934 *(8)*. Since that time, additional excavations led by B. Vandermeersch between

1967 and 1980 *(1, 9)*, and by B.M. and A.M. since 2001 have yielded 78 additional Neandertal remains. All the Neandertal fossils are poorly preserved fragments, mostly from the cranial vault *(10)*, with very few infracranial remains. In July 2010, a well preserved fragment of the left femoral diaphysis, LP10-D13 #362, was excavated by B.M. at the base of level 2a, one of the site's richest in artifacts, faunal and human remains. The layer above (2b) has been dated to 58,000 yrs BP *(10)*, locating the Neandertal occupation of Les Pradelles within Marine Isotopic Stage (MIS) 4 *(11)*. The morphology of the Neandertal femoral diaphysis is well known *(12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23)*. Features that distinguish it from modern morphology include: marked antero-posterior and medio-lateral curvatures, a lack of pilaster and a medial buttress.

Here we describe the LP femoral diaphysis and compare its morphometrical characteristics to a sample of Neandertal and Upper Pleistocene modern human femora. Neandertal features are discussed in relation to Late Pleistocene diversity.

MATERIAL AND METHODS

The comparative sample for the LP femur consists of European and Asian Neandertals (NEAND), Middle Paleolithic modern humans from Qafzeh and Skhul (MPMH) and European Upper Palaeolithic modern humans (EUP) (Table 1). Because of the debate on the Near-Eastern Mousterian fossils status, some authors divide the Neandertal sample in two sub-groups: one from Europe and one from Near-East *(19)*. However, there is no significant difference between means and variance of the Near-Eastern and European sub-groups in our NEAND comparative sample. Therefore, comparisons are made to the entire group, which is taken as a close representative of Neandertal variability.

Measurements of Les Pradelles femur were made at the mid-diaphysis. The extremities are not preserved, so the mid-diaphysis location was estimated by comparing its diaphyseal morphology to well-preserved Neandertal femora. Possible differences between the actual mid-diaphysis and the estimated one are likely insignificant at this position on the diaphysis *(23)*.

The classic measurements taken at mid-diaphysis include the antero-posterior and transversal diameters (M6 and M7) *(35)*. The pilastric index was computed using these two dimensions ((M6*100)/M7).

Adjusted z-scores (Houët in *(36)*) were used to locate the LP femur within the comparative sample's variability. The method, based the Student t-test, accounts for means, standard deviations and sample sizes of the comparative groups. As the value of the fossil studied converges to 1, it approaches the compared sample mean.

The cross-sectional geometric properties were evaluated at the midpoint of the femur length. The femur was scanned in the Tivoli private hospital (Bordeaux) using a Light speed Pro 32 medical CT scanner. The scans were made in the transversal plane, as recommended by Ruff & Leo *(37)* using a slice spacing of 0.5 mm and a pixel size of 0.1875 mm. Measurements were taken with the ImageJ *(38)* software and the macro: »Moment MacroJv1.2« (http://www.hopkinsmedicine.org/FAE/mmacro.htm). Thanks to these CT-scans, a 3D virtual cartography of the thickness variation was elaborated using AMIRA v.4.0 software. A semi-automatic segmentation method was employed using the method recommended by Spoor *et al.* *(39)*.

MORPHOMETRIC DESCRIPTION AND COMPARISON

The LP fragment is a central-proximal portion of a left femoral diaphysis from a mature individual. The

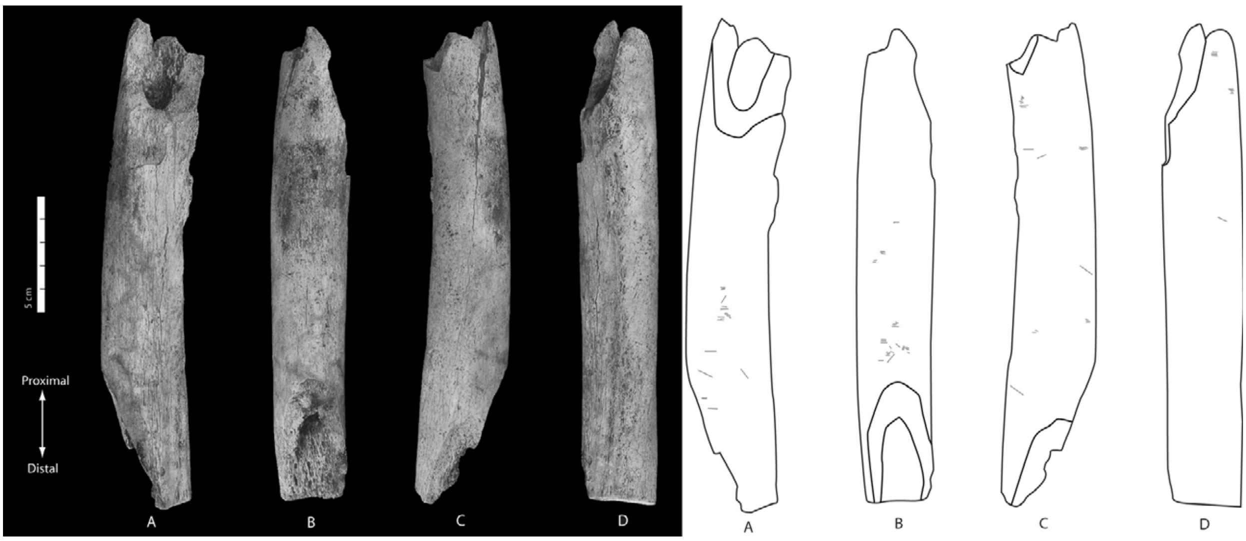

Figure 1. *The LP10-D13 #362 left femoral diaphysis, picture and localization of the cutmarks. A: lateral side, B: anterior side, C: medial side, D: posterior side.*

maximum length of the preserved diaphysis is 186 mm (it was approximately 200 mm when discovered; 15 mm of the distal extremity were removed for future isotopic and DNA analyses). Maximum diameter is 37.8 mm, maximum exposed cortical thickness 9.5 mm. The medial surface of the proximal end is better preserved than the lateral face which suffers from a 36 mm long beveled break. Soft cleaning and long drying of the bone revealed two long cracks running from the proximal edge to the posterolateral and anteromedial sides of the bone (Figure 1). Distally, the posterior face is well preserved while the anterior face is truncated by a beveled fracture 69 mm in length. The two extremities present human-made breaks with percussion pits. These anthropic modifications in-

TABLE 1

List of specimens used in the study with references for midshaft diameters, pilaster index and cross-sectional parameters.

Specimen	Group	Marine Isotope Stage	Midshaft diameters and pilaster index	Cross-sectionnal geometric properties
Les Pradelles	LP	4	This study	This study
Amud 1	NEAND	4–3	*(15)*	*(19)*
Biscegli	NEAND	5?	*(16)*	
Castel di Guido 1 and 2	NEAND	9	*(24)*	
Ehringsdorf E and 1	NEAND	7	*(25, 14)*	This study
Feldhofer 1	NEAND	3	*(26)*	Data provided by E. Trinkaus
Fond-de-Forêt 1	NEAND	?	*(14)*	*(18)*
Hohlenstein-Stadel 4	NEAND	5	Data provided by E. Trinkaus	This study
La Chapelle-aux-Saints 1	NEAND	?	*(26)*	Data provided by E. Trinkaus
La Ferrassie 1 and 2	NEAND	?	*(26)*	Data provided by E. Trinkaus
La Quina 5	NEAND	3?	*(27)*	
Rochers-de-Villeneuve 1	NEAND	3	*(23)*	Data provided by E. Trinkaus
Saint-Césaire 1	NEAND	3	*(23)*	*(20)*
Sedia del Diavolo	NEAND	5–6?	*(25)*	
Shanidar 4, 5 and 6	NEAND	?	*(25,26)*	*(19)*
Spy 2	NEAND	3	*(26)*	*(18)*
Tabun 1 and 3	NEAND	5e	*(28, 26)*	*(19)*
Qafzeh 3, 8 and 9	MPMH	5	*(29)*	*(19)*
Skhul 3, 4, 5, 6, 7 and 8	MPMH	5	*(28)*	*(19)*
Arene Candide IP	EUP	3	Data provided by E. Trinkaus	*(30)*
Barma Grande 2 and 6	EUP	3	Data provided by E. Trinkaus	*(30)*
Caviglione	EUP	3	Data provided by E. Trinkaus	
Cro Magnon 4322, 4323, 4324, 4327, 4329	EUP	3	Data provided by E. Trinkaus	Data provided by E. Trinkaus
Dolnì Vestonice 3, 13, 14, 16 and 35	EUP	3	*(31)*	*(31)*
Grotte des Enfants 4	EUP	3	Data provided by E. Trinkaus	Data provided by E. Trinkaus
La Rochette	EUP	3	*(32)*	
Mladec 27	EUP	3	*(23)*	
Nahal Ein Gev	EUP	3	Data provided by E. Trinkaus	
Paglicci 25	EUP	3	Data provided by E. Trinkaus	
Parabita 1 and 2	EUP	3	Data provided by E. Trinkaus	Data provided by E. Trinkaus
Paviland	EUP	3	*(33)*	Data provided by E. Trinkaus
Pavlov 1	EUP	3	*(32)*	*(31)*
Predmost 3, 4, 9, 10 and 14	EUP	3	*(34)*	
Sunghir 1 and 4	EUP	3	Data provided by E. Trinkaus	Data provided by E. Trinkaus
Willendorf A	EUP	3	*(14)*	

clude multiple cutmarks on all sides of the diaphysis (Figure1). Cutmarks and anthropic fractures have been observed on other human remains from Les Pradelles *(10)*. In the case of this femur, these features are presumably linked to flesh removal and bone marrow extraction activities.

The *linea aspera* is continuous and undivided along the entire shaft. Proximally it is marked with irregular sharp edged tuberosities at midshaft. Distally, the line broadens, becoming smoother and less marked. On anatomically modern humans, the *linea aspera* and the pilaster are structurally associated; like other Neandertal specimens, the LP femur exhibits no pilaster, *(12, 16, 17, 40)*. There is no nutrient foramen visible on the diaphysis. There may not have been a nutrient foramen, which is the case in 3% of the femora in one living population *(41)*. Alternatively, the nutrient foramen may have been located more distally, which occurs in 41% of this same extant population *(42)*. Despite the specimen's state of preservation, the anterior curvature, a distinctive feature of Neandertal femoral diaphyses *(12, 21, 29)*, is apparent. Like other Neandertal diaphyses, in cross-section, the medial face is regularly convex, except in the posteromedial side, where the medial buttress is well developed *(18, 19)*. The lateral face has an irregular convexity with a flat posterolateral portion.

On the medial side of the *linea aspera*, and close to the proximal end, an oval swelling 7 mm long and 4 mm wide is encircled by numerous foramina. The osseous bulge and related hypervascularization of the zone may be a consequence of a bone reaction (as a myositis ossificans) *(42, 43)*, which may be linked to the *linea aspera* tuberosities. A few osseous reactions have been described on Neandertal limb bones, however their origins (genetic, environmental, mechanical, infectious), are difficult to determine *(44)*, especially when their morphology differs from that observed on the bones of modern peoples. So its interpretation as a pathological or a mechanical response to a stress remains indeterminate.

On the distal part of the bone, a vascular imprint of one branch of the deep femoral artery (*A. Profunda Femoris*) is present and well-marked with a Y shape. The imprint begins on the *linea aspera* and continues transversally on the medial side of the bone. To our knowledge, such a vascular print has never been described on a Neandertal femoral diaphysis. The posterior surface is slightly irregular on the proximal third of the bone, an irregularity that extends laterally from the *linea aspera*. It

TABLE 2

Comparative diaphyseal diameters and cross-sectional geometric properties of the Les Pradelles femoral midshaft and the reference groups.

		M6 (SaD)	M7 (TrD)	IndPil	TA	CA	%CA	Ix	Iy	Ix/Iy	Imax	Imin	Imax/Imin	J
LP		33,1	29,2	113,6	701.1	576.9	82.3	34256	41581	0.82	45580	30257	1.51	74838
NEAND	m	30,4	30,3	100,6	660.5	531.2	80.5	33768	35624	0.94	39372	29943	1.33	69315
	s	3,4	1,9	9,6	112.5	91.5	3.9	11407	10226	0.13	12200	9590	0.17	21196
	n	19	19	21	16	16	16	16	16	16	16	16	16	16
MPMH	m	32,7	26,6	121,6	657.6	513.1	78	42363	28522	1.48	43593	27292	1.60	70885
	s	7,5	4,1	15	98.4	82.8	3.5	15920	7548	0.37	15098	8208	0.30	22225
	n	9	9	9	8	8	8	8	8	8	8	8	8	8
EUP	m	32,1	27,4	116,9	625.4	453.8	72.5	38444	24929	1.53	39217	24527	1.59	63410
	s	4,1	2,4	10,1	99.2	107.1	11.2	14411	7854	0.34	13678	7611	0.18	21855
	n	29	29	29	17	17	17	17	17	17	17	17	17	17
Adjusted Z-scores														
LP vs NEAND		0,375	–0,29	0,638	0,159	0,220	0,196	0,019	0,257	–0,383	0,225	0,014	0,454	0,136
LP vs MPMH		0,023	0,256	–0,22	0,166	0,290	0,454	–0,191	0,650	–0,663	0,049	0,136	–0,116	0,084
LP vs EUP		0,125	0,352	–0,157	0,340	0,512	0,388	–0,129	0,945	**–1,462**	0,205	0,332	–0,202	0,253

Legend: m = mean; s = standard deviation; n = number of individuals. M6(SaD) = sagittal diameter (mm), M7 (TrD) = transverse diameter (mm); IndPil = pilastric index; TA = Total area (mm2), CA = Cortical area (mm2); %CA = percent of cortical area; Ix = antero-porterior second moment of area (mm4); Iy = medio-lateral second moment of area (mm4), Imax = maximum second moment of area (mm4); Imin = minimal second moment of area (mm4); J = polar moment of area (mm4). For the adjusted z-scores, ± 1.00 encompasses the 95% limits of variation of the reference samples.

probably corresponds to the insertion area of *M. Vastus Lateralis*.

Table 2 summarized the mid-diaphyseal dimensions of the LP femur and the variation range of comparative groups.

Its mid-diaphyseal dimensions (M6, M7 and IndPil) are within the range of variation of Neandertals, as well as the sample from the MPMH and EUP. The sagittal and transverse diameters of the LP femur are closer to the MPMH mean, while its pilastric index is closer to the EUP mean (Table 2). The relatively high sagittal diameter and pilastric index of the LP femur, compared to the NEAND mean, are probably attributable to the *linea aspera* tuberosities. According to the Z-scores results on table 2, the LP transverse diameter is closer to the MPMH mean, with a weak Z-score. Taking into account the differences in standard deviation between the two comparative groups, the LP transverse diameter is effectively closer to the Neandertal mean.

If individual measurements are compared, the LP femur is closer by its mid-diaphyseal dimensions to Fond-de-Forêt 1, Feldofher 1, la Chapelle-aux-Saints 1 and Saint-Césaire 1 *(14, 23, 26)*. Twiesselmann *(14)* suggests that the values of Fond-de-Forêt "are considerable", as is also the case for Les Pradelles.

Cross-sectional geometry

The geometric properties of the lower limb result from a combination of an individual's activity level and the body mass *(45, 46, 47, 48)*. Biomechanical interpretations of the lower limb cross-sectional geometric properties should be isolated from the influences of body mass and stature *(47)*. When scaling body mass is impossible, the use of powers of bone length is strongly recommended *(47, 49)*. Because the state of preservation prevents the accurate estimation of total length, it is not possible to scale the cross-sectional dimensions of the LP femur. Cross-sectional parameters are useful only as descriptors of the bone distribution along the mid-diaphysis section and in comparisons with the reference groups. Table 2 presents the mid-diaphyseal cross-sectional parameters of the LP femur and the comparative samples.

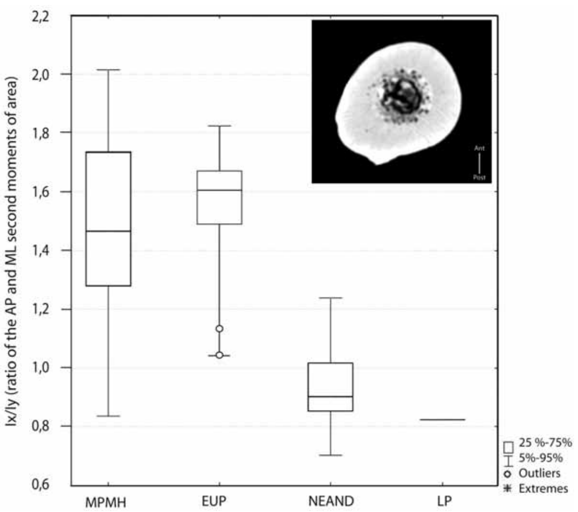

Figure 2. *Ratio of the anteroposterior and mediolateral second moment of area.*

All the cross-sectional geometric properties at mid-diaphysis of the LP femur clearly lie within the range of Neandertal variation. Its parameters are closer to the Neandertal mean than to the other comparative groups, with the exception of Imax, the ratio of Imax/Imin and J for which it is closer to the MPMH sample mean, with a weak Z-score. For the ratio of the anteroposterior and mediolateral second moments of area (Ix/Iy), LP stands in the lower part of the Pleistocene modern human range and outside of the European modern human range (Z-score higher than 1). The LP cross-section exhibits a high percentage of cortical area (%CA). According to Ruff *et al. (46)*, the proportion of cortical bone in the femoral diaphyses tends to decrease, through time, until extant modern humans. Within our samples, a significant difference is only found between the NEAND sample and the EUP modern human group: the Neandertals have a higher percentage of cortical area, but smaller variance. The most striking difference between Neandertals and modern humans, also present as the Neandertal-like in the femoral fragment from Les Pradelles, is in the bone distribution of the section along the anteroposterior and mediolateral axes and the shape of the section.

As illustrated by the ratio of the two second moments of area following these axes (Figure 2), Neandertals present an ovoid section at midshaft with transverse reinforcement of the femoral diaphysis. In sharp contrast with modern humans Neandertal specimens lack the pilaster; however a medial buttress has been observed in several Neandertal specimens *(18, 19)*.

3D virtual modeling

The cortical thickness variation cartography (Figure 3) shows lateral and medial reinforcements, with the medial buttress, the most strongly marked. Appart from the osseus tuberosities on the *linea aspera*, the medial buttress represents the maximum thickness on the diaphysis. The anterior side of the diaphysis is less thick because there are no muscle points of attachment which need reinforcement.

DISCUSSION AND CONCLUSIONS

Neandertal remains from the Mousterian site of les Pradelles, including the left femoral diaphysis discovered in 2010, show evidence of anthropic treatment including cutmarks and fracture. This femur presents many features observed on Neandertal femoral diaphyses. It possesses a well-marked anteroposterior convexity and a medial buttress, and it lacks a pilaster. According to Trinkaus *(16)*, the absence of pilaster among Neandertals "is due to their relatively wide diaphysis and secondarily related to their general femoral reinforcement". In contrast, the

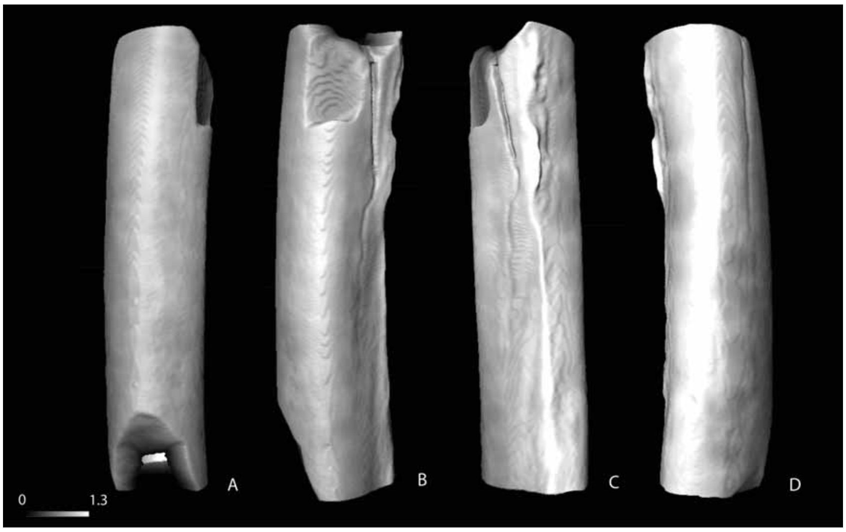

Figure 3. *CT-based 3D mapping of the topographic distribution of the cortical bone thickness in the LP10-D13 #362 left femoral diaphysis. A: lateral side, B: anterior side, C: medial side, D: posterior side.*

absence of a pilaster on modern human femora would be a feature of slender diaphyses *(13)*. The decreased anterior femoral curvature appears to be related, from biomechanical perspectives, to modifications of mobility *(21)*. The LP femur mid-diaphyseal diameters differ from the Neandertal mean because of exostoses on the *linea aspera* which tends to increase the sagittal diameter, and by consequence the pilaster index. Diaphyseal cross--sectional geometric properties of the LP femoral midshaft align with Neandertal variation: it clearly presents a high percentage of cortical bone and a ratio of the two second moments of area which indicate an ovoid section. Those features are present on all Neandertal femoral diaphyses, in contrast with modern human femurs *(18, 20, 23, 46)*. The first feature, a decreased %CA from Neandertals to EUP, may be related to decline over time in mechanical loading of the skeleton *(46)*. According to Ruff and Hayes *(50)*, a circular cross-sectional shape can result from combined bending loads applied in two perpendicular planes.

These morphological and metrical data place the femur of les Pradelles within the range of variation of European Neandertals. The data presented here reinforce our scant knowledge on MIS 4 Neandertal variability in Europe. The data also support differences in morphological and biomechanical patterns between Neandertals and modern humans which may be related to biomechanical stresses (loadings, mobility) *(21, 46, 47)*.

Acknowledgments: *We would like to thank Dr Erik Trinkaus for providing comparative data, Christianne Macauley for help with the text, the french Ministère de la Culture et de la Communication, the Service Régional de l'Archéologie from Poitou-Charentes, particularly Mr Jacques Buisson-Catil, the CNRS, Princeton University, the UMR5199-PACEA, the Charente department and the Transitions convention 20051403003AB from the Aquitaine region.*

REFERENCES

1. VANDERMEERSCH B 1976 Les Néandertaliens de Charente. *In*: Lumley D H (*ed*) La Préhistoire française. CNRS, Paris, p 584–587
2. MAUREILLE B, MANN A, BEAUVAL C, BORDES J-G, BOURGUIGNON L, COSTAMAGNO S, COUCHOUD I, LACRAMPE-CUYAUBERT F, LAUROULANDIE V, MARQUER J-C, MEIGNEN L, TEXIER J-P, VANDERMEERSCH B, Le gisement Moustérien des Pradelles (Marillac-le-Franc, Charente): passé, présent, futur, XXVIème congrès préhistorique de France, Avignon, 2004, 2007, p 249–261
3. BOURGUIGNON L 1997 Le Moustérien de type Quina : nouvelle définition d'une entité technique, Thesis of the Paris X-Nanterre University.
4. MEIGNEN L, COSTAMAGNO S, BOURGUIGNON L, BEAUVAL C, MAUREILLE B 2010 Approche interdisciplinaire d'une halte de chasse au Paléolithique moyen. *In*: Buisson-Catil J, Primault J (*ed*) Préhistoire entre Vienne et Charente. Hommes et sociétés du Paléolithique. Association des publications chauvinoises, Chauvigny, p 163–166
5. COSTAMAGNO S, BEAUVAL C, LANGE-BADRÉ B, VANDERMEERSCH B, MANN A, MAUREILLE B 2005 Homme ou carnivores? Protocole d'étude d'ensembles osseux mixtes: l'exemple du gisement moustérien des Pradelles (Marillac-le-Franc, Charente). *Archaeofauna 14:* 43–68
6. COSTAMAGNO S, MEIGNEN L, BEAUVAL C, VANDERMEERSCH B, MAUREILLE B 2006 Les Pradelles (Marillac-le-Franc, France): A mousterian reindeer hunting camp? *J Anthropol Archaeol 25:* 466–484
7. BINFORD L R 1978 Nunamiut ethnoarchaeology. Academic Press, New York, p 509
8. DAVID P 1935 Les fouilles de l'abri-repaire de Marillac, près de la Rochefoucauld. *Bull. Soc. Archéo. Histo. Char.:* 89–90
9. VANDERMEERSCH B 1971 Marillac. *In*: Oakley K, Campbell B G, Molleson T (*ed*) Catalogue of fossils Hominids Part II : Europe. Trustees of the British Mus (Nat. Hist), London, p 138–139
10. MAUREILLE B, MANN A, BEAUVAL C, BORDES J-G, BOURGUIGNON L, COSTAMAGNO S, COUCHOUD I, FAUQUIGNON J, GARRALDA M-D, GEIGL E-M, GRÜN R, GUIBERT P, LACRAMPE-CUYAUBERT F, LAROULANDIE V, MARQUET J-C, MEIGNEN L, MUSSINI C, RENDU W, ROYER A, SEGUIN G, TEXIER J-P 2010 Les Pradelles à Marillac-le-Franc (Charente). Fouilles 2001–2007: nouveaux résultats et synthèse. *In*: Buisson-Catil J, Primault J (*ed*) Préhistoire entre Vienne et Charente. Hommes et sociétés du Paléolithique. Association des publications chauvinoises, Chauvigny, p 145–162
11. SANCHEZ GONI M F 2006 Interactions végétation-climat au cours des derniers 425.000 ans en Europe occidentale. Le message du pollen des archives marines. *Quaternaire 17:* 3–25

12. BOULE M 1911 L'Homme fossile de La Chapelle-aux-Saints, Masson et Cie, Paris, p 64
13. HRDLIČKA A 1934 Contributions to the study of the femur: The crista aspera and the pilaster. *Am J of Phys Anthropol 19:* 17–37
14. TWIESSELMANN F 1961 Le fémur néanderthalien de Fond--de-Forêt (Province de Liège). *Mem Inst Roy Sci Nat Belg 148:* 1–164
15. ENDO B, KIMURA T 1970 Postcranial skeleton of the Amud man. *In*: Suzuki H, Takai F (*ed*) The Amud Man and his Cave Site. The University of Tokyo, Tokyo, p 231–406
16. TRINKAUS E 1976 The evolution of the hominid femoral diaphysis during the Upper Pleistocene in Europe and the Near East. *Z Morphol Anthropol 67:* 291–319
17. HEIM J-L 1982 Les hommes fossiles de la Ferrassie. Tome II, Masson, Archives de l'Institut de Paléontologie Humaine, Paris, p 272
18. TRINKAUS E, RUFF C B 1989 Diaphyseal cross-sectional morphology and biomechanics of the Fond-de-Forêt 1 femur and the Spy 2 femur and tibia. *Anthropol Préhist 100:* 33–42
19. TRINKAUS E, RUFF C B 1999 Diaphyseal Cross-sectional Geometry of Near Eastern Middle Palaeolithic Humans: The Femur. *Journal of Archaeological Science 26:* 409–424
20. TRINKAUS E, CHURCHILL S E, RUFF C B, VANDERMEERSCH B 1999 Long Bone Shaft Robusticity and Body Proportions of the Saint-Césaire 1 Châtelperronian Neanderthal. *J Archaeol Sci 26:* 753–773
21. SHACKELFORD L L, TRINKAUS E 2002 Late Pleistocene human femoral diaphyseal curvature. *Am J of Phys Anthropol 118:* 359–370
22. WEAVER T D 2003 The shape of the Neandertal femur is primarily the consequence of a hyperpolar body form. *P Natl Acad Sci 100:* 6926–6929
23. BEAUVAL C, MAUREILLE B, LACRAMPE-CUYAUBERT F, SERRE D, PERESSINOTTO D, BORDES J-G, COCHARD D, COUCHOUD I, DUBRASQUET D, LAROULANDIE V, LENOBLE A, MALLYE J-B, PASTY S, PRIMAULT J, ROHLAND N, PÄÄBO S, TRINKAUS E 2005 A late Neandertal femur from Les Rochers-de-Villeneuve, France. *P Natl Acad Sci 102:* 7085–7090
24. MALLEGNI F, MARIANI-COSTANTINI R, FORNACIARI G, LONGO E T, GIACOBINI G, RADMILLI A M 1983 New European Fossil Hominid Material From an Acheulean Site Near Rome (Castel Di Guido). *Am J of Phys Anthropol 62:* 263–274
25. TRINKAUS E 1983 The Shanidar Neandertals. Academic Press, New York, p 502
26. TRINKAUS E 1980 Sexual Differences in Neanderthal Limb Bones. *J Hum Evol 9:* 377–397
27. MARTIN H 1923 Recherches sur l'Evolution du Moustérien dans le gisement de La Quina. Tome 3. L'Homme fossile de La Quina, Doin, Paris, p 264
28. MC COWN T, KEITH A 1939 The stone age of Mount Carmel: the fossil remains from the levalloiso-mousterian, Oxford, p 390
29. VANDERMEERSCH B 1981 Les hommes fossiles de Qafzeh (Israël), Cahiers de Paléontologie (paléoanthropologie). Ed. du CNRS, Paris, p 319
30. SHACKELFORD L 2005 Regional variation in the postcranial robusticity of Late Upper Paleolithic humans, Thesis of the Washington University.
31. SLÁDEK V, TRINKAUS E, HILLSON S W, HOLLIDAY T W 2000 The people of the Pavlovian : skeletal catalogue and osteometrics of the Gravettian fossil hominids from Dolni Vestonice and Pavlov, Brno, p 244
32. KLAATSCH H, LUSTIG W 1914 Morphologie der paläolithischen Skelettreste des mittleren Aurignacien der Grotte von La Rochette, Dordogne. *Archiv Anthropol 41:* 81–126
33. SOLLAS W J 1913 Paviland Cave : an Aurignacian Station in Wales. *J Roy Anthropol Inst G Brit Ir 43:* 325–374
34. MATIEGKA J 1938 Homo Predmostensis. Folsilní Clovek z Predmostí na Morave II, Ceská Akademie Ved a Umení, Prague, p 91
35. MARTIN R 1914 Lehrbuch der Anthropologie, Fisher *(ed)*. Jena, p 1181
36. MAUREILLE B, ROUGIER H, HOUET F, VANDERMEERSCH B 2001 Les dents inférieures du Néandertalien Regourdou 1 (site de Regourdou, commune de Montignac, Dordogne) : Analyses métriques comparatives. *Paléo 13:* 183–200
37. RUFF C B, LEO F P 1986 Use of Computed Tomography in Skeletal Structure Research. *Am J of Phys Anthropol 29:* 181–196
38. ABRÀMOFF M D, MAGELHAES P J, RAM S J 2004 Image Processing with Image. *J Biophot Int 11:* 36–42
39. SPOOR F C, ZONNEVELD F W, MACHO G 1993 Linear Measurements of Cortical Bone and Dental Enamel by Computed Tomography: Applications and Problems. *Am J of Phys Anthropol 91*: 469–484
40. TRINKAUS E 1997 Appendicular robusticity and the paleobiology of modern human emergence. *P Natl Acad Sci 94:* 13367–13373
41. MYSOREKAR V R 1967 Diaphysial nutrient foramina in human long bones. *J Anat 101:* 813–822
42. ORTNER D J 2003 Identification of pathological conditions in Human skeletal remains. Academic Press, p 645
43. VILLOTTE S 2008 Enthésopathies et activités des Hommes préhistoriques. Recherche méthodologique et application aux fossiles européens du Paléolithique supérieur et Mésolithique. Thesis of the Bordeaux 1 University, Talence, p 380
44. MARIOTTI V, BELCASTRO M G 2011 Lower limb entheseal morphology in the Neandertal Krapina population (Croatia, 130 000 BP). *J Hum Evol 60:* 694–702
45. RUFF C B, SCOTT W Q, LIU A-C 1991 Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am J of Phys. Anthropol 86:* 397–413
46. RUFF C B, TRINKAUS E, WALKER A, LARSEN C S 1993 Postcranial Robusticity in Homo. *In:* Temporal Trends and Mechanical Interpretation. *Am J of Phys. Anthropol 91:* 21–53
47. RUFF C B 2008 Biomechanical analyses of archaeological human skeletons. *In*: Katzenberg M A, Saunders S R (*ed*) Biological Anthropology of the Human Skeleton. Alan R. Liss, New York, p 183–206
48. LIEBERMAN D E, DEVLIN M J, PEARSON O M 2001 Articular area responses to mechanical loading: effects of exercise, age, and skeletal location. *Am J of Phys Anthropol 116:* 266–277
49. SMITH R J 2005 Relative size versus controlling for size. Interpretation of ratios in research on sexual dimorphism in the human corpus callosum. *Curr Anthropol 46:* 249–273
50. RUFF C B, HAYES W C 1983 Cross-Sectional Geometry of Pecos Pueblo Femora and Tibiae- A Biomechanical Investigation: 1. Method and General Patterns of Variation. *Am J of Phys Anthropol 60:* 359–381