

The Endostructural Pattern of a Middle Pleistocene Human Femoral Diaphysis From the Karain E Site (Southern Anatolia, Turkey)

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ABSTRACT *Objective:* The human femur from Karain E Cave (Turkey) exhumed from a Mousterian level provided the opportunity to make an incursion into the structural morphology of a late adolescent, or a young adult, femoral shaft from the late Middle Pleistocene of Anatolia.

Methods: Considering the chrono-ecogeographical context, this study focuses particularly on the endostructural morphological similarities between Karain and Neanderthal fossils.

Results: Comparative analysis shows that some femoral features of the Karain specimen are frequently observed in Neanderthals, in comparison to some Middle Pleistocene *Homo* and Middle/Upper Paleolithic modern humans. In particular, we note a high degree of circularity and a strong midshaft posteromedial reinforcement of cortical thickness on the medial side. According to the mapping of cortical thickness, this latter feature can be

related to the medial spiral distribution pattern of cortical thickness in the mid-proximal shaft, which is present at Karain and in all Neanderthals available for this study. This spiral distribution was not identified in recent modern humans and may be absent from ancient *Homo* with femoral pilaster.

Conclusions: The endostructural signature of Karain could indicate a similar biomechanical strain system to that of Neanderthals that could be linked to body shape. However, the presence of posteromedial reinforcement in Berg Aukas may point to an ancestral feature and may be independent of latitude. A larger comparative sample should further clarify the taxonomical, biomechanical, and chrono-ecogeographical origins of the structural femoral features observed in an evolutionary Neanderthal context from MIS 7-9 in Karain. *Am J Phys Anthropol* 157:648–658, 2015. © 2015 Wiley Periodicals, Inc.

Over the past 15 years, postcranial robusticity and shape have become accessible through the quantification of geometric cross-sectional properties and these parameters are now frequently used for the analysis of hominin fossils (e.g., Ruff et al., 1993; Holt, 1999, 2003; Trinkaus and Ruff, 1999, 2012; Marchi et al., 2006; Shackelford, 2007; Cowgill, 2008; Marchi, 2008; Ruff, 2008; Harrington, 2010; Puymerau et al., 2012a,b; Bleuze, 2012; Chevalier, 2013; Shaw and Stock, 2013). These properties supplement the abundant compilation of more traditionally used external data. Variations in shape and rigidity extracted from the analysis of the internal structure of fossil and recent specimens result from complex multifactorial influences (i.e., systemic) (Lieberman, 1996; Lovejoy et al., 2003; Devlin and Lieberman, 2007; Wallace et al., 2014), in which body proportions (Ruff, 1995, 2000; Weaver, 2003; Ruff et al., 2006; Trinkaus and Ruff, 2012) and habitual behavior or biomechanical loading regimes (Currey, 1984; Lanyon, 1992; Trinkaus et al., 1994; Ruff et al., 2006; Shaw and Stock, 2009a,b; Marchi and Shaw, 2011; Shaw and Ryan, 2012; Warden et al., 2014), play a major role in the structure of lower limb long bones. Thereby, caution should be exercised when studying the biomechanical

characteristics of fossil bones from contrasting geographical and chronological contexts. Ecogeographical variations can produce variations in body proportions and thus lead to variations in biomechanical/structural properties (e.g., Ruff, 1995; Trinkaus and Ruff, 1999, 2012). We can assume from these studies that a more general pattern of internal structure (e.g., the pattern of cortical

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distribution) could be related to ecogeographical variations.

The objective of this article is to present a hitherto unpublished descriptive and comparative study of a Middle Pleistocene (MP) femoral shaft from Karain E Cave in the south of Anatolia in Turkey. The use of a comparative sample from a broad chronological and (eco-) geographical context, which has been described as having “warm adapted” or “cold adapted” body proportions, allows for a better appreciation of the singular femoral structure of the Karain specimen. However, considering the chrono-ecogeographical context, we focus on the structural morphological similarities between the European late MP human femur from Karain and Neanderthals in comparison to Middle/Upper Paleolithic (UP) modern humans and MP *Homo* particularly, with special attention to the distribution of cortical bone thickness.

MATERIALS

Archaeological and chronological context

The Karain E left femoral shaft was discovered in 1996 in the geological level III-4 and the archaeological level 38, in the silts and clays of the third paleosol of archaeological unit E, containing levels III-3 to III-5 (Otte et al., 1998). The fauna is made up of *Ovicapra*, *Dama dama*, *Cervus elaphus*, *Cervus capreolus*, and *Hippopotamus* (Otte et al., 1998). This archaeological level contains lithic material from the Middle Paleolithic Charentian complex, with a wide variety of side scrapers and denticulates (Otte et al., 1998). New observations suggest that this level is a cultural transition between the Charentian Mousterian and the Zagros or Karain-type Mousterian. Levels older than Karain E contain Proto-Charentian elements. As the femur-bearing level was not directly dated, we can propose a minimum age according to the absolute dating of the overlying level and a maximum age based on the lithic elements associated with the femur (i.e., Middle Paleolithic). The femur from Karain is stratigraphically located in an older layer than the Karain E mandible from level III-2, with an age ranging from 200,000 to 250,000 years [level III-2 from MIS 7-9 by thermoluminescence (TL), Valladas and Mercier in Otte et al., 1998; see also level I6-I7 from MIS 5 by Electron Spin Resonance (ESR) in Rink et al., 1994; see furthermore, Otte et al., 1995]. For the maximum age, we compiled the earliest sites with Middle Paleolithic remains in Europe and the Near East. The oldest Middle Paleolithic lithic series in Europe are chronologically positioned between MIS 9 and 7 with *Petit Bost* (Bourguignon et al., 2008), *Vaufrey* (Rigaud, 1988), and *Orgnac* (Michel et al., 2013; see also for the Middle Paleolithic, Turq et al., 2013; Wiśniewski, 2014). Michel et al. (2013) postulate that their new U/Th dates for Orgnac 3 support “the claim that the Early Middle Paleolithic emerged in Europe about 300,000 years ago.” In the Levant, the Middle Paleolithic and early Mousterian Levallois technology appears to begin during the 300,000- to 200,000-year interval in Tabun and Hayonim (Bar-Yosef, 1998; Shimelmitz and Kuhn, 2013; Mercier and Valladas 2003; Mercier et al., 2007), Rosh Ein Mor (Rink et al., 2003), and Qesem (Barkai et al., 2003; Shea, 2003). The data from Barkai et al. (2003) concerning Qesem Cave in Israel point to a long cultural transition phase between 382,000 years and 200,000 years, rather than to an abrupt transition.

Overall, these data indicate that the Karain E femoral shaft is unquestionably a MP specimen, probably chronologically situated in the MIS 7–9 interval.

Preservation and morphology

Most of the Karain shaft is preserved, from the distal metaphyseal line to about 1 cm below the lesser trochanter (Fig. 1). The middle portion of the femoral diaphysis is well preserved although slight damage affects the subperiosteal bone anteriorly, and the ends display substantial damage. Three fragments belonging to the distal epiphysis were also identified: the lateral condyle, a portion of the intercondylar zone, and part of the patellar surface. None of these fragments overlap anatomically. The lateral condyle is directly connected to the diaphysis. The three distal epiphyseal fragments, discovered in the same layer and the same zone (E15), seem to belong to the same femur.

Morphologically, diaphyseal curvature is well marked by a laterally offset proximal shaft axis in posterior view and by an anteroposterior curvature. The pectineal line is very slightly salient. The gluteal tuberosity is not clearly identified below and above the nutrient foramen (which is situated in the middle of a salient ridge). The gluteal tuberosity continues distally along a line joining the short head biceps femoris and the vastus lateralis muscle insertion lines. The medial line, which confounds the vastus medialis insertion line and the insertion ridge along the adductor longus, is the most prominent of the linea aspera, particularly in the proximal portion. At midshaft, it is located at the top of the maximum anteroposterior extension of the shaft body. This maximum extension is bordered by a posterolateral depression. We note a bulge on the posteromedial surface. Distally, it is not possible to identify the usual salient lateral supracondylar line.

Comparative samples

The Karain E late adolescent, or young adult, femoral shaft was compared to adult specimens for four distinct reasons. First, given the advanced ontogenetic development stage of the Karain femur (at least 16–18 years in comparison to extant populations), it is reasonable to assume that the internal and external particularities of this femur would not be radically impacted by the structural modifications occurring before adulthood (argument developed in the discussion). Second, only the Neanderthal adults present a clear description of Neanderthal features. Third, we note the absence of MP and Neanderthal immature femurs with a similar age to the Karain specimen. All the Neanderthal immature specimens are less than 10 years old. Fourth, there is a non-zero possibility that the Karain femur belongs to an adult. Finally, it should be noted that the immature specimens Arene Candide 1 and Dolní Věstonice 14 were used by Trinkaus and Ruff (2012) as adult specimens whereas Cowgill (2008) incorporated them with the immature samples, with respective ages of 16.4 and 17.5 years.

The samples used for comparisons include *Homo* from the MP, Neanderthal (NEA), Middle (MPMH), and UP anatomically modern humans. Some very limited comments about the cortical distribution at midshaft are added for the Early Pleistocene *Homo* (KNM ER 1481, BOU VP 2/15, BOU VP 19/63, KNM ER 1808, Kresna11). The samples are presented in Tables 1 and 2



Fig. 1. Human left femoral shaft from Karain E and mapping of cortical bone thickness distribution: posterior view (a–c) and medial view (b–d). Color scale thickness in millimeters. The colors are observable in the Web version of this article. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

and references are included in the footnotes. An additional sample of 34 recent Belgian femora (see more details below in the section on the estimation of the biomechanical length of Karain) has been used to observe the distribution of cortical thickness at midshaft.

METHODS

Age-at-death

The distal end of the femoral shaft and the associated lateral condyle reveal the fusion stage of the Karain specimen, in spite of the degradation of the bone (Supporting Information Fig. A1). One part of the diaphysis is clearly fused with the epiphysis (intercondylar area), and another part is not totally fused (condyle internal area). More precisely, on the distal end of the shaft, a restricted portion of the smooth intercondylar zone clearly indicates that part of the distal epiphysis is totally fused with the metaphysis. At the same time, the only preserved physis surface ($<1 \text{ cm}^2$) presents several foramens, as does the internal proximal portion of the lateral condyle. Baker et al. (2005) indicate that fusion occurs in late adolescence and during the early adult stage, between the ages of 15 and 20 years for extant populations, pointing out that a 15-year-old specimen would still bear a noticeable fusion line along the whole physis outline. Considering the intercondylar area in

Karain, its stage of growth is later than a 15-year-old extant specimen because the physis outline is not apparent in the intercondylar area. Thus, we consider Karain to be at least a late adolescent (>16 years old in reference to extant populations).

External morphology

The extensive references for the external measurements are presented in Table 3. Even though reference is often made to the circularity of Neanderthal diaphyses (e.g., Boule, 1912; McCown and Keith, 1939; Weidenreich, 1941; Trinkaus, 1976, 1983; Vandermeersch, 1981; Churchill, 1998; Trinkaus and Ruff, 1999; Weaver, 2003, 2009), the degree of circularity had never been measured. It was thus calculated for this study. The degree of circularity is defined by the ratio between the area of the smallest circle containing the midshaft section and the total area of the midshaft section, multiplied by 100. The anteroposterior (APD) and mediolateral diameters (MLD) were taken at midshaft. The popliteal surface and the linea aspera were chosen as a reference plane for the posterior surface. With these diameters, we calculated the pilastric index [$\text{Ipil} = (\text{APD}/\text{MLD}) \times 100$], in addition to the degree of circularity. This latter could vary considerably for the same pilastric index depending on the concavity of its posterior sides (lateral and medial).

TABLE 1. External measurements at midshaft from Pleistocene femora

	APD ^a	MLD ^a	Pilastric index ^a	Degree of circularity ^b	Biomechanical length ^c
Karain	27.7	27.6	100.4	86.8	(402.3)
MP					
<i>N</i>	21	21	22	11	5
Mean	26.9	28.6	94.8	78.8	385.6
Range	21.5–35	24–33	77.5–116.3	64.4–89.9	364–425
SD	3.4	2.3	11.3	7.2	24.5
NEA					
<i>N</i>	26	26	26	20	12
Mean	30.3	29.9	101.2	83.5	414.3
Range	22–36.5	24.1–35.7	81.5–125.4	75.5–91.5	360–458
SD	3.8	2.8	10.3	4.6	30.4
MPMH					
<i>N</i>	12	12	12	8	6
Mean	34.5	27.9	124.2	67.9	456.1
Range	27.5–41.3	26–32.4	105.7–142.5	57.9–84.3	430–477
SD	3.8	2.3	11.1	8.5	17.2
UP					
<i>N</i>	61	61	63	22	23
Mean	30.6	26.5	115.5	72.8	420.4
Range	21–40	22–33.8	89.7–142.8	58–87.9	332–486
SD	4.5	2.5	13	8.2	46.9

^aRaw data from Sollas (1913), Klaatsch and Lustig (1914), Martin (1923), Matiegka, (1938), McCown and Keith (1939), Weidenreich (1941), Twisselmann (1961), Vallois and Billy (1965), Endo and Kimura (1970), Day (1971), Day and Molleson (1973), Trinkaus (1976), Arensburg (1977), Vandermeersch (1977), Baba and Endo (1982), Heim (1982), Kennedy (1983), Mallegni et al. (1983, 1987, 1999, 2000), Mallegni (1986), Formicola (1990), Bidittu et al. (1989), Hublin (1992), Kunter and Wahl (1992), Trinkaus and Jelinek (1997), Condemi (2001), Teschler-Nicola and Trinkaus (2001), Beauval et al. (2005), Trinkaus et al. (2006), Trinkaus and Ruff (2012), Mussini et al. (2012), and Puymerau et al. (2012b). Data from Karain and Dame du Cavillon were provided by the authors.

^bSections used for calculating the degree of circularity from Matiegka (1938), Heim (1982), Hublin (1992), Trinkaus (1997, 2006), Trinkaus et al. (1999a,b), Trinkaus and Ruff (1999), Condemi (2001), Mednikova and Trinkaus (2001), Teschler-Nicola and Trinkaus (2001), Puymerau et al. (2012b), and Mussini et al. (2012). Section collected by cast for this study: Middle Pleistocene (OH28, OH34, Zhoukoudian 4, 5, 6, Castel di Guido 1, Ponte Mammolo, Sedia del Diavolo), Neanderthal (Croce Bisceglie), Middle Paleolithic modern human (Skhul 4 I, r, 5, Qafzeh 3), Upper Paleolithic (Cro-magnon 1). Section collected by CT scan for this study: Middle Pleistocene (Karain, Erhingsdorf 5), Neanderthal (Hohlenstein, Spy 16, Spy 8, La Chapelle-aux-Saints), and Upper Paleolithic (Dame du Cavillon).

^cRaw data from Sládek et al. (2000) and Trinkaus and Ruff (2012). The Karain-estimated biomechanical length comes from this study.

MP, Middle Pleistocene; NEA, Neanderthal; MPMH, Middle Paleolithic modern human; UP, Upper Paleolithic; APD, anteroposterior diameter; MLD, mediolateral diameter.

CT scan

The Karain femur was scanned in Ankara University Faculty of Veterinary Medicine Department of Surgery using a GE medical system (ingido 2) CT scanner. The scans were made in the transversal plane (helical scan type). Scans were obtained using 100 kv, 80 ma by the operator, with a Voxel size of $0.625 \times 0.625 \times 1$ (mm). The mapping of the distribution of cortical thickness and the observation of the diaphyseal cross-sections in addition to the bibliographic sources required the use of the CT scan data from the Open source information platform Nespos/Evan (Erhingsdorf, Hohlenstein), the National Museum of Natural History from Paris (La Ferrassie 1; La Chapelle-aux-Saints), the Royal Belgian Institute of Natural Sciences [Spy 8, 16 (also named Spy2), Fond-de-Forêt], and the Laboratory of Anatomy, Biomechanics and Organogenesis from the Faculty of Medicine/University of Brussels (39 20th century modern humans). The femurs from the “Dame du Cavillon” (formerly known as Menton Man), included in the group of UP humans, underwent a CT scan at the Monceau Clinic (Paris), as part of (ongoing) research for a site monograph. The mapping of cortical thickness distribution was carried out with the *Avizo 7.1* software using semi-automatic segmentation associated with manual correction.

Geometric properties

The biomechanical length and internal measurement references were taken from Sládek et al. (2000) and Trinkaus and Ruff (2012) and from Lovejoy (1982), Holt (1999), Sládek et al. (2000), Trinkaus and Ruff (2012), Mussini et al. (2012) and Puymerau et al. (2012a,b), respectively. The cross-sectional geometric (CSG) properties used are the total subperiosteal (TA, mm²) and cortical areas (CA, mm²), the second moments of area (mm⁴) along the anteroposterior (*I_x*) and mediolateral (*I_y*) axes, the maximum (*I_{max}*) and minimum (*I_{min}*) second moments of area (mm⁴) and the polar second moment of area (*J*, mm⁴). The CSG parameters were obtained using ImageJ (rsb.info.nih.gov/ij/) and MomentMacro (www.hopkinsmedicine.org/faq/mmacro.htm). The cross sections are measured at the conventional cross section for adults at 35%, 50%, and 65% of the biomechanical length. Although the Karain shaft is almost totally preserved, it was not possible to measure the cross-sectional properties at 80% and 20% of the biomechanical length on account of the proximal fracture and the badly damaged distal portion. The cross section at 50% of biomechanical length was identified easily using the middle of the shaft and the maximum pilaster development (following the recommendations of Trinkaus and Ruff, 2012). Cross sections at 65% and 35% of the

TABLE 2. Cross-sectional geometric properties from Karain and Pleistocene femora at 35%, 50%, and 65% of the biomechanical length

	35%					50%					65%				
	TA	CA	%CA	Ix/Iy	J	TA	CA	%CA	Ix/Iy	J	TA	CA	%CA	Ix/Iy	J
Karain	592.3	331.2	55.9	1.14 ^a	44,799	530.9	406.8	76.6	0.94 ^b	42,755	497.8	425.3	85.4	0.75 ^c	39,046
MP															
N	5	5	5	4	5	16	16	16	16	16	5	5	5	5	5
Mean	550.2	419.8	75.6	0.97	46,489	571.4	482.4	84.7	0.93	53,875	518	448.2	86.9	0.69	43,653
Range	394–772	262–628	66.5–83	0.75–1.29	22,445–82,359	373–814	316–708	71.2–94.3	0.59–1.42	22,408–102,649	404–622	336–543	72.5–94.4	0.5–0.9	26,364–60,708
SD	141.7	131.6	7.8	0.27	22,369	128.5	108.3	6.2	0.25	24,754	84.1	73.6	9.2	0.17	13,391
NEA															
N	10	10	10	10	10	20	20	20	20	20	16	16	16	16	16
Mean	691.9	468.6	67.8	1.09	69,180	652	522.7	80	0.93	67,581	619.1	521.8	84.6	0.83	62,365
Range	535–776	381–599	60.7–77.3	0.89–1.31	40,915–91,588	390–813	284–660	66.2–88.1	0.7–1.24	23,972–99,704	386–770	327–701	73.1–95.2	0.5–1.35	23,223–94,367
SD	77.3	63.2	4.7	0.32	15,465	114.2	99.7	5.1	0.13	21,260	114.8	94.9	5.8	0.19	21,077
MPMH															
N	6	6	6	6	6	10	10	10	10	10	6	6	6	6	6
Mean	672.3	468.6	70.8	1.41	69,184	656.7	510.2	77.8	1.53	70,790	683.7	577.3	85	1.23	73,662
Range	502–804	363–625	64.4–85.6	1.05–1.9	37,832–98,109	520–775	403–636	69.1–84.6	0.84–2.22	41,505–102,428	558–768	503–664	70.7–95.4	1.06–1.42	49,400–94,031
SD	101.8	88.2	8	0.25	20,468	95	74.5	4.4	0.38	21,120	91.8	69.4	8.9	0.14	18,064
UP															
N	27	27	27	27	27	39	39	39	39	39	32	32	32	32	32
Mean	615.1	374.5	61.7	1.22	53,881	579.3	442.9	76.6	1.44	55,697	575.2	471.6	82.2	1.08	53,886
Range	414–878	245–492	48.7–86.9	0.77–1.78	22,950–106,166	327–790	236–642	54.3–93.4	0.86–2.6	15,920–109,490	354–798	284–702	68.5–95.9	0.72–1.63	19,510–102,291
SD	118.5	71.3	9.9	0.25	20,428	120	99	7.2	0.36	23,643	119.1	100.3	5.6	0.26	21,805

Raw data from Lovejoy (1982), Holt (1999), Sládek et al. (2000), Trinkaus and Ruff (2012), Mussini et al. (2012), and Puymeraul et al. (2012a,b).

^a 35% section: $I_x = 23,837.1$, $I_y = 20,961.9$.

^b 50% section: $I_x = 2,071.1$, $I_y = 22,043.9$.

^c 65% section: $I_x = 16,782.2$, $I_y = 22,264.1$.

MP, Middle Pleistocene; NEA, Neanderthal; MPMH, Middle Paleolithic modern human; UP, Upper Paleolithic; TA, total area; CA, cortical area; %CA, relative cortical area; I_x , I_y , second moments of area (mm^4) along the anteroposterior (I_x) and mediolateral (I_y) axes; J , polar second moment of area.

TABLE 3. List of specimens used in this study, by group and measurements

Measurements/section	Samples	Specimens	
External morphology Anteroposterior and mediolateral diameter, pilastric index	MP	OH28, Ain Maarouf 1, Zhoukoudian 1, 2, 4, 5, 6, Trinil I, II, III, IV, V, Gesher-B-Ya'acov 1, 2, Venosa Notarchirico 1, Ponte Mammolo 1, Kabwe E690, Castel di Guido 1, 2, Erhingsdorf 5, Sedia del Diavolo 1, La Chaise BD-5	
	NEA	Stadelhöhle 1, Palomas 96, La Ferrassie 1 l,r, La Ferrassie 2 l, r, Croce di Bisceglie, Feldhofer 1 r, l, La Quina H5, Les Rochers-de-Villeneuve, St Césaire 1 (Roche-à-Pierrot), Spy 2 r, l, Fond-de-Forêt 1, La Chapelle-aux-Saints, Amud 1 l, r, Shanidar 4 l, r, Shanidar 5 r, Tabun 1, 3, Les Pradelles, La Chaise-de-Vouthon (CDV-Tour 1)	
	MPMH	Qafzeh 3, 8, 9 r, l, Skhul 3, 4 r, l, 5 r, l, 6 r, l, 7	
	UP	Willendorf 1, Mladeč 27, 78, Paviland 1, Barma Grande 2, Grotte des Enfants 4, Cro-magnon 1 (4327r, 4325l), Cro-magnon 4322 l, Cro-magnon 4324 l, Combe-Capelle r, l, Chancelade, La Rochette 2, Le Roc, Obercassel 1, 2, Lautsh B, Dame du Cavillon r, l, Veyrier l, r, Cap-Blanc l, r, Predmost III l, r, IV l, r, IX l, r, X l, r, XIV l, r, Dolní Věstonice 3 r, l, 13 l, r, 16 l, r, 35, Minatogawa 1 l, r, 2, 3 l, r, 4, Nahal 'En-Gev 1, Ohalo 2 l, r, Paglicci 25, Pavlov 1 l, r, Sunghir 1 l, r, 4, Veneri 1, 2, Zhoukoudian-UC 67, 68	
Degree of circularity	MP	OH28, 34, Ain Maarouf 1, Zhoukoudian 1, 4, 5, 6, Castel di Guido 1, Ponte Mammolo 1, Erhingsdorf 5, La Chaise BD-5	
	NEA	Hohlenstein, Sedia del diavolo, Croce Bisceglie, Spy 8, 16 (Spy 2 l, r), Shanidar 5, Tabun 1, 3, Amud 1, Fond-de-Forêt 1, La Chapelle-aux-Saints, Les Pradelles, La Chaise-de-Vouthon (CDV-Tour 1), La Ferrassie 1 l, r, 2 l, r, Feldhofer 1, St Césaire 1	
	MPMH	Skhul 4 l, r, 5 l, r, 7, Qafzeh 3, 8, 9	
	UP	Cro-magnon 1, 4322, 4324, Willendorf 1, Dame du Cavillon, Dolní Věstonice 3 r, l, 13 l, r, 15 l, r, 16 l, r, 35, Pavlov 1 l, r, Paviland 1, Sunghir 1 l, r, Predmost III, IV, XIV	
Internal morphology 65%	MP	OH28, Ain Maarouf 1, Gesher-B-Ya'acov 1, Broken Hill E690, Tabun E1 d	
	NEA	La Ferrassie 1 l, r, La Ferrassie 2 l, r, La Chaise-de-Vouthon (CDV-Tour 1), Feldhofer 1, La Quina 38, Spy 2, Krapina 257.32, Krapina 257.33, Fond-de-Forêt 1, Palomas 52, 92, 96, Amud 1, Shanidar 6	
	MPMH	Qafzeh 6, 8, 9, Skhul 4 l, r, 5	
	UP	Cro-magnon 1, 4322, 4324, Mladeč 27, 28, Pavlov 1 l, r, Paviland 1, r, Dolní Věstonice 3 r, l, 13 l, r, 14 l, r, 16 l, r, 41, Sunghir 1 l, r, 4, Nahal 'En-Gev 1, Ohalo 2 l, r, Minatogawa 1 l, r, 3 l, r, 4, Tianyuan 1 r, l, Willendorf 1	
	50%	MP	Ain Maarouf 1, Berg Aukas 1, Broken Hill E690, E793, Castel di Guido 1, La Chaise BD5, Ehringsdorf 5, Gesher-B-Ya'acov 1, Ponte Mammolo 1, OH28, Tabun E1, Zhoukoudian 1, 2, 4, 5, 6
		NEA	Amud 1, La Chapelle-aux-Saints, Feldhofer 1, La Ferrassie 1 l, r, La Ferrassie 2 l, r, Fond-de-Forêt 1, Palomas 96, Quina 5, Les Rochers-de-Villeneuve, Saint-Césaire 1, Shanidar 4, 5, 6, Spy 2, Tabun 1, 3, La Chaise-de-Vouthon (CDV-Tour 1), Les Pradelles
		MPMH	Qafzeh 3, 8, 9, Skhul 3, 4 l, r, 5 l, r, 6, 7
		UP	Arene Candide 1, Barma Grande 2, Cro-magnon 1 l, r, 4322, 4324, Dolní Věstonice 3 r, l, 13 l, r, 14 l, r, 16 l, r, 35, Grotte des Enfants 4, Minatogawa 1 l, r, 2, 3 l, r, 4, Mladeč 27, Ohalo 2 l, r, Paglicci 25, Paviland 1, Pavlov 1 l, r, Rochette 2, Sunghir 1 l, r, 4, Veneri 1, 2, Willendorf 1, Zhoukoudian-UC 67, 68
	35%	MP	Arago 53, Ain Maarouf 1, Broken Hill E690, Gesher-B-T. 1, OH28
		NEA	Amud 1, La Chapelle-aux-Saints, Feldhofer 1, La Ferrassie 1 l, r, La Ferrassie 2 l, r, Fond-de-Forêt 1, Spy 2, Tabun 1
		MPMH	Qafzeh 9, Skhul 4 l, r, 5, 6, 7
		UP	Cro-magnon 1, 4322, 4328, Dolní Věstonice 3 r, l, 13 l, r, 14 l, r, 16 l, r, 40, Minatogawa 1 l, r, 3 l, r, 4, Mladeč 27, Nahal 'En-Gev 1, Ohalo 2 l, r, Paviland 1, Pavlov 1 l, r, Sunghir 1 l, r, 4

MP, Middle Pleistocene; NEA, Neanderthal; MPMH, Middle Paleolithic Modern Human; UP, Upper Paleolithic. See legend in Tables 1 and 2 for data sources.

biomechanical length were positioned using the cross section at 50% of the biomechanical length and our estimation of the biomechanical length. The biomechanical length is estimated from the shaft length.

Shaft length is estimated to be 305 mm (the shaft length is measured from the base of the lesser trochanter to the distal metaphysis/epiphysis limit), based on the fact that the proximal limit is very close to the lesser trochanter and that the preserved distal limit corresponds to the metaphysis/epiphysis limit. To obtain this result, we compared the whole proximal morphology of the Karain femur (i.e., the proximal muscle insertions, the trifurcation of the linea aspera, the proximal curvature of the medial edge) to different Neanderthal casts

or modern human bones. In particular, the Feldhofer 1 specimen proved to be very useful as the direct comparison of these two femurs indicates that they present the same shaft length. This probably results in a very slight margin of error in our estimation. The morphological comparison was preferred to a regression because there are no good isolated markers for the regression.

The biomechanical length was estimated based on shaft length through linear regression. Owing to the inability to determine the sex of the Karain femur, it was preferable to use a composite sample of both female and male bones. On the other hand, given the ecogeographical context of Karain, it seems more appropriate to use a high latitude sample to estimate shaft length.

This sample is composed of 39 present-day femurs from the collection of the University of Brussels (Université Libre de Bruxelles). It includes 20th century humans from Belgium of known sex: male ($n = 20$) and female ($n = 19$). The average length of the reference sample is 320 mm (272.7–375.5 mm; SD = 24.2 mm). The following formula was obtained: biomechanical length = $41.928 + 1.1815 \times$ shaft length ($r^2 = 0.93$; SEE = 7.4; %SEE = 2.3%). Thus, the biomechanical length of Karain is estimated at 402.3 mm (vs. 419 mm for Feldhofer 1). Unfortunately, the Neanderthal sample (or the available MP data) is not sufficiently well preserved to calculate a regression. We attempted to test the formula with the very restricted sample consisting of Feldhofer 1, Spy 2, and Tabun 1 (biomechanical length from Trinkaus and Ruff, 2012; shaft length from casts). Finally, our estimations of biomechanical length are slightly underestimated (mean = 3.1%; from -0.7% to 6.4%). It is probable that the Neanderthal epiphyses are more robust than those of the extant Belgian sample. Therefore, we should consider that our approximation would be underestimated by around 3% if Karain and Neanderthal were equally robust. The consequences of the possible underestimation are slight for the localization of the cross sections at 35% and 65%. The difference would correspond to about 2 mm for the position of the sections along the diaphysis.

RESULTS

Comparative metric analysis

The biomechanical length of the Karain femur is slightly higher than the MP mean and slightly lower than the Neanderthal mean and much lower than that of late Pleistocene modern humans. The Karain shaft diameters and total areas display a low to moderate size and conform more to the MP sample than any other group, except for the MLD at midshaft. Regardless of the three sections from Karain, the cortical area and the relative cortical area are generally lower than the mean values of the comparative groups and more similar to the UP sample, whereas the relative cortical area at 65% is higher than both Neanderthal and Middle Paleolithic modern human means. The traditional pilastric index and the degree of circularity show a similar pattern of global external shape at midshaft with a rounded midshaft for Neanderthals. The MP humans and the late Pleistocene modern humans share a low to very low degree of circularity. The former is expressed by a mediolateral strengthening and the latter by an anteroposterior strengthening. With its very high degree of circularity and a pilastric index close to 100, Karain presents a very similar external shape to Neanderthal (i.e., rounded section at midshaft). Depending on the sample used, the relative bending rigidity (I_x/I_y) appears to be a poorer marker of roundness as it does not distinguish between MP and Neanderthal samples. Regarding this variable, Karain is closely related to these two later groups. The unstandardized polar second moment of area (J) is low for Karain in comparison to the average values for the different groups. However, many specimens present similar values (see detailed data in Trinkaus and Ruff, 2012).

Pattern of cortical thickness distribution

In Karain, the midshaft cross section very clearly shows a posteromedial reinforcement (Fig. 2). After

examining the different cross sections at midshaft presented in earlier studies (Ruff et al, 1993; Trinkaus and Ruff, 1989, 1999; Trinkaus, 1997, 2006; Trinkaus et al., 1999a,b; Condemi, 2001; Mednikova and Trinkaus, 2001; Teschler-Nicola and Trinkaus, 2001; Ruff, 2008; Gilbert, 2008; Puymerail et al., 2012a,b, 2013; Mussini et al., 2012) and personally observing certain cross sections from CT-scans [MP: Karain, Ehringsdorf 5; Neanderthals: Spy 8 and 16 (i.e., Spy 2), Fond-de-Forêt, Hohlenstein, La Ferrassie 1 r and l, La Chapelle-aux-Saints; UP: "Dame du Cavillon" r and l], this reinforcement is particularly posteromedially marked on many Neanderthals ($N = 8/15$). It is virtually absent from Early and MP specimens ($N = 2/7$), except for Berg Aukas and the late MP Ehringsdorf 5. With respect to our sample of modern humans, it is totally absent (MPMH, $N = 0/4$; UP, $N = 0/18$ with 13 specimens; modern Belgian, $N = 0/39$). Finally, the posteromedial reinforcement appears to be structurally more informative than the previously described "medial buttress" (Trinkaus and Ruff, 1989, 1999; Mussini et al., 2012), which is generally present within different human groups.

The distribution of the cortical thickness of the bone observed with mapping is a more comprehensive endostructural marker. Mapping is useful to show a global pattern of cortical thickness distribution. For this study, the color maps of distinct individual are unstandardized (i.e., in Supporting Information, Fig. A2, the color maps of distinct fossils do not show the same color for the same thickness but the red always corresponds to the thickest cortical bone for each individual). Accordingly, the pattern is defined by visual observation. In Karain, cortical thickness is particularly high from the proximal portion of the medial side until the midshaft portion of the posterior side (i.e., spiral distribution) (Fig. 1). In view of the mapping of the Asiatic femur Kresna 11 by Puymerail et al (2012a), the Karain endostructural femoral pattern differs from that of the Lower Pleistocene. The distribution of the high thicknesses for Kresna only concerns the medial and lateral sides. No spiral distribution of the cortical thickness on the posteromedial side was observed. The ongoing study of the Caune de l'Arago for the monograph shows the same distribution pattern as Kresna 11 in two MP femurs for which cortical thickness distribution can be described. On the other hand, the spiral distribution of the cortical thickness is lacking in our modern human comparative sample ($N = 0/34$). In contrast, the spiral distribution pattern of this cortical reinforcement is clearly visible on the cortical thickness maps of the six Neanderthal femurs observed for this study (i.e., La Ferrassie 1, Spy 8 and 16, Fond-de-Forêt, La Chapelle-Aux-Saints; Hohlenstein) (Supporting Information, Fig. A2) and on three femurs for which the mapping data were taken from publications (les Pradelles in Mussini et al. (2012) and the "grotte de la Tour" from Chaise-de-Vouthon and La chaise BD5 in Puymerail et al. (2012b, 2013). Puymerail et al. (2012b) previously emphasized the "slightly oblique reinforcement concentrated along the medial aspect of the mid-proximal shaft" from the CDV-Tour 1 and specify also this particularity in La Chaise BD5 (Puymerail et al., 2013). In addition, we note the presence of this Neanderthal characteristic on the femur maps from Spy (8 and 16), the grotte de la Tour and La Chaise BD5 even though no marked posteromedial reinforcement was present on the midshaft cross section. Finally, combining the global approach (i.e., mapping) and the

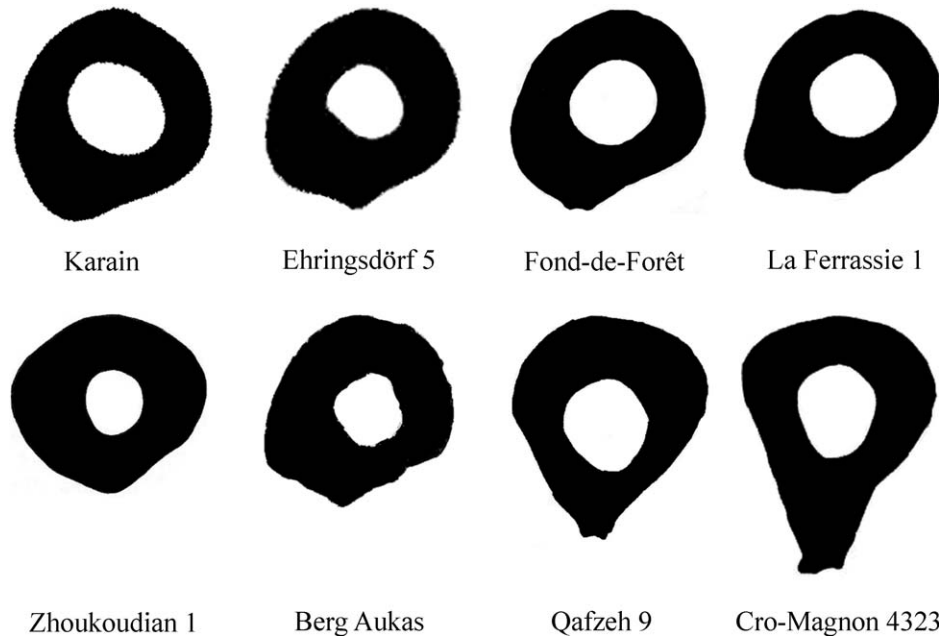


Fig. 2. Cross-sectional outlines at midshaft of human femora. The cross-sections were taken and modified from Trinkaus and Ruff (1989) for Fond-de-Forêt; Trinkaus (1997) for La Ferrassie 1 and Cro-Magnon 4323; Ruff et al. (1993) for Zhoukoudian 1; Trinkaus et al. (1999b) for Berg Aukas; Trinkaus and Ruff (1999) for Qafzeh 9. The cross-sections for Karain and Ehringsdorf 5 come from this study. All the specimens are oriented along the same laterality and presented with the same width. For sections, anterior is above and medial is to the left.

specific approach with regard to midshaft cross section, the presence of this strong posteromedial reinforcement in the middle shaft portion is as high as 80% ($N = 12/15$) in Neanderthal. The endostructural pattern in spiral distribution is also present on the Ehringsdorf 5 femur from the late MP (Supporting Information, Fig. A2). Therefore, the endostructural pattern of the shaft from Karain is concordant with the global model of reinforcement very frequently observed on Neanderthal femurs.

DISCUSSION

The left femoral diaphysis from Karain offers the opportunity to identify frequently observed Neanderthal characteristics in a MP femoral structure. Although the overall size of Karain is more similar to MP or UP samples, this diaphysis combines a high degree of circularity and a strong midshaft posteromedial reinforcement (and not only medial) of the cortical thickness on the medial side. This later and newly described feature can be related to the medial spiral distribution pattern of cortical thickness in the midproximal shaft which is present at Karain and in all the mapped Neanderthals. This spiral distribution was not identified in modern humans and further research may show that it is absent in *Homo* with femoral pilaster (i.e., MP/UP modern humans).

Given that the Karain shaft is close to the adult stage and potentially not adult, we must consider the possible structural modification before the adult stage. It has been suggested that the adult CSG properties are largely (but not only) determined by mechanical strain during ontogenetic development (Lieberman, 1997; Pearson and Lieberman, 2004; Ruff et al., 2006), implying that during this last stage of development the adult mechanical properties should be just about developed.

Moreover, according to the data from Cowgill (2008), the I_x/I_y changes little in extant populations between the ages of 12–14 years and adult age. For the TA and the CA, Ruff et al. (1994) observed a slower increase from the age of 17 years onward. Finally, the I_x/I_y values for UP samples in the final stages of development (Cowgill, 2008) clearly show UP adult characteristics (Trinkaus and Ruff, 2012; Holt, 1999) (i.e., a high index). Thus, it is likely that the general shape and size of the femoral diaphysis of Karain, if it is not an adult, would have changed very little before the adult stage.

Some structural femoral characteristics of Karain are well expressed in Neanderthals known to have cold-adapted body proportions (e.g., Trinkaus, 1981). The influence of the pelvic–femoral complex, or more general body proportions, in relation to ecogeographical variation has been previously discussed and linked to the structure of the femoral shaft (e.g., Ruff, 1995; Trinkaus and Ruff, 2012; Puymaillet et al., 2012a), while the biomechanical structure reflects a complex combination of factors (see, in particular, Ruff et al., 2006 and references therein). Thus, the Karain specimen could have similar body proportions to Neanderthals or, based on a more conservative assumption, a similar mechanical strain system that could be linked to body shape. This proposal is consistent with the chrono-ecogeographical context of Karain. However, the presence of a posteromedial reinforcement at midshaft (no mapping is available) in the probably MP femur from Berg Aukas in Namibia (Grine et al., 1995), which has relatively linear body proportions (Trinkaus et al., 1999b), may be a sign of an ancestral feature independent of latitude, although caution must be applied to the interpretation of this isolated case without a rigorous archeological context.

Finally, it is important to bear in mind that Arsuaga et al. (1991) and Bermúdez de Castro et al. (2012)

previously reported the presence of supposedly postcranial Neanderthal characters among Early Pleistocene and MP fossils from Gran Dolina and Sima de los Huesos, respectively. Although it is likely that the Karain femur belongs to *Homo heidelbergensis* or *Homo neanderthalensis* without more comparative human data, particularly from the MP (e.g., Sima de los Huesos, Caune de l'Arago), it would be premature to attribute the structural pattern of the fragmentary femur from Karain to a strict chrono-ecogeographical origin and to discuss the taxonomic affiliation of this bone.

CONCLUSION

The diaphyseal endostructural signature of the femur from Karain (i.e., posteromedial reinforcement and cortical spiral distribution pattern) was frequently observed in Neanderthal and absent in the comparative recent modern human sample. This could imply a similar mechanical strain system to Neanderthal that could be linked to body shape. Nonetheless, the Namibian Berg Aukas (MP) also presents the posteromedial reinforcement at midshaft documented within the Neanderthal sample. A larger comparative sample should clarify the taxonomical, biomechanical, and chrono-ecogeographical origins of these structural femoral features observed in an evolutionary Neanderthal context from MIS 7-9 in Karain.

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