CHAPTER XXIX-1

DESCRIPTIVE AND COMPARATIVE STUDY OF THE LOWER LIMB

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Abstract

The Upper Pleistocene lower limb remains from Spy include a complete right femur (Spy 8), a partial left femur (Spy 16), a complete left tibia (Spy 9), a left distal fibular fragment (Spy 26B) and a left patella (Spy 19). Original inventory of these remains assigned the complete right femur and left tibia to Spy I, an adult female, while the proximal left femur was designated as Spy II, a young adult male. More recent analyses have designated these bones as well as the patella to Spy II.

The current analysis investigates the morphology of each of the lower limb bones using osteometric and biomechanical data. These remains are qualitatively described and quantitatively assessed relative to relevant Neandertal and Pleistocene modern human remains. In addition to evaluating the morphology of the Spy lower limbs, the designation of each fossil is reconsidered based on age and strength indicators. Given the lack of adequate pelvic remains from the site of Spy, the lower limbs are also used to estimate stature and body mass for the individual(s) represented.

Based on anatomical and biomechanical features, all of the preserved lower limb bones from Spy are associated with the young adult male designated Spy II. The femora and tibia, which have historically been recognised as extreme examples of Neandertal robusticity, are more appropriately contextualised. In almost all anatomical details, the lower limb remains resemble other Neandertals and fall within an average range of strength and robusticity relative to other Neandertals and Pleistocene early modern humans. The femora are unique in features of the proximal femoral shaft, with particularly well-developed gluteal buttresses and consequently mediolaterally-expanded subtrochanteric femoral dimensions.

The lower limb remains from Spy include a largely complete right femur (Spy 8), a partial left femur (Spy 16), a complete left tibia (Spy 9), a left fibular fragment (Spy 26B) and a left patella (Spy 19). In the original inventory of the Spy fossils by Fraipont & Lohest in 1887, the nearly complete right femur (8) and left tibia (9) were assigned to Spy I, while the proximal left femur (16) was designated as Spy II. More recent analyses have allocated all of these lower limb bones to Spy II (Twiesselmann, 1961; Hrdlička, 1930). The patella (19) was initially identified by Fraipont & Lohest (1887) as belonging to the right side, and it was not designated to either individual. Hrdlička (1930) correctly identified Spy 19 as a left patella.

Neandertal femora have been described as large and robust with large femoral heads and distal ends relative to length, accentuated anterior diaphyseal curvature, large muscle attachments and low neck shaft angles (Boule, 1911-1913; Weidenreich, 1941; Trinkaus, 1983, 1993, 1997). Rounded subtrochanteric femoral sections and subcircular femoral diaphyses distinguish them from early modern humans of the Upper Palaeolithic (Trinkaus & Ruff, 1999). The apparently high level of tibial strength, angulation of the tibial plateau and shape contours of the tibial shaft also characterise the Neandertals (Fraipont, 1891; Hrdlička, 1930; Vandermeersch, 1981; Trinkaus, 1983; Trinkaus & Ruff, 1999). The lower limb bones of Spy, however, have been considered extreme examples of these features, particularly with respect to the size of the femoral head and stoutness of the femoral neck, large breadth of the gluteal tuberosity on the posterior femoral shaft, and shortness and stoutness of the tibia (Fraipont & Lohest, 1887; Fraipont, 1888, 1891; Leclercq, 1927; Hrdlička, 1930).

In the current analysis, each of the lower limb remains are comparatively assessed using three forms of data. First, the Spy fossils are qualitatively described. In addition, a quantitative morphological description is given, linear and angular measurements are provided and linear morphometrics of the lower limb bones are performed. Finally, the cross-sectional geometric properties of the long bone diaphyses are evaluated through computed tomographic scanning combined with image analysis software. Biomechanically-relevant cortical bone measurements from the proximal and midshaft femora and tibia are assessed.

These studies are used to re-analyse the designation of the lower limb remains using assessments of cortical bone distribution and epiphyseal fusion. In addition, the lower limb bones from Spy are investigated in the context of other Neandertal and early modern human fossils. Lastly, due to the lack of adequate pelvic remains from Spy, the femora are used to estimate stature and body mass for the individual(s) represented.

The current analyses demonstrate that the lower limb bones of Spy are largely compatible with the characteristic Neandertal femora, tibiae, fibulae and patellae. Analysis of skeletal features as well as epiphyseal sutures also demonstrate that the Spy 8 femur and Spy 9 tibia, previously attributed to the fully adult Spy I skeleton, are more compatible with the young adult age of the Spy II skull. Similarities in the right Spy 8 femur and the left Spy 16 femur indicate that these bones belong to the same individual, and that all the adult Neandertal long bones available for study belong to Spy II.

COMPARATIVE MATERIALS

Radiocarbon dates obtained from the Spy Neandertals place them chronologically in the Middle to Upper Palaeolithic transition in Western Europe. At ca. 36,000 years BP, the Spy individuals are the youngest Neandertals currently identified in Northwest Europe and are associated with a transitional culture (Semal *et al.*, 2009). Description of the lower limb remains includes comparisons to relevant Middle and Upper Palaeolithic samples (ST1).

Comparative summary statistics are included for other European and Near Eastern Neandertals. The Neandertal sample is primarily composed of last glacial remains from Western Europe and Southwest Asia. These include specimens from the sites of Amud, La Chapelle-aux-Saints, La Ferrassie, Fond-de-Forêt, Kebara, Kiik-Koba, Neandertal, Regourdou, Saint-Césaire and Shanidar. Also included are Krapina and Tabun, although they predate this time period (Mercier *et al.*, 1995; Rink *et al.*, 1995; Grün & Stringer, 2000).

Summary statistics are also included for Near Eastern Middle Palaeolithic early modern humans and European and Western Asian earlier Upper Palaeolithic (EUP) early modern humans. Middle Palaeolithic early modern human data come from the Levantine sites of Qafzeh and Skhul. Upper Palaeolithic early modern human data come from Northwestern Eurasia. These specimens are dated prior to the Last Glacial Maximum (> 18 ky BP) and primarily include individuals from the Gravettian. These derive from the sites of Arene Candide, Barma Grande, Baousso da Torre, Barma del Caviglione, Cro-Magnon, Dolní Věstonice, Grotte des Enfants, Mladeč, Nahal Ein Gev, Paglicci, Parabita, Pavil-and, Pavlov, Předmosti, La Rochette and Sunghir.

Based on the dentition and skull sutures of the crania, both Spy I and Spy II are identified as adult individuals. As such, only adult specimens are included. All analyses include males and females in order to maximise sample sizes.

COMPARATIVE METHODS

The description of the lower limb remains from Spy includes traditional osteometrics and indices (Tables 1-3, 6-7, 10). Linear and angular measurements largely follow the Martin system (Bräuer, 1988). Additional measurements are provided and defined in the notes to the tables as necessary. All measurements were taken by the author on the original fossils. When provided in the text, summary statistics are given as (mean ± s.d., N).

Given their states of preservation, cross-sectional geometric properties are also included in the description and analysis of the long bones (Tables 4 and 8). Cross-sectional properties for all long bones were modelled using computed tomographic (CT) imaging and analysed using the Artecore (v 1.0) image analysis software. CT scans were taken by Semal and colleagues (Semal *et al.*, 2005; see also Balzeau *et al.*, this volume: chapter XXII). Biomechanically-relevant cortical bone measurements for the femora and tibia are assessed.

Femoral cross-sectional biomechanical properties are evaluated at the subtrochanteric (80 %) and midshaft (50 %) levels. The tibia is analysed at proximal (65 %) and midshaft (50 %) sections, with 0 % at the distal end of the bone. This places the proximal section at the approximate level of the nutrient foramen. The strength of the long bone sections in axial loading are evaluated using measures of cortical area relative to body mass. The overall strength of the bones in bending and torsional loading is approximated by the polar moment of area relative to appropriate measures of body mass and moment arm lengths. The general distribution of cortical bone at these cross-sections is considered using indices of external diameters as well as second moments of area.

Body mass is estimated for Spy using the femoral head diameters of Spy 8 and Spy 16 as well as using a non-mechanical method. Further information on body mass estimation is provided below.

FEMORA

Inventory

Spy 8 (right)

Spy 8 is a largely complete right femur that is absent the greater trochanter (Figure 1). The damage to the greater trochanter extends medially into the trochanteric fossa and posteriorly along the intertrochanteric crest and the surface of the lesser trochanter. These damaged regions are covered by a smooth, brown matrix. Other than slight damage to the surface of the femoral head, the remainder of the proximal end is intact, allowing a maximum length measure to be recorded (426.0 mm, Table 1). The distal end of the femur has minor surface damage, particularly to the medial and lateral epicondyles, that is partially obscured by matrix. In the distal quarter of the diaphysis there is a repaired post-mortem break.

Fraipont (1891) designated Spy 8 to the Spy I skeleton.

Measurement	*Martin #*	*Spy 8 (right)*	*Spy 16 (left)*
Maximum length	M-1	426.0	(289.0)[1]
Bicondylar length	M-2	424.5	--
Biomechanical length[2]		405.0	--
Anterior curvature chord	M-27	300.0	--
Anterior curvature subtense		14.0	--
Subtrochanteric A-P diameter	M-10	27.8	34.3
Subtrochanteric M-L diameter	M-9	35.6	40.2
Midshaft A-P diameter	M-6	28.9	28.3
Midshaft M-L diameter	M-7	29.1	29.2
Midshaft circumference	M-8	100.5	101.0
Head-neck length	M-14	80.0	82.8
Anatomical biomechanical neck length		81.0	84.0
Trochanteric biomechanical neck length		(103.0)	106.0
Head sagittal diameter	M-19	(53.6)	--
Head vertical diameter	M-18	54.0	53.8
Neck sagittal diameter	M-16	36.2	29.8
Neck vertical diameter	M-15	37.2	37.2
Neck-shaft angle (in degrees)	M-29	120.0	118.0
Anteversion angle (in degrees)	M-28	19.0	--
Greater trochanter depth	M-26(1)	(41.4)	43.4
Gluteal tuberosity breadth		21.1	21.6
Distal epicondylar breadth	M-21	90.7	--
Bicondylar breadth		87.1	--
Medial condylar breadth	M-21c	34.3	--
Lateral condylar breadth	M-21e	29.8	--
Bicondylar angle (in degrees)	M-30	11.0	--
Medial patellar projection	M-24b	62.8	--
Lateral patellar projection	M-22	69.0	--
Median patellar projection		59.7	--
Patellar surface circumference		51.0	--
Patellar surface breadth	M-26(3b)	49.5	--
Patellar surface depth		12.9	--
Patellar surface depth position		29.0	--

[1] Maximum preserved length.
[2] Biomechanical length = average distance parallel to the diaphyseal axis between the distal condyles and the proximal neck just medial to the greater trochanter (Ruff, 1981).

Parentheses indicate estimated values.

Table 1. Osteometric dimensions of the Spy 8 and 16 femora (in mm unless otherwise noted).

Figure 1. Spy 8 (right femur). From left to right: anterior, medial, posterior and lateral views. Photograph by P. Semal (RBINS). Scale = 1 cm.

Spy 16 (left)

Spy 16 is a partial left femur that includes the proximal end and approximately two-thirds of the proximal femoral shaft (Figure 2). Both the greater and lesser trochanters of Spy 16 are damaged with the superior portion of the lesser trochanter largely absent. The damage to the greater trochanter continues onto the external surface of the proximal femoral neck and medial portion of the femoral head.

Figure 2. Spy 16 (left femur). From left to right: anterior, medial, posterior and lateral views.
Photograph by P. Semal (RBINS). Scale = 1 cm.

Approximately 2/3 of the femoral shaft is present, with the maximum preserved length of the Spy 16 femur measuring 289.0 mm.

In his observations on the original specimens, Fraipont (1891) notes that Spy 16 is even stronger than the Spy 8 femur and strongly resembles the characteristic Neandertal femur. As such, he designated it as part of the Spy II skeleton.

Length estimation for Spy 16

Given that Spy 16 represents the proximal end and 2/3 of the femoral diaphysis, it is possible to estimate the full length of this bone. Several regression models have been developed to estimate maximum femoral length from a fragmentary femur (Steele & McKern, 1969; Steele, 1970; Simmons *et al.*, 1990; Bidmos, 2008). These models predict maximum femoral length with varying degrees of accuracy, but rarely with greater than 65 % correlation. Also since these regression models have been developed using recent human populations, there is a tendency to over-predict the length of Neandertal femora.

An equation from Steele & McKern (1970) derived from a prehistoric American Indian population based on a proximal femoral segment (segment 1: from the most proximal point of the head to the midpoint of the lesser trochanter) was used to estimate the length of Spy 16. With this formula, Spy 16 was estimated to have a maximum length of 459 ± 14 mm (445 – 473 mm). The mean maximum length for Neandertals is 439 ± 7.49 mm (N = 12), making the average estimated length for Spy 16 outside the range of variation for Neandertal femora.

If the length of the Spy 8 femur is estimated from the same femoral segment with the identical regression equation, its length is estimated to be 457 ± 14 mm (443 – 471 mm). Given its measured maximum length of 426 mm, this regression formula grossly over-estimates its actual size. For this reason, it is likely that the length of Spy 16 is also over-estimated using this formula.

Since this bone almost certainly belongs to the same individual as Spy 8 and there is very little directional or systematic length asymmetry in the lower limb (Auerbach & Ruff, 2006), the length of the right Spy 8 femur gives the best estimate for Spy 16 at 426 mm. This estimated length is used for further analysis.

Body mass estimation

The functional significance of a skeletal trait in body size reconstruction has argued for the use of lower limb bone dimensions to predict body mass in fossil hominins (see review in Ruff, 2002). Two distinct methods provide reliable estimates of body mass. The first is a mechanical method, which incorporates lower limb articular dimensions. Lower limb articular dimensions, specifically femoral head size, have successfully estimated body mass in fossil and modern human populations given their mechanical significance for weight-bearing in bipedal locomotion (Ruff *et al.*, 1991; McHenry, 1992; Grine *et al.*, 1995). Unlike the use of lower limb diaphyseal breadth, articular dimensions are relatively insensitive to variations in the mechanical environment that can over- or under-estimate body mass in behaviorally variable populations (McHenry, 1976; Rightmire, 1986; Hartwig-Scherer, 1994; Ruff *et al.*, 1994; Holliday, 2002).

A second method of body mass estimation uses a non-mechanical model for reconstruction by modeling the human body as a cylinder using stature and bi-iliac breadth (Ruff, 1991, 1994, 2000). Estimates from stature and bi-iliac breadth for modern populations are reliable when appropriate reference samples are used (Ruff, 1994, 2002; Holliday & Ruff, 1997; Auerbach & Ruff, 2004). This method requires the preservation of the long bone and pelvis of an individual or a considerable amount of estimation. Often estimation from femoral head diameter may be preferable for the analysis of fossil material given preservation bias. However, body mass estimates from these two methods give similar results when applied to fossil humans (Ruff *et al.*, 1997; Auerbach & Ruff, 2004).

Given the preservation of the Spy fossils, body mass can be predicted most reliably using femoral head size. Several models have been provided for estimating body mass in fossil hominins using the size of the femoral head (Ruff *et al.*, 1991; McHenry, 1992; Grine *et al.*, 1995). These three models are generally comparable although they each perform slightly differently due to differences in the reference samples used to generate the formulae (Auerbach & Ruff, 2004). The Ruff *et al.* (1991) sex-specific model performs most accurately in a middle size range, tending to under-estimate at the upper end of the body mass distribution and over-estimate at the lower end of the distribution. McHenry's (1992) model was derived to predict body mass in small, early hominins and used small-bodied populations as reference samples. As a result, it is most accurate when predicting body mass for small-bodied humans. Conversely, Grine *et al.* (1995) used large-bodied populations to create a model for predicting body mass, making it more accurate in prediction at the upper end of the body mass distribution. In order to accommodate these variations, each prediction model was used to estimate body mass for the Spy femora and then averaged (Auerbach & Ruff, 2004).

The body mass for Spy 8 estimated from femoral head diameter is 82.4 kg (average of three estimates: 85.1 kg, 80.1 kg, 81.9 kg). That of Spy 16 is 82.8 kg (average of three estimates: 85.5 kg, 80.6 kg, 82.3 kg). Given the error range for each of these models, there is virtually no difference in the predicted body mass for these specimens between estimates.

While this method requires the least estimation, many researchers prefer a non-mechanical model that incorporates stature and bi-iliac breadth (Ruff, 1991, 1994, 2000). Given the lack of adequate pelvic remains from Spy, both stature and bi-iliac breadth must be estimated. Stature for Spy II was estimated using Trotter & Gleser (1952)'s Euroamerican sex-specific formula. Bi-iliac breadth was taken as the mean of those available for archaic *H. sapiens* (La Chapelle-aux-Saints 1 and Kebara 2) following

Ruff *et al.* (1997; see also Trinkaus *et al.*, 1999). The resultant estimated body mass for Spy II is 83.6 kg, which is comparable to the estimates from femoral head diameter (see also Ruff *et al.*, 1997).

Prior research has demonstrated that features of robusticity scale allometrically with body size, thereby maintaining approximately equivalent mechanical strain levels in long bones under dynamic loading (Rubin & Lanyon, 1984; Ruff, 1984; Ruff *et al.*, 1993). As such, features of robusticity must be scaled to appropriate measures of body size and issues of body size are inevitably associated with aspects of robusticity. The estimated body masses for Spy 8 and Spy 16 calculated from their femoral head diameters are used for scaling cross-sectional geometric properties in the following analyses as appropriate.

Morphology

Proximal epiphyses

Spy 8 and Spy 16 have been considered extreme in the size and strength of their femoral heads and necks. The most unique features of these femora are found in the proximal shaft (Figure 3).

Figure 3. Spy 8 (on right side) and Spy 16 (on left side). Posterior view showing proximal epiphysis and shaft with large gluteal tuberosity and medial buttress on Spy 8. Scale = 1 cm.

Vertical head diameters for Spy 8 (54.0 mm) and Spy 16 (53.8 mm) fall at the top of the range of variation for Neandertals (49.8 ± 3.9 mm, N = 10). Sagittal head diameter is only available for Spy 8 (estimated at 53.6 mm due to slight damage), and it again falls at the top of the Neandertal range of variation (47.4 ± 5.7 mm, N = 9). While Neandertals have relatively large femoral heads compared to early modern human samples, when scaled to measures of body size, neither vertical head diameter ($p = 0.558$) nor sagittal head diameter ($p = 0.771$) discriminate between the comparative samples.

With respect to the stoutness of the femoral neck, in measures of vertical diameter, Spy 8 (37.2 mm) and Spy 16 (37.2 mm) again fall at the top of the range of variation for Neandertals and well above that of the other comparative samples (Table 2). When scaled to measures of body size, the comparative samples are indistinguishable from one another ($p = 0.977$). Spy 8 also has an extremely large sagittal diameter, making the femoral neck appear almost round in cross-section. Again, the comparative samples are indistinguishable from one another ($p = 0.911$), but at 36.2 mm, Spy 8 falls more than two standard deviations above the range of variation for Neandertals.

As is typical for the Neandertals, Spy 8 and 16 have relatively low neck shaft angles at 120° and 118°, respectively. The mean values for the Neandertals and EUP early modern humans are virtually indistinguishable, and Spy 8 falls within this range, although it is well below that of the Middle Palaeolithic sample from Qafzeh-Skhul (Table 2), which is closer to that of modern, urbanised populations (Trinkaus, 1993; Anderson & Trinkaus, 1998; Trinkaus *et al.*, 2006).

Spy 8 has traces of an epiphyseal fusion line visible at the proximal end where the diaphysis meets the femoral head.

Diaphyses

Neandertals and early modern humans are distinctive in diaphyseal shape at the proximal and midshaft femur, and the Spy femora demonstrate their own unique blend of characteristics in these regions. The most distinctive fea-

	Neandertals	*Qafzeh-Skhul*	*Earlier Upper Palaeolithic*
Curvature subtense (mm)	12.9 ± 2.0 10	9.0 ± 2.0 4	9.7 ± 2.1 12
Sagittal neck diameter (mm)	26.7 ± 3.8 8	25.3 ± 2.7 3	26.4 ± 2.1 5
Vertical neck diameter (mm)	32.6 ± 3.5 8	32.3 ± 2.8 5	33.1 ± 2.7 5
Neck shaft angle (°)	121.0 ± 4.7 9	133.2 ± 2.6 6	121.5 ± 8.0 16
Gluteal tuberosity breadth (mm)	12.9 ± 2.0 10	9.0 ± 2.0 4	10.9 ± 2.8 16
Bicondylar angle (°)	9.6 ± 3.0 4	9,10[1]	9.9 ± 2.1 12

[1]Right and left values are provided for a single individual.

Table 2. Comparisons of femoral osteometric values.
Mean ± standard deviation and N are provided for comparative samples.

tures of Spy 8 and 16 are found in the subtrochanteric region where the femoral diaphysis is mediolaterally broad.

On the posterolateral surface of the Spy femora there are well-developed, broad, rugose gluteal tuberosities for the insertion of *M. gluteus maximus*. There is a significant difference in the breadth of the gluteal tuberosity across comparative samples ($p = 0.001$), indicating a hypertrophy of the hip extensors in the Neandertals. Measuring 21.1 mm in Spy 8 and 21.6 mm in Spy 16, these muscle insertion sites are at the top of the range of variation in gluteal tuberosity breadth for Neandertals (Table 2; Figures 3-4). In each specimen, the gluteal ridge extends mediodistally to merge with the linea aspera, which is mildly developed. On both Spy 8 and 16, the gluteal tuberosity is bordered laterally by a prominent proximolateral gluteal buttress, creating a very broad subtrochanteric mediolateral diameter. A clear sulcus separates the gluteal tuberosity and buttress.

The relative development of the gluteal buttress can be evaluated by the meric index as well as by cross-sectional geometric properties at the subtrochanteric level. The meric index, which compares external diameters at the subtrochanteric level, effectively separates the comparative samples ($p < 0.001$) (Table 3). In this comparison, the EUP sample has the lowest values and consequently relatively mediolaterally-broad proximal diaphyses. Alternatively,

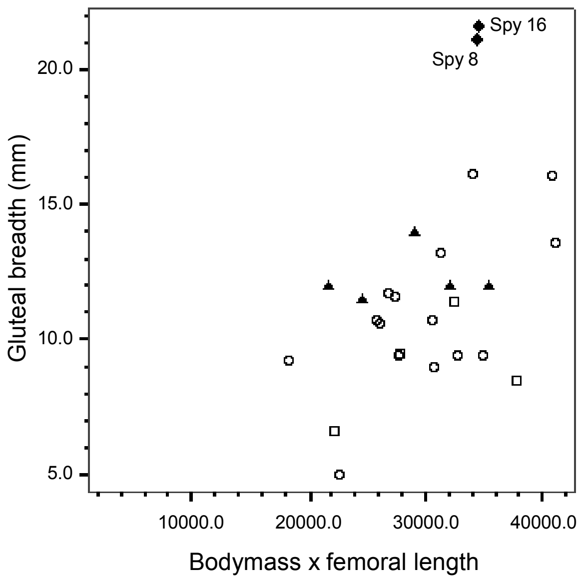

Figure 4. Gluteal tuberosity breadth versus body mass multiplied by femoral length for Spy 8 and 16 (black diamonds), Neandertals (black triangles), Qafzeh-Skhul early modern humans (open squares) and earlier Upper Palaeolithic early modern humans (open circles).

the Neandertals have relatively high meric indices, indicating more circular proximal diaphyses. The Qafzeh-Skhul specimens fall between these samples but generally similar to the Neandertals in having relatively round proximal femoral shafts (Figure 5). In this respect, Spy 8 falls strictly with the Upper Palaeolithic early modern humans who demonstrate relat-

	Pilastric index	*Meric index*	*Crural index*
Spy 8	99.3	78.1	--
Spy 16	96.9	85.3	--
Spy II[1]	--	--	78.6
Neandertals	106.9 ± 3.7 10	82.7 ± 2.1 9	77.4 ± 0.64 8
Qafzeh-Skhul	126.6 ± 6.7 5	84.8 ± 5.7 4	85.3 ± 0.70 5
Earlier Upper Palaeolithic	116.5 ± 2.4 19	75.8 ± 1.7 24	84.5 ± 0.78 27

[1]The crural index for Spy II was calculated using the length measurements for Spy 8 (right femur) and Spy 9 (left tibia).

Table 3. Diaphyseal indices for the Spy femora and comparative samples. Mean ± standard deviation and N are provided for comparative samples.

ively broad mediolateral diaphyses. Its meric index (78.1) falls at the lowest end of the range of variation for Neandertals and within the range of variation of the EUP early modern humans. This low value reflects the very wide mediolateral diameter resulting from its prominent gluteal buttress. Spy 16 has a relatively high meric index (85.3), reflecting a relatively round proximal diaphysis.

Comparisons of second moments of area at the subtrochanteric level effectively quantify the shape of the proximal femur. Because of the torsion of the femoral head and neck, the maximum diameter of the cross-section across the gluteal buttress is evaluated rather than the true mediolateral diameter (Twiesselmann, 1961; Sládek *et al.*, 2000; Trinkaus *et al.*, 2006). The perpendicular distance is taken as the minimum diameter of the cross-section.

This ratio of maximum to minimum second moments of area at the subtrochanteric level is used here to assess the shape of the proximal femur (Figure 5). This comparison provides less discrimination between samples, but the Spy femora still remain within the range of the EUP early modern humans.

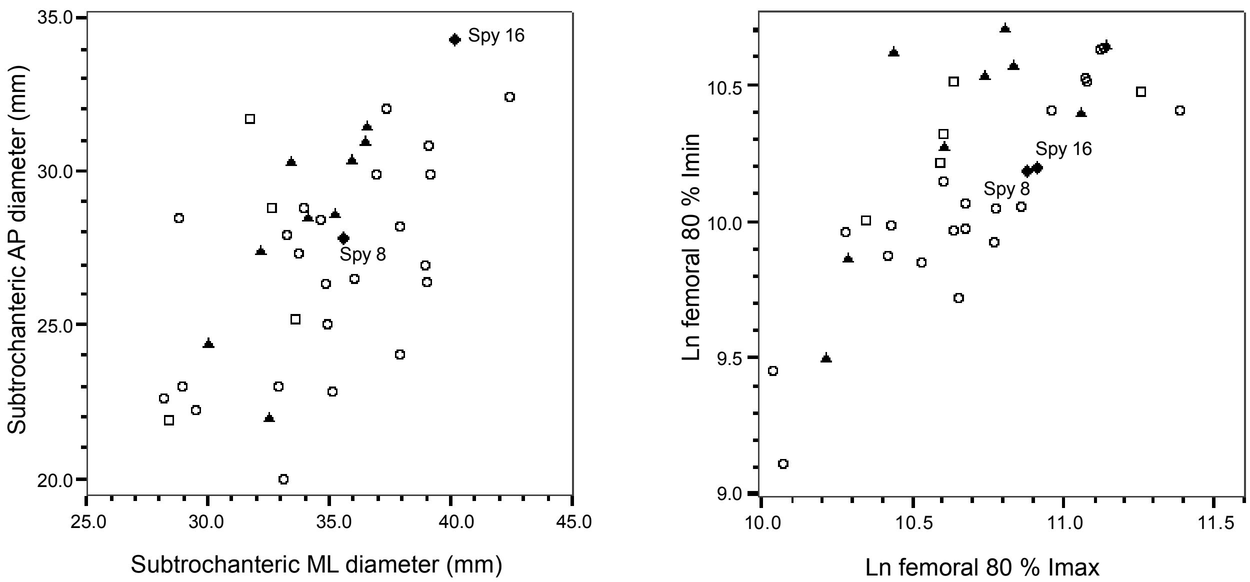

Figure 5. Subtrochanteric femoral diaphyseal proportions. Anteroposterior versus mediolateral external diameters (left) and anteroposterior versus mediolateral second moments of area (right). Symbols are as in Figure 4.

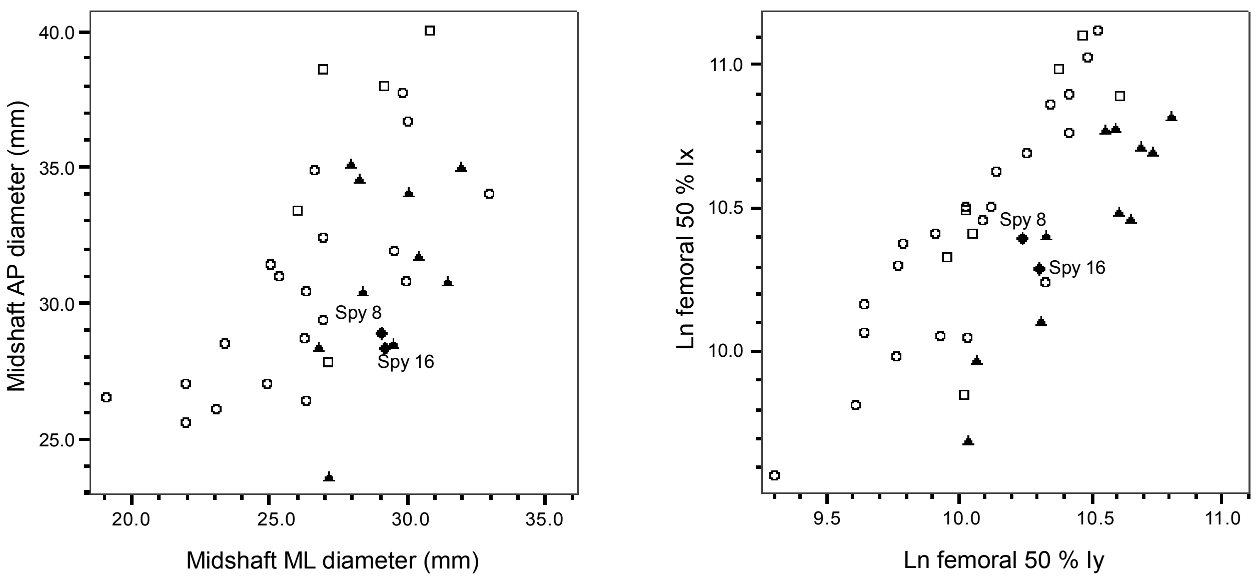

Figure 6. Midshaft femoral diaphyseal proportions. Anteroposterior versus mediolateral external diameters (left) and anteroposterior versus mediolateral second moments of area (right). Symbols are as in Figure 4.

Neandertals and early modern humans also show distinctly different cross-sectional shapes at the femoral midshaft. Neandertals have sub-circular cross-sections at the midshaft due to relatively strong mediolateral cortical reinforcement and the lack of a femoral pilaster, a crest of bone along the posterior midshaft; in contrast, the midshaft cross-sections of early modern humans have a distinctive tear-drop-shape due to the pilaster (McCown & Keith, 1939; Trinkaus, 1976, 1984; Vandermeersch, 1981; Kennedy, 1984; Trinkaus & Ruff, 1999).

The shape of the femoral midshaft can be quantified by its external diameters via the pilastric index and a ratio of the second moments of area. The comparative samples are effectively separated by both indices, demonstrating the different shapes of the midshaft between Neandertals and early modern humans (Table 3; Figure 6). The cross-sectional shapes of the Spy femora fall with the Neandertals and are effectively separated from the early modern humans with a pilastric index of 99.3 for Spy 8 and 96.9 for Spy 16. The ratio of second moments of area at the midshaft also places Spy 8 (1.16) and Spy 16 (0.97) within the range of variation for Neandertals (0.965 ± 0.16, N = 11) and outside the range of variation for EUP early modern humans (1.47 ± 0.25, N = 21) and the Qafzeh-Skhul early modern humans (1.47 ± 0.39, N = 7).

The Spy 8 diaphysis is mediolaterally straight with the minimum breadth just proximal to the midshaft. As noted originally by Fraipont (1891), as well as many individuals who have since analysed the Spy femora, the diaphysis of Spy 8 has accentuated anterior curvature. This is indicated by a curvature index of 4.67, which falls within the range of variation of Neandertals (4.92 ± 1.3, N = 5) and Qafzeh-Skhul early modern humans (4.89 ± 1.7, N = 3) and at the upper end of the range of variation of EUP early modern humans (4.13 ± 0.86, N = 11).

Diaphyseal robusticity

The relative cortical area in a cross-section ([cortical area/total area]*100) indicates the differential endosteal resorption versus subperiosteal deposition through the life cycle of an individual (Ruff & Hayes, 1983; Ruff *et al.*, 1994). The percent cortical area is not significantly different across Middle and Upper Palaeolithic samples at the midshaft ($p = 0.289$) or proximal ($p = 0.215$) femur (SF1). Spy 8 and Spy 16 femora are aligned with the Neandertal sample, although there is little discrimination between groups (Tables 4 and 5).

Contrary to this measurement, cortical area can be evaluated relative to body mass to assess compressive and tensile strength of a bone in axial loading (Ruff *et al.*, 1993). The Spy

Cross-sectional property	*Spy 8*	*Spy 16*
50 % Cortical area (CA)	475.8	478.0
50 % Total area (TA)	637.2	628.8
50 % AP 2nd moment of area (I_x)	32695.7	29316.1
50 % ML 2nd moment of area (I_y)	28158.7	30131.1
50 % Max 2nd moment of area (I_{max})	33663.0	30835.1
50 % Min 2nd moment of area (I_{min})	27191.4	28612.1
50 % Polar moment of area (J)	60854.4	59447.2
50 % I_x/I_y	1.161	0.9730
80 % Cortical area (CA)	537.0	515.8
80 % Total area (TA)	705.7	724.2
80 % AP 2nd moment of area (I_x)	28501.1	28677.1
80 % ML 2nd moment of area (I_y)	51282.4	53050.6
80 % Max 2nd moment of area (I_{max})	53305.4	54974.2
80 % Min 2nd moment of area (I_{min})	26478.1	26753.5
80 % Polar moment of area (J)	79783.5	81727.7
80 % I_{max}/I_{min}	2.013	2.055

Table 4. Cross-sectional geometric properties of the Spy 8 and Spy 16 femora. Areas in mm^2, second moments of area in mm^4. 0 % is distal.

femora are relatively gracile with respect to resisting axial loads when compared to all comparative samples at the midshaft and proximal femur (Tables 4 and 5; SF2), although the samples are not well differentiated amongst themselves (midshaft: $p = 0.089$; proximal: $p = 0.557$).

Overall strength of the femoral diaphysis is estimated in these analyses by the polar moment of area (J). Analyses across species as well as investigations of long bone strength in humans have shown that neither bone length nor body mass alone is a reliable scaling factor for cross-sectional properties reflecting bending regimes in the lower limbs. Instead, bending rigidity is highly correlated with an approximation of the bending moment created by the product of body mass and bone length (Polk *et al.*, 2000; Ruff, 2000; Stock, 2002). This is particularly relevant to this study due to the difference in body proportions between Neandertals and early modern humans. This difference in body proportions is well-established, with Neandertals having relatively broad pelves and short limbs that are associated with an arctic climate, while early modern humans have more narrow pelves and longer

		Neandertals		*Qafzeh-Skhul*		*Earlier Upper Palaeolithic*	
	p-value	*Spy 8*	*Spy 16*	*Spy 8*	*Spy 16*	*Spy 8*	*Spy 16*
Midshaft (50 %)							
AP/ML	0.011*	0.648	0.853	1.83	1.99	1.66	1.89
CA/TA	0.289	1.29	0.981	0.696	0.381	0.202	0.0357
CA/BM	0.089	1.84	1.84	1.61	1.61	0.950	0.950
I_x/I_y	<0.001*	1.19	0.0486	0.891	1.43	1.23	1.97
J/BM x len	0.092	1.09	1.18	0.820	0.891	0.344	0.440
Subtrochanteric (80 %)							
AP/ML	0.040*	0.718	0.421	0.587	0.0418	0.271	1.13
CA/TA	0.215	0.585	1.39	0.209	0.843	0.197	0.478
CA/BM	0.557	0.847	1.42	1.23	1.47	0.736	0.946
I_{max}/I_{min}	0.077	1.46	1.57	0.359	0.351	0.170	0.283
J/BM x len	0.044*	0.555	0.549	0.0484	0.0426	0.0924	0.0190

* $p < 0.05$ with a multiple comparison correction.

Table 5. Spy 8 and Spy 16 femoral metric comparisons. The *p*-values are from ANOVA comparisons across the three comparative samples used for analyses. The Spy values are z-scores relative to each comparative sample [(|Spy values – sample mean|)/standard deviation]. Abbreviations are as follows: AP: anterior-posterior diameter; ML: medial-lateral diameter; CA and TA: cortical and total subperiosteal areas; I_x, I_y, I_{max}, I_{min}: anteroposterior, mediolateral, maximum and minimum second moments of area, respectively; J: polar moment of area; BM x len: estimated body mass multiplied by femoral length.

limbs that are better adapted to the warmer climates in which they emerged (Trinkaus, 1981; Ruff, 1991, 1994; Holliday, 1997). Given these differences in body proportions between comparative samples, polar moment of area is scaled to body mass multiplied by bone length (Figure 7).

Overall strength at the femoral midshaft does not differ significantly between Neandertals and early modern humans when body proportions are considered ($p = 0.092$). In this section, the Spy femora cluster at the gracile margin of the Neandertal distribution, but are within the ranges of variation for both Neandertals and early modern humans, as expected (Tables 4 and 5).

This relationship between polar moment of area and body mass multiplied by bone length has been shown empirically for properties of the lower limbs, with the exception of the proximal femur in humans. Ruff (1995, 2000) has demonstrated that cross-sectional dimensions of the proximal femur scale to body mass multiplied by bi-iliac breadth since the magnitude of the bending moment arm at the hip is dominated by pelvic dimensions rather than femoral shaft length.

Although it is most appropriate to evaluate the overall strength of the proximal femur relative to the product of body mass and bi-iliac breadth, this measure is not available for Spy. Bi-iliac breadth could be estimated from the two available Neandertal pelves or estimated from femoral length. Alternatively, the polar moment of area could be evaluated relative to body mass multiplied by femoral length as was done for the femoral midshaft. This method has been shown empirically to be less accurate than using bi-iliac breadth; it does, however, avoid the redundancy of using femoral length to estimate bi-iliac breadth. Overall strength at the proximal femur was evaluated relative to body mass multiplied by femoral length (Figure 7). This allowed for the inclusion of a greater number of individuals in all comparative samples. An analysis was also performed using only those fossil specimens with known bi-iliac breadths and with the bi-iliac breadth for Spy 8 and 16 estimated as the average for the known Neandertal pelves (La Chapelle-aux-Saints 1 and Kebara 2). The results of these two analyses were not substantially different.

Measures of overall strength at the subtrochanteric section provide greater discrimination between the samples than at the midshaft section ($p = 0.044$). This is due in large part, however, to the small Dolní Věstonice 3 and Na-

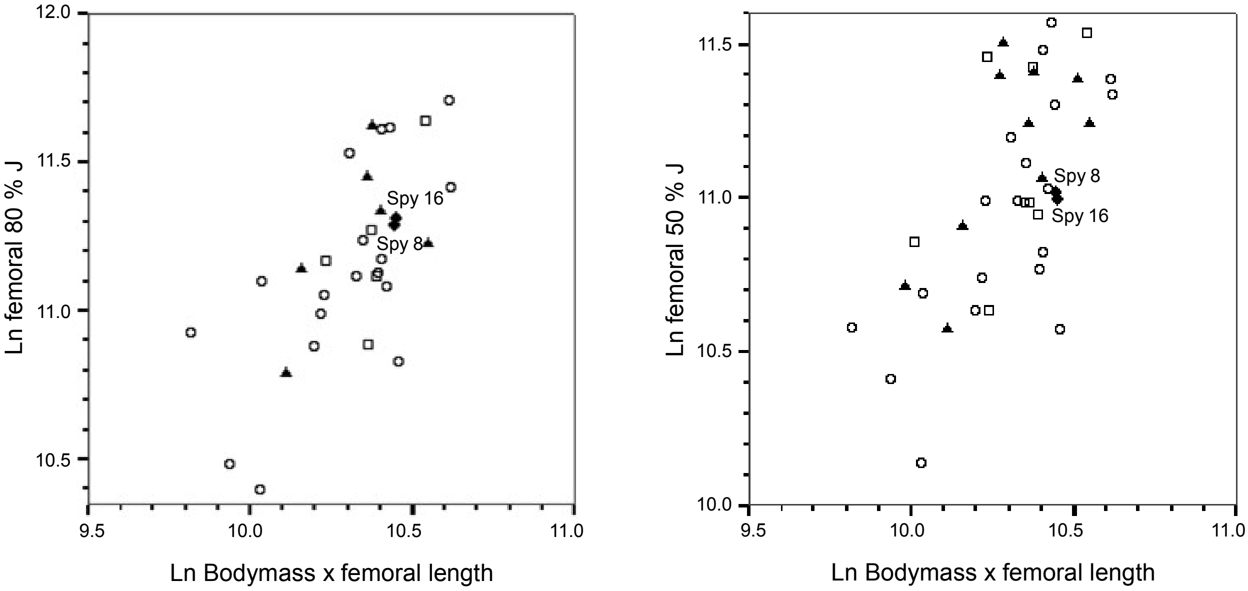

Figure 7. Comparison of the polar moment of area (J) versus body mass multiplied by femoral length at the proximal (80 %) and midshaft (50 %) femoral diaphysis as a measure of overall bending and torsional strength. Symbols are as in Figure 4.

hal Ein Gev 1 specimens, which are outliers. When these specimens are removed, there is no longer a significant difference between samples (p = 0.063).

Distal epiphysis

The distal epiphysis of Spy 8 is broad and typically rounded. The lateral condyle projects further anteriorly (lateral patellar projection = 69.0 mm) than does the medial condyle (medial patellar projection = 62.8 mm). A bicondylar angle of 11° places Spy 8 in the range of other fossil hominids (Table 2).

Traces of an epiphyseal fusion line are present where the distal end of the femoral shaft joins the distal epiphysis.

TIBIA

Inventory

Spy 9 (left)

Spy 9 is a complete left tibia that has two post-mortem, repaired breaks in the diaphysis: one just proximal to the midshaft and one just

Figure 8. Spy 9 (left tibia). From left to right: anterior, lateral, posterior and medial views. Scale = 1 cm.

proximal to the distal epiphysis (Figure 8). It has slight damage around the proximal and distal articular surfaces, but is complete and well-preserved. At its proximal end, there is minor damage to the lateral sides of the medial and lateral condyles, and damage to the anterior shaft inferior to the condyles but superior to the tibial tuberosity. At its distal end, there is slight damage around the talar articular surface. Maximum length of the Spy 9 tibia is 335.0 mm (Table 6).

Measurement	*Martin #*	*Spy 9 (left)*
Maximum length	M-1a	335.0
Medial total length	M-1b	325.0
Lateral total length	M-1	335.0
Medial articular length	M-2	316.0
Lateral articular length	M-2	322.0
Midshaft A-P diameter	M-8	32.3
Midshaft M-L diameter	M-9	22.8
Midshaft circumference	M-10	98.0
Proximal A-P diameter	M-8a	39.6
Proximal M-L diameter	M-9a	26.8
Proximal circumference	M-10a	114.0
Distal minimum circumference	M-10b	93.0
Proximal epiphyseal maximum breadth	M-3	76.6
Medial condyle breadth	M-3a	38.0
Lateral condyle breadth	M-3b	33.4
Medial condyle depth	M-4a	42.2
Lateral condyle depth	M-4b	39.6
Condylar displacement		43.0
Medial retroversion angle (in degrees)	M-12	110.0
Lateral retroversion angle (in degrees)		109.0
Medial inclination angle (in degrees)	M-13	107.0
Lateral inclination angle (in degrees)		103.0
Torsion angle (in degrees)	M-14	23.0
Distal maximum breadth	M-6	55.9
Distal maximum depth	M-7	40.8
Talar trochlear articular breadth		32.1
Medial talar articular depth		15.2
Lateral talar articular depth		33.0

Table 6. Osteometric dimensions of the Spy 9 tibia (in mm unless otherwise noted).

Spy 9 was originally designated as part of the Spy I skeleton (Fraipont, 1891).

Morphology

Proximal epiphysis

Spy 9 is characterised by marked posterior inclination of the tibial plateau relative to the anatomical axis of the diaphysis (tibial retroversion). This posterior displacement of the tibial condyles is a characteristic feature of European and Near Eastern Neandertals (Fraipont, 1891; Boule, 1911-1913; Lustig, 1915; McCown & Keith, 1939; Vandermeersch, 1981; Heim, 1982; Trinkaus, 1983; Trinkaus & Rhoads, 1999). This configuration at the knee led to the early conclusion that Neandertals walked with habitually-bent knees and stooped posture as do the great apes rather than like modern humans (Fraipont, 1891; Boule, 1911-1913; Hrdlička, 1930).

This marked tibial retroversion is also seen in human populations that frequently adopt a squatting posture, leading other early authors to designate Neandertals as habitual squatters (Charles, 1893). As subsequent researchers have indicated, posterior inclination of the tibial plateau did not preclude normal extension of the knee in standing or walking (Arambourg, 1955; Trinkaus, 1983, 1985).

Posterior displacement of the tibial plateau effectively increases the *M. quadriceps femoris* moment arm by increasing the anterior distance between the patellar ligament and rotation axis of the knee (Trinkaus, 1983; Trinkaus & Rhoads, 1999). This feature, combined with the thicker patellae that was also characteristic of Neandertals, would displace the *M. quadriceps femoris* tendon anteriorly, resulting in greater muscle force generated by the knee extensors. These elements were interpreted as part of a general package of postcranial hypertrophy among the Neandertals relative to early modern and recent humans (Trinkaus, 1983, 1986; Trinkaus & Rhoads, 1999).

More recent studies have demonstrated, however, that Neandertals are similar to other Pleistocene humans and nonindustrial recent humans in their degree of tibial retroversion when this measure is evaluated relative to appropriate measures of body size. Given that the baseline load on the knee joint is body weight, tibial retroversion must be considered relative to the body weight moment arm at the knee multiplied by body mass or a proxy for it (Trinkaus & Rhoads, 1999). Thus, the comparative samples are not differentiated by this feature, but Spy 9 does fall above the mean of all samples in its degree of tibial retroversion (Figure 9).

Proximal epiphyseal lines are present on the Spy 9 tibia.

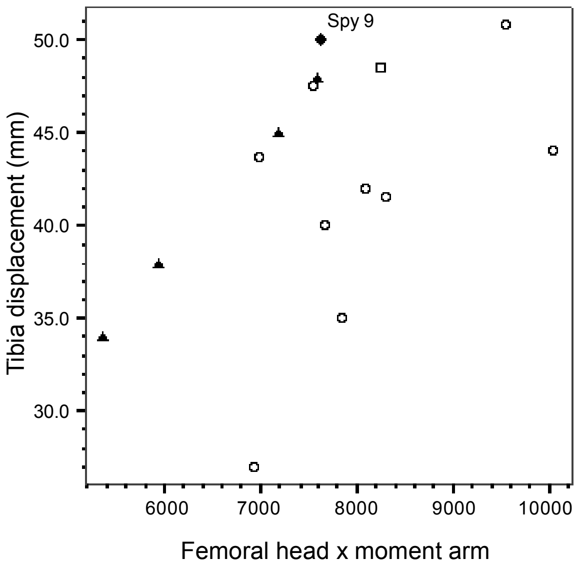

Figure 9. Comparison of tibial condylar displacement versus femoral head diameter multiplied by the body weight moment arm (see text for further explanation). Spy 9 (black diamond), Neandertals (black triangles), Qafzeh-Skhul early modern humans (open squares) and earlier Upper Palaeolithic early modern humans (open circles).

Diaphysis

The Spy 9 tibia has been described as remarkably short and stout (Hrdlička, 1930). At 335.0 mm, Spy 9 falls precisely in the range of variation for Neandertal tibial length (338.8 ± 8.1 mm, N = 9), which is well below that of Middle Palaeolithic (412.5 ± 13.2 mm, N = 6) or Upper Palaeolithic (385.9 ± 5.7 mm, N = 28) early modern humans. The relatively shortened distal limb segments of Neandertals are a well-established adaptation to the arctic environments in which they lived (Trinkaus, 1981; Ruff, 1991, 1994; Holliday, 1997), and the limb proportions of Spy are comparable to other Neandertals (Table 3). Like other Neandertal tibiae, Spy 9 is generally amygdaloid in cross-section.

The cnemic index of Spy 9 (67.7) is near the Neandertal mean. The comparative samples are significantly different with respect to this index (p = 0.039), with the Neandertals having a more eurycnemic tibial shaft (Table 7). These shape differences between samples can also be quantified by means of a ratio of second moments of area at the proximal tibial section. This ratio of maximum to minimum second moments of area provides less discrimination between samples, but the Spy tibia still remains within the range of the Neandertals (2.65 ± 0.41, N = 5) and below that of the early modern humans (Qafzeh-Skhul: 2.92 ± 0.43, N = 4; EUP: 3.07 ± 0.47, N = 8; SF3).

	Midshaft index	*Cnemic index*
Spy 9	70.6	67.7
Neandertals	69.9 ± 6.1 8	69.4 ± 5.6 7
Qafzeh-Skhul	69.7 ± 5.9 6	65.4 ± 4.9 6
Earlier Upper Palaeolithic	64.5 ± 7.2 12	61.0 ± 6.8 12

Table 7. Diaphyseal indices for Spy 9 and comparative samples. Mean ± standard deviation and N are provided for comparative samples.

A ratio of external diameters at the tibial midshaft shows a similar result as that given above, with Spy 9 falling near the Neandertal mean (Table 7). The Neandertals and Qafzeh-Skhul early modern humans are virtually indistinguishable from one another, though they both are distinctly different from the more platycnemic EUP early modern humans. The cross-sectional shape of Spy 9 is also demonstrated by the ratio of second moments of area at the midshaft, which falls in the range of the Qafzeh-Skhul early modern humans (2.17 ± 0.31, N = 5) and at the low end of the range of variation for the Neandertals

(2.39 ± 0.45, N = 8), effectively separating it from the EUP sample (2.64 ± 0.65, N = 12; SF4).

Diaphyseal robusticity

Cross-sectional geometric properties for Spy 9 are provided in Table 8.

Percent cortical area ([cortical area/total area]*100) is not significantly different across Middle and Upper Palaeolithic samples at the midshaft ($p = 0.491$) or proximal ($p = 0.989$) tibia. Spy 9 falls within the range of variation for all samples, and it lies roughly in the middle of the Neandertal and EUP ranges of variation for relative cortical area at the tibial midshaft (Table 9; SF5). At the proximal tibia, Spy 9 falls at the low end of these ranges of variation, demonstrating relatively less cortical area at this section.

Cortical area was evaluated relative to body mass as an indicator of resistance to axial loading on the tibia. As in the femur, there was no significant separation between comparative samples at the midshaft ($p = 0.093$) or proximal ($p = 0.172$) tibia, but Spy 9 falls at the low end of the ranges of variation for the Neandertals (6.02 ± 1.7, N = 5) and EUP early modern humans (5.55 ± 0.91, N = 8) and below that of the Qafzeh-Skhul early modern humans (7.00 ± 0.80, N = 4; SF6).

Cross-sectional properties	*Spy 9*
50 % Cortical area (CA)	414.8
50 % Total area (TA)	574.9
50 % AP 2nd moment of area (I_x)	35273.8
50 % ML 2nd moment of area (I_y)	17770.2
50 % Max 2nd moment of area (I_{max})	36466.1
50 % Min 2nd moment of area (I_{min})	16577.9
50 % Polar moment of area (J)	53044.0
50 % I_{max}/I_{min}	2.200
65 % Cortical area (CA)	376.8
65 % Total area (TA)	722.3
65 % AP 2nd moment of area (I_x)	48871.1
65 % ML 2nd moment of area (I_y)	22144.8
65 % Max 2nd moment of area (I_{max})	50484.4
65 % Min 2nd moment of area (I_{min})	20531.5
65 % Polar moment of area (J)	71015.9
65 % I_{max}/I_{min}	2.459

Table 8. Cross-sectional geometric properties of the Spy 9 tibia. Areas in mm^2, second moments of area in mm^4. 0 % is distal.

Overall strength of the tibial diaphysis is estimated by the polar moment of area (J). Polar moment of area was analysed relative to tibial length multiplied by body mass in order to account for variation in body proportions between Neandertals and early modern humans

	p-value	*Neandertals*	*Qafzeh-Skhul*	*Earlier Upper Palaeolithic*
Midshaft (50 %)				
CA/TA	0.491	0.595	0.544	1.18
CA/BM	0.0930	0.877	2.22	0.883
I_{max}/I_{min}	0.250	0.423	0.0974	0.683
J/BM x len	0.144	0.310	0.979	0.228
Proximal (65 %)				
CA/TA	0.989	1.22	2.49	4.13
CA/BM	0.172	0.922	3.22	1.24
I_{max}/I_{min}	0.290	0.468	1.08	1.29
J/BM x len	0.072	0.369	0.715	0.687

Table 9. Spy 9 tibial metric comparisons. The *p*-values are from ANOVA comparisons across the three comparative samples used for analyses. The remaining values are z-scores relative to each comparative sample [(|Spy values – sample mean|)/standard deviation]. Abbreviations are as follows: CA and TA: cortical and total subperiosteal areas; I_{max}, I_{min}: maximum and minimum second moments of area, respectively; J: polar moment of area; BM x len: estimated body mass multiplied by tibial length.

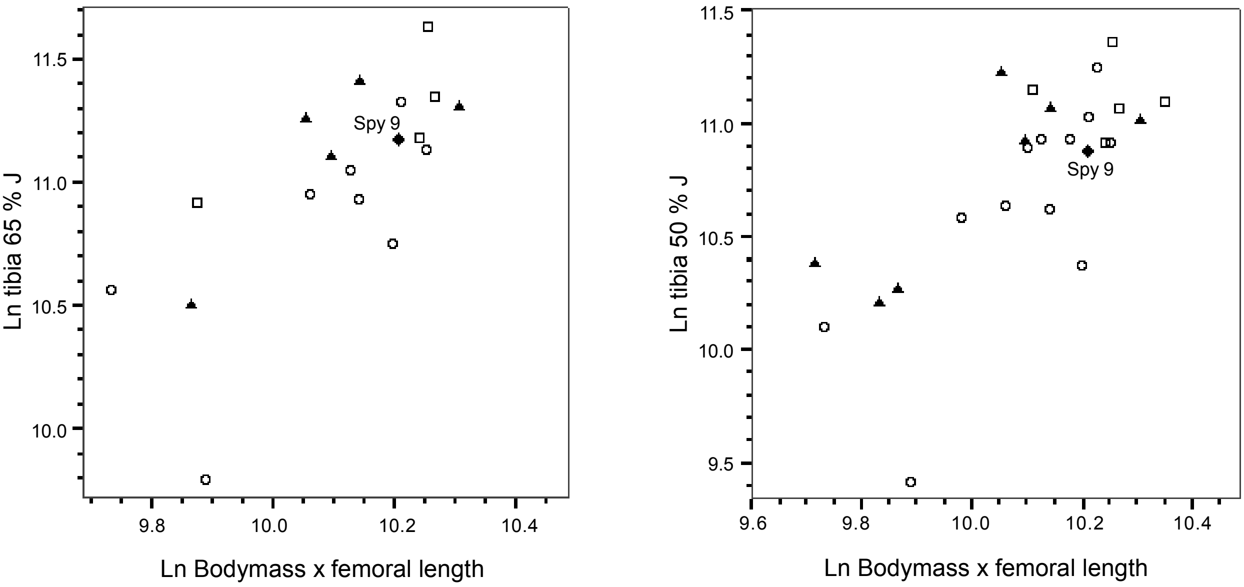

Figure 10. Comparison of the polar moment of area (J) versus body mass multiplied by tibial length at the proximal (65 %) and midshaft (50 %) tibial diaphysis as a measure of overall bending and torsional strength. Symbols are as in Figure 9.

(Figure 10). At the tibial midshaft, there is clearly overlap between comparative samples ($p = 0.144$), and Spy 9 clusters with the Neandertals in its relative strength. At the proximal tibia, greater discrimination is seen between samples ($p = 0.072$) but this is due almost entirely to the anomalously gracile Dolní Věstonice 3 specimen. When Dolní Věstonice 3 is removed from the comparison, there is no longer any significant differentiation between samples ($p = 0.370$). In either case, Spy 9 can be seen to cluster with other Neandertals specimens in overall strength though there are no meaningful differences between samples.

Distal epiphysis

The distal epiphysis of Spy 9 is well-preserved, allowing the articular surface to be assessed. The talar articular surface has a maximum breadth of 32.1 mm. At its maximum anteroposterior depth, this surface measures 33.0 mm; at its minimum anteroposterior depth, it is 15.2 mm.

FIBULA

Spy 26B is a left fibular fragment that includes the distal epiphysis and approximately one-fourth of the distal fibular shaft (Figure 11). The maximum length of the fragment is 94.4 mm. There is slight, postmortem abrasion around the border of the malleolar articular surface, as well as damage to the lateral malleolus. The distal epiphysis is relatively robust, but morphologically

Figure 11. Spy 26B (left fibular fragment). From left to right: posterior, medial, anterior and lateral views. Photograph by P. Semal (RBINS). Scale = 1 cm.

similar to modern humans. On the posterior surface, the groove for the *fibularis longus* and *fibularis brevis* tendons is well-developed. Epiphyseal fusion lines are visible on Spy 26B where the diaphysis joins the distal epiphysis.

PATELLA

Spy 19 is a left patella that is complete with only slight damage to its borders (Table 10; Figure 12). Neandertal patellae are typically described as similar to those of modern humans but with increased thickness resulting from biomechanical considerations at the knee (Heim, 1982; Trinkaus, 1983, 2000; Pap *et al.*, 1996; Trinkaus & Rhoads, 1999). Neandertals have also been shown to have relatively symmetrical medial and lateral patellar facets (Trinkaus, 2000). Spy 19 is characteristically thick (23.1 mm), similar to other Neandertals (23.0 ± 4.4 mm, N = 6) and slightly above that of early modern humans (Qafzeh-Skhul: 21.5 ± 1.4 mm, N = 2; EUP: 20.8 ± 1.7 mm, N = 18). Its height, at 46.2 mm, is similar to Neandertals (44.2 ± 4.8 mm, N = 10) and Qafzeh-Skhul early modern humans (46.7 ± 3.3 mm, N = 2), though not significantly different from EUP early modern humans (42.7 ± 3.7 mm, N = 17). The breadth of the lateral facet (29.9 mm) is greater than that of the medial facet (25.5 mm).

Measurement	*Martin #*	*Spy 19 (left)*
Patellar height	M-1	46.2
Patellar breadth	M-2	50.5
Patellar thickness	M-3	23.1
Articular breadth		49.8
Articular depth		13.0
Medial facet breadth	M-5	26.0
Lateral facet breadth	M-6	31.0

Table 10. Osteometric dimensions for the Spy 19 patella (in mm).

Figure 12. Spy 19 (left patella).
From left to right, top row: lateral, posterior, medial and anterior views. From left to right, bottom row: superior and inferior views.
Photograph by P. Semal (RBINS). Scale = 1 cm.

ASSIGNMENT OF BONES

In their original assessment, Fraipont & Lohest (1887) determined that Spy I represented a fully adult female (or possibly a weak male). Spy II was considered a young adult male. This designation was based primarily on the crania, although these authors also used features of the postcrania to support their assignment. Spy 8, the right femur, was described as having a more distally-projecting lateral condyle relative to the medial condyle when the shaft was held in a vertical position, a feature that they considered more typical of females than males (see also Genoves, 1954). It was originally assigned to Spy I along with Spy 9, the left tibia. The Spy 16 partial femur, judged to be more robust than Spy 8, was designated as part of the Spy II skeleton.

Hrdlička (1930), in an assessment of the skeletons of Spy I and II, indicated the improbability that the right femur and left tibia should be assigned to Spy I based on the strength of these bones relative to the weak arm bones and clavicle assigned to this individual. His revised assignment was strengthened by the presence of epiphyseal lines in the distal femur and proximal tibia that indicated a young adult age that was incompatible with the advanced adult age of the Spy I skull. These features were much more consistent with the age of the Spy II skull.

In a treatise on the sex of the Spy skeletons, Genoves (1954) makes mention of the assignment of the postcranial bones. He supports Hrdlička's reassignment of the partial femur and tibia to Spy II, and relates that the same assessment has been made by Twiesselmann.

This analysis of the original fossils demonstrates that Spy 8 shows traces of epiphyseal fusion lines at both the proximal and distal femur. In males, secondary ossification centers at the proximal femur close between years fourteen to sixteen, followed by a period of synostosis lasting from approximately years sixteen to nineteen. Closure of the distal femoral epiphyses is completed around age eighteen, followed by a period of synostosis from approximately age eighteen to twenty (McKern, 1970). Given that the proximal and distal epiphyses of Spy 8 are fused but the epiphyseal lines are still present, this femur indicates that the individual was a young adult at the time of death.

Traces of the proximal epiphyseal lines are also visible on Spy 9. In males, secondary ossification centers at the proximal tibial shaft close at approximately age eighteen, after which time there is a period of senescence from approximately age eighteen to twenty-one (McKern, 1970). Since the proximal epiphysis of Spy 9 is fused but the epiphyseal lines are still present, this tibia further supports the contention that the individual was a young adult at the time of death.

The presence of these age markers strongly indicates that the Spy 8 femur and Spy 9 tibia belong to the same individual, Spy II, who was a young adult male at the time of death. The left proximal femoral shaft, Spy 16, matches the right in shape, strength and features, indicating that its original attribution to Spy II should remain.

The presence of epiphyseal fusion lines on the Spy 26B distal fibular fragment suggests that this bone can also be assigned to Spy II. Union of the distal epiphysis is generally completed in males by age eighteen, indicating that it belonged to an individual who was a young adult at the time of death (McKern, 1970). This places it securely with the young, male Spy II skeleton.

The attribution of the Spy 19 patella is less secure; however, given its size it is most likely associated with the robust Spy II skeleton. In measures of patellar thickness, Spy 19 falls near the mean value for Neandertals. Its height, however, places it at the upper end of the range of variation for Neandertals. These features make it more likely that the patella should be assigned to Spy II.

CONCLUSIONS

Previous assessments of the lower limb bones from Spy have indicated that these skeletons are typical of the Neandertals, particularly in femoral and tibial strength, the large size of the femoral epiphyses and the exaggerated anterior curvature of the femoral shaft (Fraipont & Lohest, 1887; Fraipont, 1888, 1891; Leclercq, 1927; Hrdlička, 1930). Most notably, early studies of the Spy 9 tibia recognised the marked posterior inclination of the tibial plateau relative to the diaphyseal axis (Fraipont & Lohest, 1887; Fraipont, 1888, 1891; Hrdlička, 1930). This feature was used to augment the argument that Neandertals were incapable of fully extending their legs, and thus walked with habitually bent knees (Fraipont, 1891; Boule, 1911-1913; Hrdlička, 1930).

Like previous assessments by Fraipont (1891) and Hrdlička (1930), this analysis of the Spy lower limb remains demonstrates the resemblance of the femora, tibia and patella to other European and Near Eastern Neandertals. This morphological similarity is seen in most aspects of the femora although, contrary to previous studies, the Spy femora cannot be considered excessively robust relative to other Neandertals in most features. The Spy femora are also unique in dimensions of the proximal femoral shaft, where Spy 8 and 16 show unusually well-developed gluteal buttresses and consequently mediolaterally-expanded subtrochanteric femoral sections relative to other Neandertals. Similarly, the morphology of the Spy 9 tibia is typical of the Neandertals though it does not fall at the upper end of the range of variation in most reflections of strength and robusticity.

Unlike its original attribution by Fraipont (1891), it is most likely that both femora, the tibia and the fibular fragment belong to Spy II, a young adult male. Features of the Spy 8 femur, Spy 9 tibia and Spy 26B fibula indicate that death occurred around the age of eighteen to twenty years. This assessment places them more securely with the skull of Spy II rather than Spy I, a fully adult female. The size and strength of these bones is also more consistent with the strength and robusticity of the upper limb skeleton of Spy II. The similarities between the Spy 8 and Spy 16 femora in size and robusticity also suggest that these bones belong to the same individual, Spy II. While the patella cannot be securely associated with either skeleton, its large height and breadth are consistent with the other features of Spy II. These features of strength and robusticity have been recognised and continue to identify the Spy skeletons as morphologically similar to the Neandertals.

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