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Body size, body proportions, and mobility in the Tyrolean "Iceman"

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Abstract

Body mass and structural properties of the femoral and tibial midshafts of the "Iceman," a late Neolithic (5200 BP) mummy found in the Tyrolean Alps, are determined from computed tomographic scans of his body, and compared with those of a sample of 139 males spanning the European early Upper Paleolithic through the Bronze Age. Two methods, based on femoral head breadth and estimated stature/bi-iliac (pelvic) breath, yield identical body-mass estimates of 61 kg for the Iceman. In combination with his estimated stature of 158 cm, this indicates a short but relatively wide or stocky body compared to our total sample. His femur is about average in strength compared to our late Neolithic (Eneolithic) males, but his tibia is well above average. His femur also shows adaptations for his relatively broad body (mediolateral strengthening), while his tibia shows adaptations for high mobility over rough terrain (anteroposterior strengthening). In many respects, his tibia more closely resembles those of European Mesolithic rather than Neolithic males, which may reflect a more mobile lifestyle than was characteristic of most Neolithic males, perhaps related to a pastoral subsistence strategy. There are indications that mobility in general declined between the European Mesolithic and late Neolithic, and that body size and shape may have become more variable throughout the continent following the Upper Paleolithic.
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Introduction

The Tyrolean "Iceman" (nicknamed "Ötzi" in the popular press) is a mummified corpse that was discovered in 1991 in the Tyrolean Alps near the Italian-Austrian border, at an altitude of about 3200 m (Seidler et al., 1992; Dickson et al., 2003). Radiocarbon analyses of samples from the mummy and equipment found with him yield dates centered around 5200 BP (Bonani et al., 1994; Kutschera et al., 2000), placing him within the late Neolithic−Copper Age (Milisauskas, 2002). Chemical analyses of his bones, teeth, and intestinal contents, as well as paleobotanical evidence, indicate that he spent most of his life south of the discovery site, died in late spring, and was probably not a chance wanderer into the high mountains, i.e., he was familiar with the terrain and local environment (Oeggl et al., 2000; Muller et al., 2003). His sex assignment is based on preserved soft tissue, and his age has been estimated at about 46 years (range: 40−53 yr), based on macroscopic and microscopic analyses of the skeleton (Sjovold, pers. comm.; see: www.uibk.ac.at/c/c5/c552/Forschung/

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Iceman/agepress-en.html). He is currently housed in a special climate-controlled chamber in the South Tyrol Museum of Archaeology in Bolzano, Italy.

Because of his state of preservation, including soft tissue and the remains of clothing and tools, and chronological age (the earliest known mummy from Europe), the Iceman has been one of the most intensively studied prehistoric individuals in the world (for recent reviews, see Dickson et al., 2003; Muller et al., 2003; Murphy et al., 2003). As part of those investigations, a series of CT scans of his body were carried out beginning shortly after his discovery (Murphy et al., 2003). We report here on information extracted from one of these examinations that sheds further light on his body size, proportions, and lower limb-bone structural properties, with implications for reconstructing his activity patterns. Comparisons are made to a large sample of prehistoric European skeletons, ranging from early Upper Paleolithic through the Bronze Age. Based on these comparisons, we also offer some more general observations regarding temporal trends in body shape and mobility in this region.

Materials and methods

The CT scans used in this investigation were taken in May, 1994, using a spiral CT scanner at the University of Innsbruck (Somatom Plus 40; Siemens). Images were examined and linear and angular skeletal dimensions were measured using the software application Osiris 4.0.7. Images were imported into a version of NIH Image 1.62 with a custom-designed macro for determination of bone cross-sectional geometric properties (for a copy of the macro, see: www.hopkinsmedicine.org/fae/mmacro.htm). Geometric section properties were determined at two locations: the midshaft of the right femur and the midshaft of the left tibia (with midshaft defined relative to bone length', see Ruff, 2002). The right femur was chosen because it is fixed more nearly parallel to the long axis of the Iceman's body (and thus transverse to the plane of the CT images) than the left femur (for an illustration of the whole body, see Dickson et al., 2003). Although the right tibia is also slightly more longitudinally oriented than the left tibia, it could not be used for this analysis because a large piece of the cortex is missing from the midshaft region. The exact positioning of each bone in three-dimensional space was determined by comparing x, y coordinates of articular centers and other bony landmarks and relating these to standardized positioning protocols (Ruff, 2002). Slight anteroposterior (A-P) and mediolateral (M-L) angling of the femoral and tibial shafts ($< 10°$) was corrected trigonometrically. In addition, the right femur in the mummy is twisted $25°$ about its longitudinal axis and the left tibia $65°$ about its longitudinal axis, relative to standardized orientations (Ruff, 2002); this was corrected by rotating the sections within the NIH Image analysis program prior to analysis.

Body mass of the Iceman was calculated using two different but complementary techniques based on: a) estimated stature and bi-iliac (maximum pelvic) breadth and b) femoral head breadth (Auerbach and Ruff, 2004). For the stature/bi-iliac technique, a recently revised equation was used

(Ruff et al., 2005). Three equations based on femoral head breadth are available (Ruff et al., 1991; McHenry, 1992; Grine et al., 1995); because the Iceman is intermediate in body size (i.e., not very small or very large relative to most living humans), an average of all three estimates was used here (for discussion and justification, see Auerbach and Ruff, 2004). Bi-iliac breadth and femoral head breadth (of the right femur) were measured directly from appropriate CT scan slices (see below for images). Because only A-P breadth of the femoral head can be measured on a transverse CT slice, and all body-mass estimation formulae are based on S-I (superoinferior) breadth, A-P breadth was corrected to S-I breadth using a relationship derived from a diverse modern human sample (Ruff, 2000b): S-I = $1.004 \times$ A-P (SEE = 0.67 mm). Stature was estimated both from regression formulae based on femoral length and from direct measurement of the body (Seidler et al., 1992).

Comparative samples are listed in Table 1. All are European and range from the early Upper Paleolithic (30,000 BP) through the Bronze Age (3,500 BP), thus bracketing the time period of the Iceman. The Upper Paleolithic and Mesolithic samples are derived from sites throughout Europe (Holt, 2003), while the Neolithic and Bronze Age samples are almost entirely derived from sites in central Europe, specifically lower Austria, Moravia, and Bohemia (Sládek et al., 2006, in press). The possible effects of this unequal geographic distribution on comparisons are discussed below. It should also be noted that our comparative Neolithic sample is late Copper Age, or Eneolithic, and thus slightly younger than the Iceman. The Mesolithic sample includes some Scandinavian material (Holt, 2003), explaining the relatively late (5,300 BP) upper limit for this period.

Because the Iceman is male, all of our comparative analyses included only (adult) males. A total of 139 individuals were included in the study, with most ($n = 100$) possessing both an intact femur and tibia (Table 1). Cross-sectional properties of the midshaft femur and tibia were determined through analysis of section contours obtained from external molds and biplanar radiographs or CT scans (Holt, 2003; Sládek et al., 2006, in press).

Body mass for the comparative sample was determined in the same way as for the Iceman, using a combination of estimations from stature/bi-iliac breadth and femoral head breadth (Auerbach and Ruff, 2004), as available. Body masses for the majority of individuals (62% of the males) were estimated using femoral head breadth (with A-P breadths corrected to S-I

Table 1
Comparative samples (males)

Period	Years BP	Individuals	Femora[1]	Tibiae[1]
Early Upper Paleolithic	20,000–30,000	11	11	7
Late Upper Paleolithic	10,000–19,000	14	14	12
Mesolithic	5,300–9,000	32	30	26
Neolithic	4,200–4,800	36	30	29
Bronze	3,500–4,200	46	41	33

[1] Included in cross-sectional geometric analyses.

breadths as necessary using the formula given above), again taking the average of the three femoral breadth formulae results. Bi-iliac breadth could be measured in only 19% of the males; body-mass estimates from stature/bi-iliac breadth were averaged with those from the femoral head for these individuals, except for two individuals for whom femoral head breadths were not available. In the remainder of the sample (19%), body mass was estimated from stature and estimated bi-iliac breadth, with bi-iliac breadth estimated from femoral length using a previously described technique employing the average slope between the two variables in recent humans, keyed to the mean bi-iliac breadth and femoral length of the appropriate sample (i.e., the five periods shown in Table 1) (Trinkaus and Ruff, 1999). Estimated bi-iliac breadths were only used for body-mass calculations and not analyses of body shape. Statures were estimated from maximum femoral length. Following from known differences in relative limb length (Holliday, 1997; Formicola, 2003), Trotter and Gleser's (1952) formula for U.S. blacks was used for early Upper Paleolithic specimens, while Sjovold's (1990: Table 1, "Femur 1") "Caucasian" formula, based on modern Euro-americans, was used for specimens from subsequent time periods. Other possible stature estimation equations for the later time periods, including Trotter and Gleser's (1952) U.S. white formula and Formicola and Franceschi's (1996) formulae based on a European Neolithic sample, were found to produce more variance between body-mass estimates when compared to estimates based on the femoral head. The Sjovold technique was also used in the original stature estimate for the Iceman, and compared well with direct measurement of his body (Seidler et al., 1992; see below). In a few cases, body mass could not be determined for an individual in the comparative sample due to the lack of a femur (or bi-iliac breadth), but tibial cross-sectional data were still collected. Conversely, in a few other cases, body mass could be estimated but cross-sectional data were incomplete.

The LOWESS nonparametric plotting technique (Cleveland, 1979) was used to examine temporal trends within the comparative sample, using a smoothing window width of 0.5. All statistics and graphics were generated using SYSTAT (SYSTAT: Statistics, 1990).

Results

Body size

Maximum pelvic breadth of the Iceman, measured through the iliac crests, is 26.4 cm (Figure 1a). Although the sacroiliac joint space appears to be somewhat reduced due to desiccation of articular cartilage, the orientation of the two innominates to each other and to the sacrum appears undistorted and approximately in anatomical position (as also confirmed by examination of photographs of the whole body; see Dickson et al., 2003). Correcting for the addition of soft tissue (Ruff et al., 1997) yields an estimated "living" bi-iliac breadth of 27.9 cm.

Stature of the Iceman based on measurements taken directly on his body is 158 cm (Seidler et al., 1992). Maximum femoral length, measured as the distance between appropriate CT slices following trigonometric positional correction, is 411 mm. Using this length, Sjovold's (1990) "Caucasian" formula yields an identical stature estimate of 158 cm; similar results are obtained using Trotter and Gleser's (1952) U.S. white male formula (159 cm), and Formicola and Franceschi's (1996) European Neolithic male formulae (158 cm and 157 cm for least squares and major axis formulae, respectively). Thus, a stature estimate of 158 cm for the Iceman seems to be well justified. Based on this stature and a living bi-iliac breadth of 27.9 cm, body mass of the Iceman is estimated as 61.0 kg, using a formula derived from a worldwide sample of living males (Ruff et al., 2005).

Anteroposterior femoral head breadth of the Iceman is 44.1 mm (Figure 1b), producing an estimated S-I breadth of 44.3 mm (see above). Entering this value into the formulae of Ruff et al. (1991), McHenry (1992), and Grine et al. (1995) yields body-mass estimates ranging from 59.3 to 64.0 kg, with an average of 61.07 kg. This value is almost identical to that obtained from the stature/bi-iliac technique. Thus, two complementary but independent approaches converge on the same body-mass estimate of 61 kg.

Temporal trends in stature and body mass for the comparative male sample and the Iceman are shown in Figure 2. There is a relatively sharp decline in both body-size measures in the comparative sample from the early Upper Paleolithic
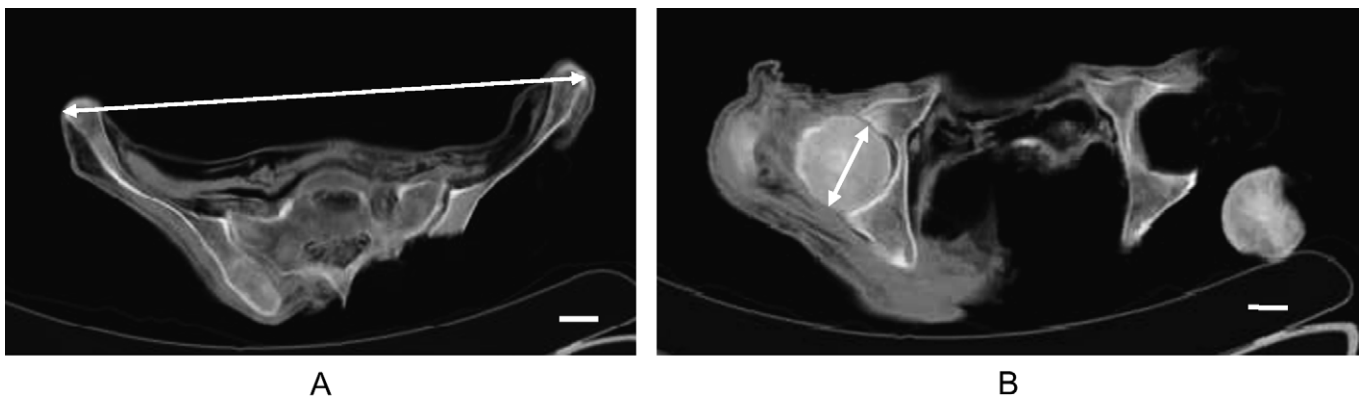

Fig. 1. Transverse CT slices through the Iceman (viewed from below). Scale bars = 2 cm. (A) Measurement of bi-iliac breadth (26.4 cm). (B) Measurement of femoral head breadth (44.1 mm). Light grey regions are remains of desiccated soft tissue. Note (postmortem) dislocation of left femur from acetabulum.
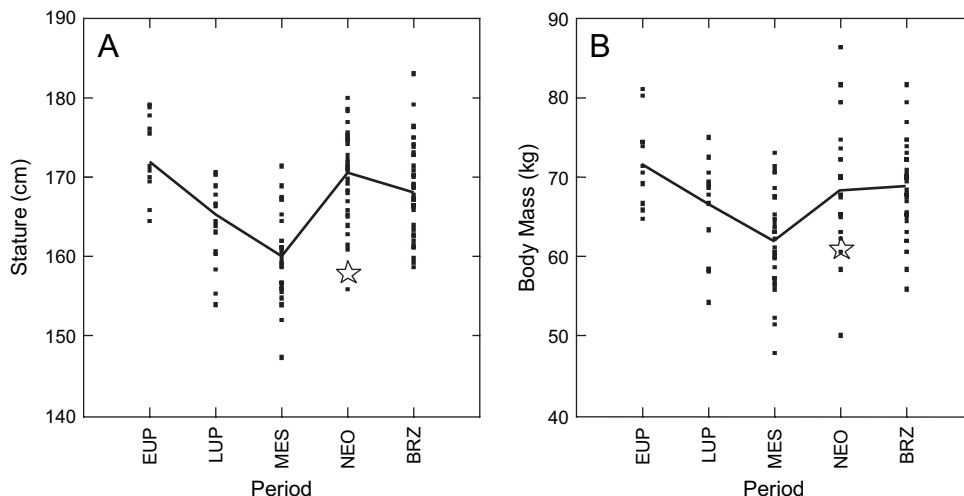
Fig. 2. Temporal trends and position of the Iceman (open star) relative to the comparative male sample for stature (A) and body mass (B). LOWESS line fit through comparative data. Abbreviations are as follows: EUP, early Upper Paleolithic; LUP, late Upper Paleolithic; MES, Mesolithic; NEO, Neolithic; BRZ, Bronze Age (see Table 1).

through the Mesolithic, as documented for stature or long-bone lengths by previous researchers (Frayer, 1980, 1984; Jacobs, 1985; Formicola and Giannecchini, 1999). In our sample, there is then an increase in both body-size measures in the Neolithic that is then maintained in the Bronze Age. However, it is likely that this apparent increase is brought about at least in part by the nonrandom geographic sampling of our two later samples (see Discussion). The Iceman is quite small compared to our Neolithic male sample, particularly in stature (second smallest in our sample of 30 with statures, fourth smallest in our sample of 36 with body masses). Relative to the entire comparative sample he is less of an outlier but is still small: 1.26 standard deviations (SDs) below the overall sample mean for stature (166.8 ± 7.0 cm, $n = 124$) and 0.92 SDs below the mean body mass (67.4 ± 7.0 kg, $n = 135$).

Femoral and tibial cross-sectional geometry

CT images of the Iceman through the femoral and tibial midshafts are shown in Figure 3. Images were rotated to maintain a constant orientation relative to standardized reference axes (Ruff, 2002) and are presented as if the bones were from the right side, viewed proximodistally. Section properties and their definitions are given in Table 2.

Relative cortical area, summarized as %CA (CA/TA × 100), is high in the Iceman (femur: 85.6%; tibia: 84.9%) compared to our total sample of males (femur: $76.1\% \pm 6.2$; tibia $78.1\% \pm 7.4$) or Neolithic males only (femur: $73.9\% \pm 5.6$; tibia: $72.9\% \pm 5.5$). In fact, the relative medullary size and cortical thickness of his femoral midshaft is similar to that of early-middle Pleistocene *Homo*, although within the range of modern humans (Ruff et al., 1993). Relative cortical thickness, however, is not a direct measure of mechanical competence, which depends on both bone area and the distribution of bone in cross section (Nordin and Frankel, 1980; Ruff, 1992). Because in vivo mechanical loading of limb-bone diaphyses is dominated by bending (Rubin and Lanyon,

1982), combined with some torsion (Carter, 1978), cross-sectional properties that reflect bending/torsional strength, i.e., second moments of area (or area moments of inertia), are more critical for assessing mechanical strength.

The polar second moment of area, J, can be used as a measure of torsional and (twice) average bending rigidity (although it is less applicable to torsional analyses in strongly asymmetrical sections like the tibial midshaft) (Ruff, 2000b; Daegling, 2002). When divided by the average radius of a section, it approximates the average section modulus, or (twice) average bending or torsional strength of the section (Ruff, 2002), here designated as the polar section modulus, Z_p.[1] Section moduli derived from maximum and minimum second moments of area (I_{max} and I_{min}) are designated here as Z_{max} and Z_{min}, which refer to bending strengths calculated in the same planes as I_{max} and I_{min}. Because bone breadths were not available for all sections in the comparative sample, section moduli were derived as corresponding second moments of area taken to the 0.73 power (Ruff, 1995, 2000b). Section moduli, in turn, were standardized for differences in body size by dividing by the product of estimated body mass and maximum bone length, based on previous allometric studies (Selker and Carter, 1989; Polk et al., 2000; Ruff, 2000b). Standardized values for Z_p, Z_{max}, and Z_{min} are presented for the femoral and tibial midshafts of the Iceman and the comparative samples in Table 3. Also shown are the ratios of A-P to M-L

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[1] As Lieberman et al. (2004) have shown, section moduli may misrepresent true bending strengths (more specifically, maximum strains in the plane of bending) when the neutral axis does not pass through the section centroid, as is common in weight-bearing limb bones. However, as discussed later in this paper, this is less of an obstacle to interpretations when comparisons are made between (or within) similar species and skeletal locations, where general mechanical loading regimes are also similar. In such situations, section moduli still represent the best available indices of in vivo bending/torsional strength (Ruff et al., 2006).
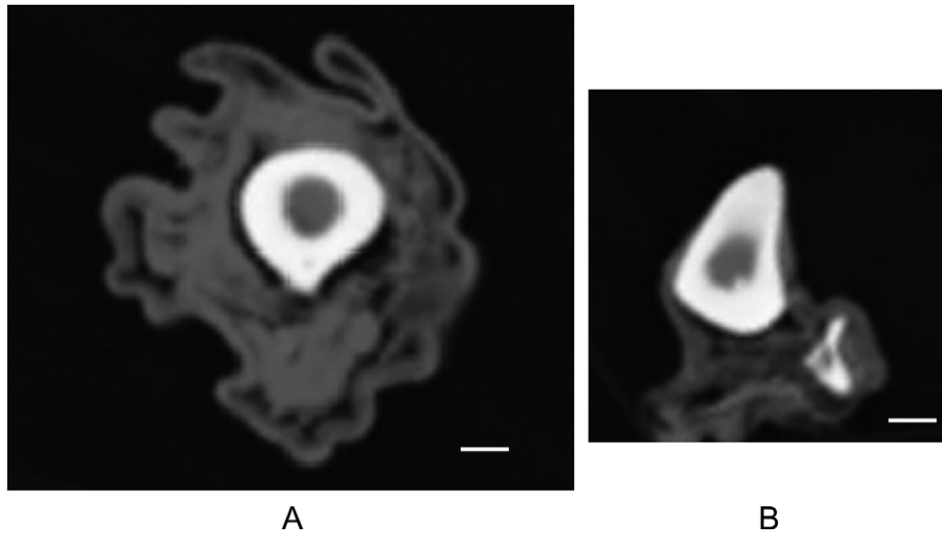
Fig. 3. Transverse CT slices through the Iceman: (A) femoral midshaft and (B) tibial midshaft. Scale bars = 1 cm. Anterior is up and lateral is to the right (original sections rotated as necessary).

bending strength, Z_x/Z_y, at each location, used in bone-shape analyses (see below).

Figure 4 shows temporal changes in femoral and tibial midshaft Z_p relative to body size in the male comparative sample and in the Iceman. The Iceman's femur is close to the average for Neolithic males, but his tibia is well above average. Both femoral and tibial Z_ps show little change from the early Upper Paleolithic through the Mesolithic and then decline from the Mesolithic to the Neolithic, with tibial average relative strength continuing to decline in the Bronze Age. The Iceman's tibia is thus closer in average relative strength to those of pre-Neolithic males (within about 0.6 SD of the Mesolithic mean, see Table 3), but his femur is closer to the average for Neolithic and Bronze Age males. Similar patterns are evident in Z_{max} and Z_{min} (Table 3).

Possession of a larger polar second moment of area (J) in the tibial midshaft than in the femoral midshaft—characteristic of the Iceman (Table 2)—is unusual but not exceptional: 13% of the male comparative sample also displays this characteristic. When converted to the section modulus (Z_p) and size-standardized (by dividing by bone length; body mass is constant), thus estimating true relative strength, femoral and tibial midshafts are nonsignificantly different within individuals in the total sample ($p = 0.73$; paired t-test) (also see Table 3). The Iceman's ratio of 1.27 for size-standardized tibial-to-femoral Z_p is quite high but within the overall range of the comparative sample (3 of 82 individuals with all necessary

data are equal or higher). Similar ratios for size-standardized tibial/femoral Z_{max} and Z_{min} for the Iceman are also within the range of the total sample. Thus, the Iceman has unusual but not unprecedented tibial/femoral strength proportions.

Differences in cross-sectional shape can be summarized by considering ratios of bending rigidities or strengths in perpendicular planes (e.g., A-P/M-L or maximum/minimum). The Iceman's femoral midshaft is relatively round, with an I_x/I_y ratio of 0.982 and I_{max}/I_{min} ratio of 1.21 (Figure 3; Table 2). His tibial midshaft is much more strongly asymmetrical, as is usual for this section (Ruff and Hayes, 1983a), with $I_x/I_y = 2.11$ and $I_{max}/I_{min} = 2.55$. To put shape differences into context, A-P/M-L bending strengths (ratios of section moduli) of the Iceman's femur and tibia are plotted along with the male comparative sample in Figure 5. The Iceman's femur is somewhat rounder than average (i.e., closer to 1.0) compared to our Neolithic males, but within 0.6 SD of the mean for this time period (Table 3). Conversely, his tibia is somewhat less round (farther from 1.0) than other Neolithic males, falling about 0.85 SD above the mean. Both femoral and tibial A-P/M-L bending strengths generally decline through time in the comparative sample, but the major decline in the femoral index occurs between the early Upper Paleolithic and Mesolithic, and in the tibial index, between the Mesolithic and Neolithic. As with overall strength (Z_p) relative to body size, then, the Iceman's tibial shape is more similar to that of Mesolithic males (within 0.4 SD) than to that of

Table 2

Cross-sectional properties of femoral and tibial midshafts of the Iceman

Bone	CA[1]	TA	MA	I_x	I_y	I_{max}	I_{min}	J
Femur	415	485	70	18440	18779	20373	16846	37219
Tibia	400	471	71	27549	13057	29178	11428	40606

[1] Abbreviations are as follows: CA, cortical area; TA, total subperiosteal area; MA, medullary area; I_x, second moment of area about M-L axis; I_y, second moment of area about A-P axis; I_{max}, maximum second moment of area; I_{min}, minimum second moment of area; J, polar second moment of area. Areas are in mm^2; second moments of area are in mm^4.

Table 3
Relative femoral and tibial midshaft strengths in the Iceman and comparative samples[1]

Sample	Femur								Tibia							
	Z_p[2]		Z_{max}[3]		Z_{min}[4]		Z_x/Z_y[5]		Z_p[2]		Z_{max}[3]		Z_{min}[4]		Z_x/Z_y[5]	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Iceman	86.6	—	55.8	—	48.5	—	0.99	—	110.2	—	86.6	—	43.7	—	1.72	—
Early Up. Pal.	96.7	17.4	67.7	13.7	48.3	7.3	1.36	0.13	95.6	14.7	76.2	13.8	36.4	5.6	1.85	0.30
Late Up. Pal.	100.0	12.1	68.5	9.0	51.5	7.3	1.26	0.19	100.6	9.1	80.0	8.6	38.4	6.4	1.98	0.32
Mesolithic	97.4	12.8	62.6	9.2	53.2	7.9	1.09	0.11	99.0	17.8	77.4	14.2	41.3	9.9	1.84	0.30
Neolithic	85.7	10.7	56.0	7.2	47.1	6.4	1.08	0.16	86.9	11.8	66.9	9.9	36.1	5.3	1.50	0.26
Bronze Age	83.6	9.6	55.3	7.6	45.3	5.0	1.04	0.17	80.6	9.1	62.3	7.6	33.2	4.9	1.57	0.26

[1] All properties are standardized over estimated body mass × bone length (femoral or tibial) and multiplied by 1000; section moduli in mm^3, body mass in kg, bone length in mm.
[2] Polar section modulus (torsional/average bending strength).
[3] Maximum section modulus (maximum bending strength).
[4] Minimum section modulus (minimum bending strength).
[5] A-P/M-L bending strengths (section moduli).

Neolithic males. The same is true for the Iceman's tibial midshaft Z_{max}/Z_{min} ratio, which is within 0.1 SD of the Mesolithic mean but about 0.5 SD above the Neolithic mean (data not shown).

Femoral cross-sectional shape has been shown, theoretically and empirically, to be sensitive to differences in mechanical loadings about the hip joint, which in turn can be related to overall body shape (Ruff, 1995). Specifically, femoral shafts become more mediolaterally buttressed as pelvic interacetabular distance relative to femoral length increases. Theoretically, tibial cross-sectional shape should not be as affected by pelvic proportions, since the tibia is more mediolaterally centered under the body's center of gravity during weight support (Pauwels, 1980; Ruff, 2005). Although interacetabular distances were not measured on the present comparative sample, bi-iliac (maximum pelvic M-L) breadths may be used as a rough guide to general body proportions (Ruff, 2000b), and were available for 21 individuals with matching femoral and tibial cross-sectional data in the comparative sample.

Figure 6 shows the ratios of femoral-to-tibial M-L (Z_y) and A-P (Z_x) bending strengths, relative to pelvic bi-iliac breadth/stature in the comparative sample and the Iceman. As above, bending strengths are size-standardized over corresponding bone lengths (body mass is constant). Theoretically, M-L bending strength should be more dependent on pelvic (body) proportions more proximally in the lower limb, i.e., in the femur, while A-P bending strength should show no such locational dependence (Pauwels, 1980; Ruff, 2005). The results shown in Figure 6 support this prediction: the greater the relative pelvic breadth, the greater the increase in M-L bending strength of the femur relative to the tibia (Fig. 6A, r = 0.420, p = 0.058), while there is not a similar relationship between bi-iliac breadth/stature and femoral/tibial relative A-P bending strength (Fig. 6B, r = 0.090, p = 0.70). Thus, individuals with relatively stocky bodies, i.e., wide pelves relative to stature, tend to have increased femoral M-L, but not A-P bending strength, relative to similar measures in the tibia. The Iceman falls well within the data scatter for femoral/tibial M-L strength in
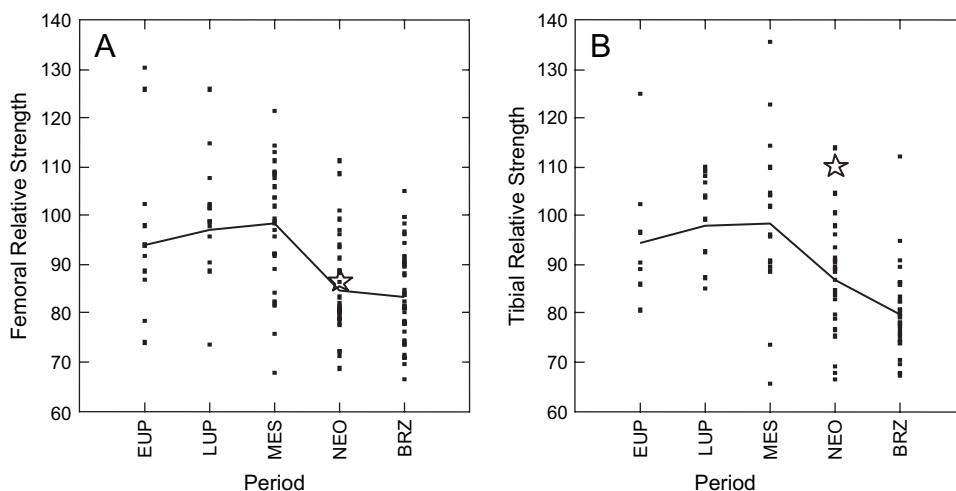

Fig. 4. Temporal trends and position of the Iceman (open star) relative to the comparative male sample in relative strength of the femoral midshaft (A) and tibial midshaft (B). Relative strengths calculated as polar section modulus/(body mass × bone length), with section modulus in mm^3, body mass in kg, and bone length in mm; resulting ratios multiplied by 1000. See Figure 2 for period abbreviations. Line through comparative sample plotted using LOWESS.
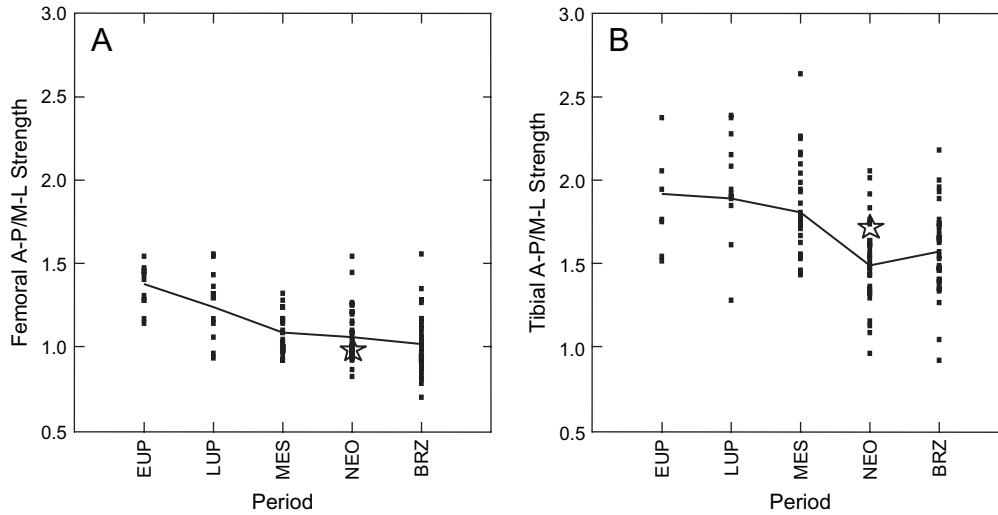
Fig. 5. Temporal trends and position of the Iceman (open star) relative to the comparative male sample for A-P/M-L bending strengths (section moduli) of the femoral midshaft (A) and tibial midshaft (B). See Figure 2 for period abbreviations. Line through comparative sample plotted using LOWESS.

Figure 6A—within 0.8 standard errors of the value predicted for his body shape (bi-iliac breadth/stature). In contrast, his femoral/tibial A-P strength is near the bottom of the available comparative sample (Fig. 6B), reflecting his A-P strengthened tibia (Fig. 5).

Discussion

The Tyrolean Iceman was a relatively small individual when compared to most European males in our Upper Paleolithic through Bronze Age samples. However, despite the superficial appearance given by photographs of his mummified body (Dickson et al., 2003), he was not thin or lightly built: his body (bi-iliac) breadth relative to stature falls in the top third (8 of 26 individuals) for all males with available bi-iliac breadths and exceeds all four of our other Neolithic males with

comparable data. His bone strength relative to body size ranges from slightly to well-above average for other Neolithic males, and his relative tibial strength in particular is among the highest in our comparative sample. His "emaciated" appearance in photographs can thus be attributed to desiccation following his death: given the general interdependence of muscle and bone strength (Burr, 1997), it is likely that his muscles, like his bones, were well developed during life (Murphy et al., 2003). This conclusion is also implied by his estimated body mass of 61 kg, which is not small for an individual whose stature is about 158 cm. These values give an estimated "body mass index" (BMI = weight/stature^2, with stature in meters) of 24.4, which is slightly below average for recent US white males in their fifth decade (Must et al., 1991). However, given the increased prevalence of obesity (i.e., excess fat) in recent industrialized societies (Cronk and Roche, 1982;
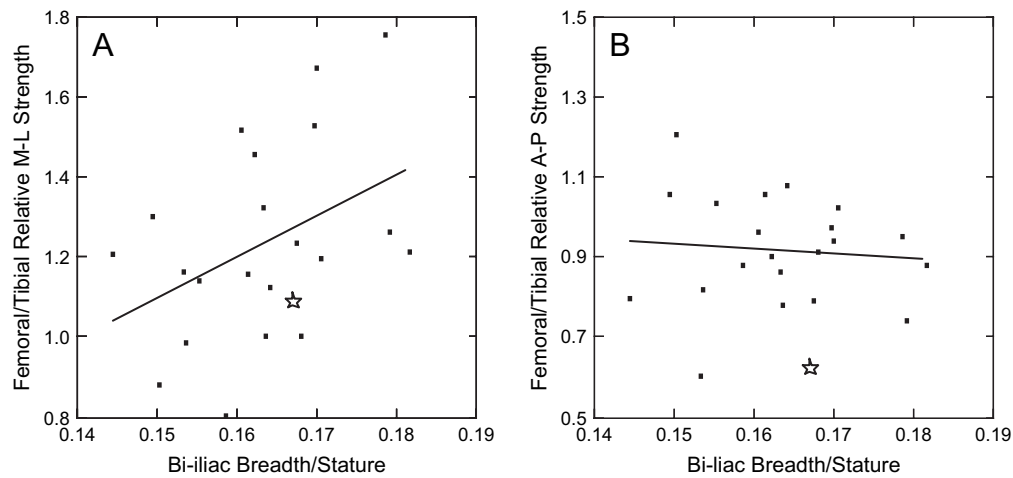

Fig. 6. Relationship between femoral-to-tibial relative strengths (section moduli/bone length) and body shape in the available comparative sample ($n = 21$) and the Iceman (open star). Least squares regression lines plotted through comparative sample. (A) Femoral/tibial relative M-L bending strength vs. bi-iliac breadth/stature. Regression equation: y = 10.34(x) − 0.45, r = 0.420, p = 0.058. (B) Femoral/tibial relative A-P bending strength vs. bi-iliac breadth/stature. Regression equation: y = −1.24(x) + 1.12, r = 0.090, p = 0.70.

Stamler, 1993), and the unlikelihood of such a body composition in the Iceman, perhaps a better comparison is with the male Olympic athletes measured by Tanner (1964): the Iceman falls slightly above the average BMI for Tanner's Euroamerican athletes (23.4, average of event-specific means) and falls closest to the wrestlers and decathlete (means of 24.2 and individual value of 24.3, respectively). Thus, the Iceman was likely very sturdily built.

As noted earlier, nonrandom geographic sampling may have contributed to the apparent increase in body size in our Neolithic and Bronze Age samples relative to our Mesolithic sample, since pre-Neolithic samples were pan-European while the later samples were from only a relatively limited area in central Europe (present-day Czech Republic and Austria). As discussed by previous authors (Frayer, 1984; Formicola and Giannecchini, 1999), stature estimates for the European Mesolithic vary significantly depending on which particular samples are included, implying considerable heterogeneity across the continent. Thus, in two different analyses including somewhat different samples, Frayer (1980) found either a slight increase or slight decrease (1984) in average stature between the Mesolithic and Neolithic. Formicola and Giannecchini (1999) specifically noted a contrast between eastern and western European Mesolithic samples in average stature, with eastern European samples being taller. If this pattern is also characteristic of the Neolithic, then it could explain the taller statures of our Neolithic sample (assuming that they are more closely related to eastern Europeans—Formicola and Giannecchini included Serbian as well as Ukranian and Russian samples among their eastern Europeans). Interestingly, Formicola and Giannecchini found no evidence for any geographic heterogeneity in stature among Upper Paleolithic European samples, suggesting that whatever factors were responsible for later differentiation (different population origins, reduced gene flow between populations, local adaptations), they were not present earlier in Europe, an idea that has a long history in anthropological research (von Bonin, 1935).

Significant geographic variation in body size among Neolithic Europeans is also suggested by a recent report on a late Neolithic skeletal sample from Liguria in northern Italy (Marchi et al., 2005; Marchi, pers. comm). Average stature and body mass for the eight males in this sample, calculated using the same methods as in the present study, are 160.4 cm (range: 154.1−167.3 cm) and 61.2 kg (range: 58.0−63.9 kg), respectively, very similar to the dimensions obtained here for the Iceman (158 cm and 61 kg). The average bi-iliac breadth/femoral length ratio for the four males in the Ligurian sample with measurable pelves is 0.657 (range: 0.621−0.669), again close to that for the Iceman (0.642) and deviating from our male Neolithic sample (range: 0.558−0.609; $p < 0.01$, t-test with Ligurian sample). Thus, in general, body form in the Ligurian sample appears to deviate from our Neolithic sample in the same direction as the Iceman: short, but relatively broad-bodied. The samples are small and may not be wholly representative of geographic variation across Europe, but they suggest possible north-south as well as east-west variation in body size, with the Iceman conforming more to the southern pattern (at least as represented in northern Italy). These observations also highlight the importance of controlling for body size in comparisons of relative bone strength.

The relatively thick cortices of the Iceman's femur and tibia have been noted previously (Murphy et al., 2003) and are confirmed here through comparisons with other penecontemporaneous European samples. Individual age is not likely to be a significant factor in these comparisons, since %CA reaches its maximum in the fourth decade and declines thereafter (Garn, 1970; Ruff and Hayes, 1983b)—the Iceman should have been slightly beyond his peak in this respect. Diaphyseal response to increased mechanical loading is primarily endosteal after mid-adolescence (Ruff et al., 1994; Bass et al., 2002; Kontulainen et al., 2002), and continued high levels of mechanical loading are probably necessary to maintain (and increase) bone mass in adults (Valdimarsson et al., 2005), so the thick cortices and small medullary cavity of the Iceman's bones suggest an active lifestyle maintained throughout his life. Comparisons of actual bending/torsional strength relative to body size support this conclusion. This is especially true with regard to tibial strength, for which the Iceman falls among the strongest individuals in our comparative sample.

In a comparative analysis of several Holocene forager groups, Stock (2004) found that relative strength of distal limb bones (e.g., the tibia) showed a stronger correlation with habitual activity patterns than did relative strength of proximal limb bones (e.g., the femur), which showed a stronger correlation with climate. Another way to interpret these results is that the structure of proximal limb bones is more influenced by body shape (which itself is in part climatically determined; see Ruff, 1994) than is the structure of distal limb bones, so that differences in activity alone may be more clearly discernable in the distal limb. The bone-shape analyses carried out in the present study support this hypothesis: differences in basic body shape (bi-iliac breadth/stature) are associated with variation in femoral-to-tibial M-L bending strength. Thus, the relatively wide body of the Iceman may explain his relatively mediolaterally wide femoral shaft, while his body shape would be expected to have less effect on tibial morphology, which is strongly (for Neolithic males) A-P buttressed. In fact, in all respects, the Iceman's tibia is much more like that of our Mesolithic rather than Neolithic males, which suggests a corresponding similarity in habitual activities. Although the exact nature of the Iceman's lifestyle and subsistence strategy are still debated (Dickson et al., 2003), one likely possibility is that he was involved in some kind of transhumance, or seasonal migrational activities associated with driving livestock back and forth between higher and lower elevations (Oeggl et al., 2000; Muller et al., 2003). In any event, his discovery high in the Alps implies that he was capable of traveling long distances over rough terrain. In this respect, then, his lifestyle, at least in terms of lower-limb loadings, may have been more similar to that of Mesolithic foragers than to that of more sedentary agricultural populations. The combination of such an active lifestyle together with a short, stocky body build may account for the somewhat contradictory structural

characteristics of his tibia and femur. In effect, he combines a relatively broad body (a ''female'' characteristic), which would be expected to increase M-L bending of the femur, with great mobility over rough terrain (a ''male'' characteristic), which would be expected to increase A-P bending of the entire lower limb, but especially the region about the knee (Ruff, 1987). The latter appears to be more expressed in his tibia, possibly because of the overriding effect of body shape more proximally.

These observations also have implications for more general interpretations of body shape and mobility patterns among late Pleistocene−early Holocene Europeans. Although the exact timing and magnitude of change in stature in Europe following the early Upper Paleolithic has been debated (in part due to disagreements regarding stature estimation technique; see Formicola, 2003), it seems clear that average stature across Europe declined between the early Upper Paleolithic and Mesolithic, at least (Frayer, 1980, 1984; Jacobs, 1985; Formicola and Giannecchini, 1999). This is also true in our sample (see above; ANOVA, stature on time period, $p < 0.001$). At the same time, bi-iliac breadth shows no change from the early Upper Paleolithic through Mesolithic (ANOVA, bi-iliac breadth on time period, $p > 0.80$). Our sample sizes for bi-iliac breadth are very small ($n = 6$, 4, and 3 males for early and late Upper Paleolithic and Mesolithic, respectively), but even restricting the sample to these individuals, stature reduction is still statistically significant (ANOVA, $p < 0.05$). Changing body proportions may thus have contributed to femoral cross-sectional shape changes from the early Upper Paleolithic through Mesolithic, along with a general reduction in mobility (for discussion, see Holt, 2003). However, the marked change in tibial cross-sectional shape between the Mesolithic and Neolithic that we observed here may indicate an even more marked change in mobility between these time periods, especially since it is not accompanied by any similarly large change in femoral cross-sectional shape (which could reflect a body shape influence). These observations will need to be verified on larger, more geographically comprehensive Neolithic and Bronze Age samples, but if found to be generally true, they may indicate more of a reduction in mobility between the Mesolithic and Neolithic than between the early Upper Paleolithic and Mesolithic in Europe. The outlier position of the Iceman with respect to such a general temporal trend would again highlight his relatively unusual activity patterns compared to most males of his time period. Marchi et al. (2005) also found an unusually high degree of skeletal robusticity in the lower limb in their Neolithic Ligurian sample, which they also attributed to a pastoral subsistence strategy carried out over rough terrain.

Finally, it is appropriate to include a word here regarding the general use of long-bone cross-sectional geometric properties to reconstruct mechanical loadings, and by implication, activity patterns in humans. Results of several recent studies have emphasized the complexities involved in extrapolating from diaphyseal structural properties to in vivo loading patterns (Demes et al., 1998, 2001; Lieberman et al., 2004; Pearson and Lieberman, 2004). Such studies argue for caution,

particularly in broad comparisons between widely divergent species with very different locomotor repertoires and body designs. However, in comparisons of the same bone within species or between closely related species, where ''musculoskeletal design and function'' and ''patterns of bending'' are comparable, relative differences in cross-sectional properties between individuals or samples should still provide reasonable approximations of relative differences in in vivo mechanical loadings (Lieberman et al., 2004: 168; Ruff et al., 2006). This is exactly the situation in the present study: all of the samples included here are of ''anatomically modern'' humans, who were almost certainly very similar in terms of basic lower-limb function, bone-muscle relationships, mechanisms of gait, etc., but who varied in body proportions and activity patterns, i.e., the relative importance of specific components of this loading milieu. Thus, under these circumstances, it is reasonable to infer that variation in cross-sectional properties reflects, at least in part, such subtle but important morphological and behavioral differences (Ruff et al., 2006). Similar comparative studies of modern human archaeological samples have yielded structural results that are consistent for the most part with documented behavioral differences between populations (Ruff, 1987, 2000a; Stock and Pfeiffer, 2001; Weiss, 2003).

Conclusions

Two different methods of estimating the body mass of the Iceman yield the same result of 61 kg. Thus, although he was relatively short (about 158 cm), he was not thin; rather, he was relatively stockily built compared to a sample of Upper Paleolithic through Bronze Age European males. His femur was of average strength relative to body size for Neolithic males, but his tibia was well above average. His femur also shows evidence for adaptation to relatively high M-L loads, possibly a result of his relatively wide body, while his tibia is adapted for high A-P loads, which is consistent with an active lifestyle that included long-distance travel over rough terrain. We find evidence for a general reduction in the lower limb, particularly tibial strength, from the Mesolithic to Neolithic, which may reflect a reduction in mobility. In many respects, the Iceman's tibia more closely resembles that of Mesolithic rather than Neolithic and Bronze Age males, which may reflect high levels of mobility compared to that of at least some more sedentary penecontemporaneous populations. There is preliminary evidence for greater variability in both body size/shape as well as behavioral patterns in the European Mesolithic and Neolithic compared with the Upper Paleolithic; the Iceman's combination of structural features is consistent with such increased variability.

Acknowledgements

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