

THE HUMAN POSTCRANIAL REMAINS FROM MLADEČ

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Introduction

The paleontological analysis of Late Pleistocene human postcranial remains from Europe has highlighted a series of changes in morphology associated with the emergence of modern humans and the eventual replacement of a late archaic human (specifically Neandertal) morphological pattern with one of robust early modern humans. This has involved aspects of body proportions (Trinkaus, 1981; Holliday, 1997; 2005a), upper limb diaphyseal strength and muscularity (Trinkaus, 1983; 1997; 2000; 2005a; Churchill, 1994), lower limb diaphyseal shape (especially femoral) (Trinkaus, 1976; 2005b; Trinkaus et al., 1999a), and vertebral spinous process robusticity (Matiegka, 1938; Heim, 1976; Trinkaus, 1983). Other aspects of lower limb robusticity, such as diaphyseal robusticity, articular hypertrophy, knee moment arms and femoral curvature, largely disappear once appropriately analyzed and/or scaled to body mass and limb length (Trinkaus et al., 1999a, b; 2005b; Trinkaus and Rhoads, 1999; Trinkaus, 2000; Shackelford and Trinkaus, 2002).

Despite these observations, it is also apparent that most of the postcranial comparisons are between Middle Paleolithic Neandertals and earlier Upper Paleolithic modern humans dating to ≤ 28 kyr BP (Gravettian *sensu lato*). The rare exceptions to this are the Châtelperronian Saint Césaire Neandertal partial skeleton (Vandermeesch, 1984; Trinkaus et al., 1999a), the Fontana Nuova 4 talus (Chilardi et al., 1996), isolated phalanges from Brassempouy (Henry-Gambier et al., 2004), and the collection of human remains from Mladeč Cave. Indeed, although distinctive Neandertal remains have been dated to ca. 30 kyr BP in at least southwestern Europe (Hublin et al., 1995), diagnostic and well-dated early modern human remains ≥ 30 kyr BP in Europe are poorly known. Indeed, only the remains from the Peștera Muierii (Nicolăescu-Plopșor, 1968), the teeth and phalanges from Brassempouy (Henry-Gambier et al., 2004), and the craniofacial remains from the Peștera cu Oase (Trinkaus et al., 2003a, b; 2005) provide secure paleontological information on modern humans ≥ 30 kyr BP in Europe, and all of them except for an incomplete scapula and fibula from the Peștera Muierii and phalanges from Brassempouy are cephalic. The remainder of the European early modern human remains are immature mandibles, isolated teeth and/or insecurely dated to this time period.

The only other human limb bone which has been considered in this sample, the Vogelherd 3 humerus (Churchill and Smith, 2000), is now known to be Holocene in age (Conard et al., 2004). Similarly, the Cro-Magnon and La Rochette human remains (including postcrania) are now dated to the succeeding Gravettian of Western Europe (Orschiedt, 2003; Henry-Gambier, 2003).

As a result, the key sample of early modern human postcrania for providing current information on the postcranial morphology of the earliest European modern humans are the disassociated human axial and limb remains from Mladeč. Incompletely described (Szombathy, 1925) and only partially integrated into appropriate analyses (e.g., Wolpoff, 1989; Liston et al., 1989; Churchill, 1994; Chilardi et al., 1996; Stockton, 1997; Trinkaus, 2005a, b), the postcranial remains from the karstic cave system at Mladeč appear to represent the oldest currently known sample (as opposed to isolated

elements) of early modern humans limbs in Europe. Directly associated with early modern human craniofacial remains, these postcrania provide important information on the early modern human biology in Europe. We therefore provide here a detailed description and assessment of these elements.

Inventory

This description of the Mladeč human postcranial remains is based principally on those specimens excavated by Josef Szombathy in 1881 and 1882 (Szombathy, 1881; 1882; 1904) in Chamber D, originally described by him (1925) and currently curated in the Naturhistorisches Museum Wien. Other human postcranial remains have been found in the Mladeč Caves and briefly described (e.g., Maška, 1905; Knies, 1906); the majority were destroyed in 1945 in Mikulov Castle or their whereabouts is not known, but several hand bones excavated by Jan Knies in Chamber E between 1903 and 1911 are preserved in the Moravské zemské muzeum in Brno. Given the apparent depositional complexity of the Mladeč karstic cave system and the fact that different Chambers, “Sites,” or “Halls,” may have accumulated archeological and human remains at different times (Oliva, 1989; Svoboda, 2000; Svoboda, this volume, chap. 3), the focus here is principally on those remains which are currently available and appear to derive from one discrete depositional event, the Chamber D remains. The Chamber E remains, essentially the aforementioned hand bones, are also included but considered as a separate sample.

The Mladeč human postcranial remains that are no longer available for analysis (see Wolpoff et al., this volume, chap. 8 (inventory)) are listed and briefly described in chap. 14 based on the original publications of them (Wolpoff et al., this volume). Since it cannot be adequately assessed whether they are of the same geological age as the remains from Szombathy’s excavations in Chamber D, they are not considered further in this presentation.

The Mladeč human postcranial remains in the Naturhistorisches Museum Wien were originally inventoried in a hand written document by Josef Szombathy (December 12, 1922) as presented in Table 1. Comments and notes follow each of his original entries. The inventory of currently available human postcranial remains in the Naturhistorisches Museum Wien and the Moravské zemské muzeum in Brno are presented by catalog number in Table 2. Although the identifications of the

Table 1. Szombathy’s handwritten December 12, 1922 inventory of Mladeč human postcranial remains in the Naturhistorisches Museum Wien, with comments on current identifications

1 Halswirbel, etwa Nr V oder VI	Mladeč 11
1 Körper eines ähnlichen Halswirbels	Mladeč 34, probably non-human
16 Rippenfragmente	13 are currently present; Mladeč 12 to 19 and 20a to 20e; Mladeč 13 is a clavicle
1 Schlüsselbein eines Säuglings (?)	Whereabouts unknown
4 Beckenfragmente	Mladeč 21 and 22; one is non-human, one is missing
2 Oberarmfragmente	Mladeč 23 and 24
1 prox. Ulnafragment	Mladeč 25c
4 Radiusfragmente	Mladeč 25a, 25b and 26. The fourth is not known, and it may be the piece of immature proximal femur (Mladeč 102)
1 fragliches Radiusfragment, kindlich	Non-human postcranial element
2 Oberschenkelknochenstücke	Mladeč 27 and 28
3 Metatarsalknochen III, IV, V I.	Mladeč 32 (metatarsal 3), Mladeč 31 (metacarpal 3, mislabeled “IV”), the bone identified as a metatarsal 5 is absent.
1 Fingerknochen I	Whereabouts unknown
1 Sprungbein I.	Mladeč 30
1 distale Epiphyse des Schienbeins r.	Mladeč 29

Table 2. Summary list, by specimen number, of the human postcranial remains from Mladeč currently known and available in the Naturhistorisches Museum Wien (Mladeč 11 to 32 and 102) and the Moravské zemské muzeum in Brno (Mladeč 88 to 91)

Specimen number	Identification	Specimen number	Identification
11	Cervical vertebra C3 to C6	24	Humerus right
12	Rib 1 left	25a	Radius right
13	Clavicle right immature	25b	Radius right
14	Rib 2 or 3 left	25c	Ulna right
15	Middle rib left	26	Radius left
16	Middle to caudal rib right	27	Femur right
17	Caudal rib right	28	Femur left
18	Rib 12 left	29	Tibia immature right
19	Rib 11 or 12 right	30	Talus left
20a	Rib section, side indeterminate	31	Metacarpal 3 immature right
20b	Rib section, side indeterminate	32	Metatarsal 3 immature left
20c	Rib section, side indeterminate	88	Manual proximal phalanx 2 left?
20d	Rib section, side indeterminate	89	Manual proximal phalanx 3 left?
20e	Rib section, side indeterminate	90	Metacarpal 3 right
21	Os coxae left	91	Metacarpal 4 right
22	Os coxae immature right	102	Femur immature left
23	Humerus right		

larger postcranial elements are the same as those of Szombathy, several of the smaller pieces have been reidentified based on further considerations. The current identifications, based on our work and that of M. Teschler-Nicola, are presented in Tables 1 and 2.

It should be noted that most of the human remains from Mladeč in the Naturhistorisches Museum Wien bear the museum catalog number 5459. This same number is on the section of a proximal immature human femur, a piece which was not originally included in the comprehensive Mladeč catalog (chap. 8, Inventory). Since it is now recognized as both human and deriving from the same collection as the remainder of the Mladeč postcrania, based on museum association and preservation, including similar adhering matrix, it has been given the number of Mladeč 102.

There is no indication in Szombathy's inventory of the possible associations between these bones, but it is apparent that at least three and probably more individuals are represented by the postcrania. This is based on duplication of the Mladeč 23 and 24 right humeri, the size differences between the Mladeč 25b and 26 radial diaphyses, the size and maturity contrasts between the Mladeč 21 and 22 pelvic pieces, and the morphological contrasts between the Mladeč 27 and 28 femora. A series of associations are possible, and they are discussed after the descriptions of the individual elements.

The hand remains from Chamber E include Mladeč 88 to Mladeč 91. Mladeč 88 and 89 are proximal hand phalanges, whereas Mladeč 90 and 91 are right metacarpal bones.

Comparative materials

The description of human fossil remains entails, by its very nature, comparisons to relevant samples of human remains. Since the Mladeč fossils derive from the central European earlier Upper Paleolithic and are cranially attributable to early modern humans (Szombathy, 1925; Smith, 1984; Frayer, 1986; Wolpoff et al., 2001; see this volume, chaps. 9 and 10, male and female crania), the most relevant sample is that of earlier Upper Paleolithic northwestern Old World early modern humans. Comparative data as appropriate and available have therefore been assembled for European and western Asian earlier (> 18,000 years BP) Upper Paleolithic early modern humans. These specimens derive

from the sites of Arene Candide, Barma Grande, Cro-Magnon, Dolní Věstonice I and II, Fanciulli (Grotte-des-Enfants), Fontana Nuova, Lagar Velho, Nahal-Ein-Gev, Ohalo II, Paglicci, Pataud, Paviland, Pavlov I, Předmostí, La Rochette, Sunghir, Veneri (Parabita) and Willendorf. The majority of them date to after 30,000 years BP, and the sample is therefore predominantly Gravettian (or Middle Upper Paleolithic) in age. Several of the specimens, as noted above, were originally attributed to the Aurignacian (e.g., Cro-Magnon and La Rochette), but reassessment and dating (Orschiedt, 2002; Henry-Gambier, 2003) have placed them within the Gravettian. The only Aurignacian specimen within this postcranial comparative sample is the Fontana Nuova 4 talus, despite uncertainties as to its association with the Aurignacian of that site (Chilardi et al., 1996).

At the same time, given that the Mladeč fossils represent one of the earlier populations of early modern humans in central Europe, overlapping the time period of the latest Neandertals and probably resulting in part from a dispersal of early modern humans from southeast Europe and eventually southwest Asia (Smith and Trinkaus, 1991; Smith et al., 1999; Trinkaus et al., 2003b), the sample may well have close affinities to the earliest modern humans from southwest Asia, the Middle Paleolithic Qafzeh-Skhul sample. Data for the adult and immature remains from those two sites are therefore included in the comparisons.

In addition, it has also been argued (Smith, 1984; Frayer, 1986; Smith and Trinkaus, 1991; Wolpoff et al., 2001) that the Mladeč remains exhibit evidence of some degree of genetic continuity between central European Neandertals and their early modern human temporal successors. It is therefore necessary to compare the Mladeč postcranial remains to those of last glacial Neandertal specimens. Unfortunately, such Neandertal postcranial remains are rare and fragmentary in central Europe, consisting principally of those from the Middle Paleolithic of Subalyuk (Pap et al., 1996) and Vindija G₃ (Wolpoff et al., 1981; Malez and Ullrich, 1982; Ahern et al., 2004) and the initial Upper Paleolithic of Vindija G₁ (Ahern et al., 2004). The Subalyuk 1 and Vindija G₃ postcranial elements are small and/or fragmentary, and only the probably immature Vindija 228, 253 and 266 distal humeri, the Vindija 13.8 proximal radial shaft, and the metatarsal 3 of Subalyuk 1 anatomically match those of the Mladeč sample. Given that the Mladeč remains preserve several relatively complete portions of major long bones, the comparative Neandertal sample consists principally of last glacial remains from western European and southwestern Asian Neandertals. These are from the sites of Amud, La Chapelle-aux-Saints, Cova Negra, Dederiyeh, La Ferrassie, Font-de-Forêt, Kebara, Lezetxiki, La Quina, Neandertal, Regourdou, Roc de Marsal, Rochers-de-Villeneuve, Saint Césaire, Shanidar and Spy. The Krapina remains predate this time period (Rink et al., 1995), as do the Tabun Layers B and C human remains (Mercier et al., 1995; Grün and Stringer, 2000); they are therefore not included in the comparative samples.

Measurements affected by pathological lesions or post-traumatic remodeling [e.g., Neandertal 1 humeral diaphyses (Trinkaus et al., 1994)] are not included. The comparative data were assembled from personal investigation of the original specimens and the primary published descriptions of specimens, supplemented by data particularly from Churchill (1994, pers. comm.), Holliday (1995), and Holt (1999).

Comparative methods

The comparative assessment of the Mladeč postcranial remains involves three forms of data. The material are qualitatively described and compared to other samples. A full set of comparative linear and angular metrics are provided; most of these measurements follow the Martin system (Bräuer, 1988), but additional measurements are provided and defined in the notes to the tables. The majority of the Mladeč postcranial measurements were taken by three of us (FHS, TCS and ET) on separate occasions; in 1998 they were all rechecked on the originals by ET to resolve

differences in measurement techniques. The presented data represent the result of that combined effort.

In addition, cross-sectional geometric parameters (cross-sectional areas and second moments of area) are provided for the Mladeč long bone and metapodial diaphyses. All of them were reconstructed using polysiloxane molding putty (Cuttersil Putty Plus) to transcribe the anatomically oriented subperiosteal contours and biplanar radiography to determine parallax corrected cortical thicknesses. The endosteal contours were then interpolated and the resultant cross sections were projected enlarged onto a Summagraphics III digitizing tablet and digitized twice. Cross-sectional parameters were computed using a PC-DOS version (Eschman, 1992) of SLICE (Nagurka and Hayes, 1980), and the results of the repeated digitizing of each section averaged.

None of the Mladeč diaphyses is complete, and the sections are located at percentages of bone lengths; it was therefore necessary to estimate the positions of the cross sections. For the two most complete long bones (Mladeč 24 and 27) plus the two metapodials (Mladeč 31 and 32), lengths were estimated, and the sections were located at the appropriate calculated percentages of bone biomechanical length. For the other diaphyses, the positions of the sections were estimated using anatomical landmarks (including proximity to epiphyses and diaphyseal muscle markings); their locations are therefore more approximate. The orientations of the sections relative to anatomical planes were assessed principally using diaphyseal shape indicators, in particular the anterior crests on the humeri, the interosseus crests on the radii, and the linea aspera on the femora. Only for the Mladeč 25c proximal ulna, the Mladeč 31 metacarpal and the Mladeč 32 metatarsal could articulations be employed for anatomical orientation. For this reason, the orientations of the maximum second moments of area (θ) are not provided, and the anatomically oriented second moments of area (I_x and I_y) should be considered approximate.

Since the humeral diaphyses of Late Pleistocene humans frequently exhibit pronounced levels of asymmetry (Trinkaus et al., 1994; Churchill and Formicola, 1997), and since the dominant arm in almost all of the individuals providing data on asymmetry is the right one, comparisons should be made solely to the same side bone for those portions of humeral remains which exhibit significant levels of asymmetry. For this reason, the Mladeč humeral diaphyses, both of which are right, are compared only to right humeri. The few forearm and hand bones are compared to both right and left sides, even though there may be some systematic asymmetry in at least diaphyseal features related to handedness (Sakaue, 1999). The lower limbs may exhibit asymmetry, but it is generally lower in magnitude and random with respect to side (Ruff and Hayes, 1983; Trinkaus et al., 1994; Anderson and Trinkaus, 1998). The forearm, hand and lower limb comparisons therefore pool right and left specimens in the comparative samples, averaging the right and left values for specimens which preserve both sides prior to any sample calculations or graph composition.

Given the incompleteness of the Mladeč postcranial remains and the need to have length measurements for long bones to scale their diaphyseal and articular properties, lengths have been estimated for several of the Mladeč bones. For the Mladeč 24 humerus and Mladeč 27 femur, lengths were estimated from landmarks adjacent to the epiphyses. For the Mladeč 31 metacarpal and the Mladeč 32 metatarsal, both of which lack their unfused head epiphyses, lengths were estimated based on the distance from the dorsal tubercles to the proximal facet using mature metacarpals. In each case, the reference samples were mature recent human bones; given the immature status of the Mladeč 31 and 32 bones and the absence of the epiphyses on Mladeč 24 and 27, the resultant lengths may slightly underestimate the original mature lengths of these bones. Given that this would have the effect of overestimating the robusticities of these bones, and that one of the concerns is whether they exhibit the reduction in robusticity seen in some earlier Upper Paleolithic human remains (Trinkaus, 2000), this possible bias should be conservative for the comparisons.

In the comparisons, assessments of the degrees of difference between the three comparative samples were done using parametric tests (ANOVA and t-tests) for linear and angular measurements, and

non-parametric (Kruskal-Wallis and Wilcoxon) tests for ratios (indices) and discrete data. Metric comparisons which are not amenable to ratios are presented graphically. The differences between the samples are assessed with linear residuals relative to the reduced major axis lines through the pooled comparative sample, which are then compared parametrically.

The Mladeč 11 cervical vertebra and the Mladeč 34 vertebral body

Preservation, identification and maturity

Mladeč 11 is a largely complete adult cervical vertebra, almost entirely covered with a thin layer of carbonate crust (see chap. 8, Plate VIII). The crust, however, is sufficiently thin to permit assessment of most aspects of its preserved morphology and proportions. The superior (cranial) margins of the uncinat processes, as well as the antero-caudal margin of the vertebral body, are slightly abraded. The inferior and superior articular facets are complete, with only slight damage to the superolateral aspect of the left superior facet and the inferior aspects of the right and left inferior articular facets.

Moderate damage has occurred to the lateral and posterior (dorsal) portions of the vertebra. The most lateral portions of the posterior tubercles and the entire anterior tubercles of the transverse processes are absent. The right costotransverse bar (intertubercular lamella) is complete while only a very thin bridge of bone remains on the left side. The transverse foramina are complete and unobscured, as are the laminae, pedicles, neural arch and neural canal. The spinous process, however, is damaged and only the base remains. The preserved length of the spinous process is only 11 mm. The vertebra provides a total preserved transverse diameter of 57.3 mm and a preserved dorsoventral maximum dimension of 42.4 mm.

The annular rings are fully fused to the centrum, and there are no traces of pathological degenerations on the bone. These suggest a minimum age-at-death at the end of the second decade (Scheuer and Black, 2000) and probably not an advanced age for the individual.

The presence of foramina in each transverse process, superior articular facets that face superiorly and posteriorly, posterolateral lips (uncinate processes) on the superior surface of the centrum, and a triangular neural (vertebral) canal indicate that Mladeč 11 is a cervical vertebra. Determining the position of Mladeč 11 within the cervical vertebral sequence has proven to be difficult, however, since no other vertebrae in the sequence were recovered and damage to the spinous process makes it impossible to determine the length or degree of bifidity. It is clearly not a C1 or C2, and the absence of any thoracic-like morphology (e.g., the inferior surface of the centrum is not flat and the transverse processes do not appear large) precludes it from being a C7. Therefore, based on morphology alone, it is equally likely that Mladeč 11 is a C3, C4, C5 or C6.

Szombathy (1925, 24) identified this specimen as a C6 but did not make explicit his reasons for doing so. This is unfortunate because the single feature that can be used to differentiate between C6 and C3–C5 (a large anterior tubercle of the transverse process known as the carotid tubercle) (McMinn et al., 1993) is not markedly large on the Mladeč 11 specimen. Therefore, although only a single vertebra is preserved in the Mladeč sample and carotid tubercle development is variable (Stockton, pers. observ.), the absence of a large anterior tubercle of the transverse process of Mladeč 11 makes it unlikely (but not impossible) that this specimen is a C6.

Metric data do not help to resolve the issue. This is in part due to variation within populations that occurs naturally in the vertebral columns of fossil and recent humans, but it is also caused by overlapping ranges of morphometric variation between different (not necessarily consecutive) vertebrae in the cervical vertebral column. For example, despite the well-supported assumption that the more caudal vertebral bodies are larger than the cranial ones as a virtue of weight transmission in orthograde primates (Taylor and Twomey, 1984), the considerable ranges of overlap in within-sam-

ple and between-sample vertebral body size from one vertebra to the next preclude accurate positional assessment from a single isolated vertebra (Hasebe, 1912; Lanier, 1939; Pal and Routal, 1986).

One feature which may help is the essentially horizontal orientation of the Mladeč 11 spinous process. Cervical spinous processes do become more horizontal as they go caudally, including among Late Pleistocene humans (Matiegka, 1938; Heim, 1976; Trinkaus, 1983), making it more likely that Mladeč 11 is a C5 or a C6.

For these reasons, the Mladeč 11 vertebra is compared to available data for C3 to C6 vertebrae from the Late Pleistocene comparative samples. Yet, given the limited sample sizes available for even C5 and C6 (Tables 4 and 5), it is principally to the more caudal two vertebrae that proportional metrics are compared.

The Mladeč 34 specimen is a vertebral body, which was originally identified as human (see chap. 8, Plate VIII). It is partially obscured by a massive carbonate encrustation on its cranial body surface and its ventrolateral surface. It is abraded along its dorsal surface. The strong dorsoventral concavity of its caudal body surface with the caudally turned ventral edge indicates that it is a cervical vertebra. Its number is unknowable, but its small size suggests that it derives from the middle of the cervical column. The caudal annular ring is partially fused. It is completely fused along the ventral midline, but partially fused bilaterally ventrolaterally. This suggests a late adolescent age for the individual (Scheuer and Black, 2000).

The unusually small size of Mladeč 34 (the body dorsoventral diameter is 13.4 mm and its transverse diameter is 19.5 mm; the dorsal and ventral body heights are 11.7 and 10.9 mm respectively) bring into question whether this specimen is indeed human. Moreover, the carbonate encrustation obscures most of the relevant morphology. It is therefore put into a suspense account and is not considered further.

Morphology

The Mladeč 11 vertebra exhibits large foramina transversaria for the vertebral arteries and a small foramen on the dorsal side of each one. The right articular facets are concave craniocaudally and appear to be slightly displaced dorsally relative to the left ones. The spinous process is incomplete, but the preserved portions of it suggest that it tapered markedly from its base towards its dorsal tip. For example, the craniocaudal height of the process is 10.6 mm at its juncture with the laminae, but is reduced to 7.5 mm near its dorsal break, only 12.4 mm from the vertebral canal. At the same time, viewed in *norma lateralis*, the spinous process appears to have been largely horizontal (estimated angle of 0°) relative to the planes defined by the cranial and caudal body surfaces.

Relatively horizontal cervical spinous processes, although once considered as a Neandertal or “archaic” characteristic (e.g., Boule, 1911–13), have been shown repeatedly (e.g., Kleinschmidt, 1938; Arambourg, 1955; Straus and Cave, 1957; Toerien, 1957; Stewart, 1962; Heim, 1976; Trinkaus, 1983; Arensburg, 1991) to be present in variable frequencies among recent humans (see also Cunningham, 1886). They are also present in the Předmostí sample (Matiegka, 1938) and on Cro-Magnon 2 (Trinkaus, pers. observ.). The apparently horizontal orientation of the Mladeč 11 spinous process is therefore unremarkable.

At the same time, what appears to contrast more consistently between late archaic and early modern human cervical spinous processes is the degree of tapering of the process, in which the cranial and caudal margins of Neandertal lower cervical processes remain largely parallel, especially close to the laminae, while those of early modern humans become progressively thinner dorsally (Matiegka, 1938; Piveteau, 1963–66; Heim, 1976; Trinkaus, 1983, pers. observ.). There is nonetheless some overlap in this feature between the two samples. In this aspect, the Mladeč 11 spinous process, especially if it represents a C5 or a C6, is closer to the pattern seen in the few earlier Upper Paleolithic specimens available for comparison.

Table 3. Osteometric dimensions of the Mladeč 11 cervical vertebra (in mm and degrees). Values in parentheses are estimated

Body ventral height (M-1)	9.5
Body dorsal height (M-2)	12.2
Body median height (M-3)	9.3
Body cranial dorsoventral diameter (M-4)	16.7
Body caudal dorsoventral diameter (M-5)	(17.0)
Body cranial transverse diameter (M-7)	25.5
Body caudal transverse diameter (M-8)	24.6
Cranial external transverse diameter ¹	(53.2)
Cranial internal transverse diameter ²	22.1
Caudal external diameter ¹	53.6
Caudal internal transverse diameter ²	20.5
Spinal canal cranial dorsoventral diameter (M-10)	11.9
Spinal canal caudal dorsoventral diameter	13.6
Spinal canal transverse diameter (M-11)	22.4
Pedicle dorsoventral diameter – right	6.3
Pedicle dorsoventral diameter – left	6.8
Pedicle mediolateral diameter – right	5.6
Pedicle mediolateral diameter – left	7.0
Cranial facet angle – right ³	62°
Cranial facet angle – left ³	59°
Spinous process angle ⁴	(0°)

¹ Maximum transverse dimension measured to the lateral margins of the superior or inferior articular facets.

² Transverse diameter measured to the medial margins of the cranial or caudal facets.

³ Angle between the facet and the mid-sagittal plane in the horizontal plane of the cranial body.

⁴ Angle between the cranial body and the midline of the spinous process.

The Mladeč 11 measurements (Table 3) fall near the mean values of the comparative samples. Additionally, the inability to distinguish between samples based on the vertebral metrics presented here holds true at each level of the spinal sequence: C3, C4, C5 and C6. There is, however, one interesting aspect of these data that deserves mention.

While the overall vertebral morphology of European Neandertals and of more recent humans is very similar, the cervical bodies of European Neandertals have been described as relatively low and broad (McCown and Keith, 1939; Piveteau, 1963–66; Heim, 1976). Relatively low and broad centra are also found in southwest Asian late archaic human vertebrae from Shanidar (Trinkaus, 1983), Kebara (Arensburg, 1991), and the Mousterian associated third cervical vertebra from Hayonim (Arensburg and Nathan, 1980). Wolpoff (1989) observed that the low and broad vertebral body of Mladeč 11 resembled European Neandertals more than Skhul 5 or the small sample ($N = 3$) of early modern humans from Předmostí and argued that the Mladeč 11 proportions provided evidence for Neandertal to early modern human morphological continuity in central Europe. Wolpoff, however, regarded Mladeč 11 as a C3 and therefore only compared it to other third cervical vertebrae.

To reevaluate the body heights of Mladeč 11 in light of additional data, absolute heights are provided in Table 4 and indices comparing it to C5 and C6 proportions (samples of the paired measurements are too small to be meaningful for C3 and C4) are in Table 5. From these, it is apparent that the ventral body height of Mladeč 11 is relatively small. Only the Skhul 5 C4 and the Regourdou 1 and Shanidar 1 C5s have ventral heights as small as Mladeč 11. However, its dorsal height is well within the ranges of variation of all of the samples. Moreover, although the earlier Upper Paleolithic

Table 4. Comparative cervical vertebral body heights for Mladeč 11. Mean and standard deviation (N) provided for samples greater than 4; individual values provided for smaller samples. T-test P-values for the Neandertal versus earlier Upper Paleolithic samples. * P < 0.05 with a multiple comparison correction ($\alpha/8$)

	Mladeč 11	Neandertals	Skhul 5	Earlier Upper Paleolithic	Nean/EUP P
C3					
Ventral height	9.5	11.0, 11.0, 12.2	–	11.9 ± 1.0 (6)	0.414
Dorsal height	12.2	10.0, 12.5, 13.0	10.5	12.4 ± 1.2 (5)	0.608
C4					
Ventral height	9.5	11.1 ± 0.2 (5)	8.5	12.1 ± 0.8 (5)	0.033
Dorsal height	12.2	12.3 ± 0.8 (4)	9.5	12.4 ± 1.3 (8)	0.797
C5					
Ventral height	9.5	10.5 ± 1.3 (7)	10.0	12.0 ± 1.0 (6)	0.037
Dorsal height	12.2	11.8 ± 1.0 (6)	10.0	13.3 ± 1.0 (8)	0.013
C6					
Ventral height	9.5	10.9 ± 0.9 (7)	12.2	11.9 ± 1.0 (7)	0.062
Dorsal height	12.2	12.3 ± 0.7 (7)	13.5	13.7 ± 0.9 (9)	0.003*

Table 5. Comparative body proportions of the Mladeč 11 cervical vertebra. Mean and standard deviation (N) provided for samples greater than 3; individual values provided for smaller samples. T-test P-values provided for the Neandertal versus earlier Upper Paleolithic samples. ** P < 0.01 with a multiple comparison correction ($\alpha/8$)

	Mladeč 11	Neandertals	Skhul 5	Earlier Upper Paleolithic	Nean/EUP P
C5					
Ventral height / Cranial body breadth	37.3	46.9 ± 6.4 (5)	45.5	47.8 ± 3.5 (5)	0.794
Ventral height / Canal breadth	42.4	40.4 ± 5.4 (6)	40.0	50.5 ± 5.7 (5)	0.015
Dorsal height / Cranial body breadth	47.8	54.3 ± 6.1 (5)	45.5	56.2 ± 2.0 (5)	0.532
Dorsal height / Canal breadth	54.5	44.8 ± 4.7 (6)	40.0	58.3 ± 3.8 (6)	0.001**
C6					
Ventral height / Cranial body breadth	37.3	47.4 ± 11.9 (4)	52.0	45.6 ± 5.2 (6)	0.789
Ventral height / Canal breadth	42.4	37.1, 41.0, 50.6	54.2	46.3 ± 4.8 (4)	0.501
Dorsal height / Cranial body breadth	47.8	52.2 ± 9.5 (4)	40.0	52.3 ± 5.9 (6)	0.844
Dorsal height / Canal breadth	54.5	43.9, 48.5, 54.9	41.7	53.4 ± 5.1 (4)	0.280

sample has consistently higher mean values than the Neandertals for these heights, only the C6 dorsal value is significantly greater. When the Mladeč 11 heights are compared to body cranial breadth or canal breadth for C5s and C6s (Table 5), only its ventral height to body breadth value is even moderately low (being approached or matched by values for La Chapelle-aux-Saints 1 and Shanidar 1). Moreover, contrary to previous impressions, only the C5 dorsal height to canal breadth index is significantly different between the Neandertal and earlier Upper Paleolithic samples, and Skhul 5 exhibits relatively low heights as well.

Therefore, morphologically the Mladeč 11 cervical vertebra falls well within the ranges of variation of Late Pleistocene C3 to C5 vertebrae. Its moderate ventral body height (but not dor-

sal body height) suggests closer affinities to the Mousterian late archaic and early modern human remains, whereas its strongly tapering spinous process aligns it closer to early modern human vertebrae.

The Mladeč costal remains

Preservation, identification and maturity

Twelve rib pieces are associated with the Mladeč human postcrania, all of them heavily encrusted with dark carbonate (see chap. 8, Plates IX–XI). Only the Mladeč 12 left first rib is essentially complete; the others are missing significant portions. Their identifications as to side are based on their patterns of proximodistal torsion. Their attributions to rib number are based on morphology for the cranial three ribs and the eleventh and twelfth rib; the remainder which have been assigned numbers (even approximate) have been so identified based on general degrees of size and curvature. Their preservations and inferred numbers are as follows.

Mladeč 12

An essentially complete left first rib, with slight abrasion to the costal cartilaginous surface. The head epiphysis appears to have been unfused, with a portion of the metaphyseal surface preserved cranially. Maximum length is 70.2 mm.

Mladeč 14

A left second or third rib with the head metaphysis, the articular facet, the tubercle and the angle area. Portions of the middle of the head metaphysis are preserved, indicating that the head epiphysis was unfused. The attribution to the second or third rib given preservation depends upon the assessment of the degree of curvature, and it appears more likely that it derives from a second rib. Maximum preserved length is 62.5 mm.

Mladeč 15

A left middle rib, probably from the fourth, fifth or sixth one, from the distal margin of the articular facet around to the region of the angle. Its maximum preserved length is 50.6 mm.

Mladeč 16

A right middle or more caudal rib; it may be from the sixth to the ninth rib. It is present from the curve near the angle to the distal tapering for the costal cartilage, and its maximum preserved length is 106.8 mm.

Mladeč 17

A right middle to caudal rib preserved from the head (or head metaphysis) to the middle of the body, for a preserved length of 127.5 mm. It could be a ninth or a tenth one. The head metaphysis is preserved across the caudal half of the surface, indicating that it was unfused.

Mladeč 18

A twelfth rib from the left side, preserved from the distal articular facet most of the way to its distal end. Maximum preserved length is 111.2 mm. It is encrusted similarly to the other ribs, and the distocaudal margin is abraded.

Mladeč 19

A piece of a right rib, preserved from the distal facet margin towards the angle. It should derive from an eleventh or twelfth rib. Maximum preserved length is 42.5 mm.

Mladeč 20a

A piece of a middle to more cranial right rib, with a preserved length of 75.7 mm.

Mladeč 20b

A piece probably of a middle to more cranial rib, with an original preserved length of 69.0 mm. It was shortened to 64.2 mm in 1998 through the removal of a sample for accelerator mass spectrometry radiocarbon dating; the dating attempt failed due to low carbon yield and contamination.

Mladeč 20c

A piece probably of a middle to more caudal rib, with a preserved length of 65.6 mm.

Mladeč 20d

A piece of a probably distal rib of indeterminate side. Preserved maximum length is 29.6 mm.

Mladeč 20e

A polished piece of proximal rib, possibly from the left side. Maximum preserved length is 35.2 mm.

It is not possible to determine how many individuals are represented by these ribs. Given the apparent lack of duplication, they could derive from one thorax. However, three of the ribs (Mladeč 12, 14 and 17) have unfused head epiphyses. This indicates a late second decade to young third decade age-at-death, and they may represent the same individual.

Morphology

As an essentially complete left first rib, Mladeč 12 provides some indications of overall morphology. However, among Late Pleistocene humans, largely intact first ribs are rare, being preserved mainly for Dolní Věstonice 13, 14 and 15 plus Skhul 4 among early modern humans and for Kebara 2 and Regourdou 1 for the Neandertals (McCown and Keith, 1939; Arensburg, 1991; Kuželka, 1992; Sládek et al., 2000; Holliday, 2005b); fragments are preserved for a number of others (Trinkaus, 1983; Franciscus and Churchill, 2002).

The Mladeč 12 rib, as far as can be determined through the carbonate encrustation, is gently convex caudally and gently concave cranially with a modest development of a cranial ridge externally near the distal end. It narrows dorsally for the neck relative to the dorsal projection of the angle, and

it presents a modest torsion proximodistally. In terms of overall dimensions, the rib measures 69 mm from the ventral costal cartilage surface to the dorsal head, 44 mm from the dorsal cartilage surface to the ventral head, 25 mm from the dorsal head to the dorsal angle, and 73 mm from the dorsal angle to the ventral costal cartilage surface. The internal margin is maximally 25 mm from a line drawn between the ventral head and the dorsal cartilage surface.

The Mladeč 14 left second or third rib has its margins generally rounded along the length of the preserved rib.

The Mladeč 16 right middle or more caudal rib (possibly number 8) has a strong flange of bone for the intercostal muscles and connective tissue near the angle, which then tapers to nothing distally. The rib arcs caudally as it goes distally, in addition to the normal axial torsion.

Table 6. Osteometric dimensions of the Mladeč ribs (in mm). Estimated values are in parentheses

Number	Side	Neck height ¹	Neck thickness	Facet height ²	Facet thickness	Angle height ³	Angle thickness
12	1 - Lt	6.1	8.1	6.6	12.6		
14	2/3 - Lt	10.0	5.4	10.7	8.6	12.4	8.0
15	Mid - Lt	-	-	9.4	8.3	-	-
16	Mid/Caud - Rt	-	-	(13.4)	(7.4)	18.3	9.2
17	Caudal - Rt	(15.5)	7.0	10.0	9.0	16.4	9.1
18	12 - Lt	-	-	10.6	6.8	14.2	6.3
19	11/12 - Rt	-	-	11.3	6.6	-	-

¹ Diameters in the middle of the costal neck.

² Diameters taken just distal of the articular facet.

³ Diameters taken in the middle of the angle.

Table 7. Minimum to maximum diameter indices from diameters taken at the posterior angle for Mladeč and comparative Late Pleistocene and recent Euroamerican male right ribs (N = 18–19). Comparative data from Trinkaus (1983), Arensburg (1991), Sládek et al. (2000) and Franciscus and Churchill (2002). Right and left indices, when available for the fossils, are averaged. For Mladeč 14 and 17, given uncertainties in rib number, comparative data for the adjacent probable ribs are provided

	Rib 2	Rib 3	Rib 8?	Rib 9?	Rib 10?	Rib 12
Mladeč 14	64.5					
Mladeč 16			50.3			
Mladeč 17				55.5		
Mladeč 18						44.4
Neandertals						
Kebara 2	46.4	58.4	57.9	52.4	60.0	62.3
Shanidar 3	66.3	55.8	52.1	53.8	62.2	56.5
Shanidar 4	70.8	-	-	-	-	52.8
Shanidar 5	71.0	-	-	-	-	-
Qafzeh-Skhul						
Skhul 4	-	48.1	65.8	39.6	65.5	55.8
Skhul 5	50.0	57.3	68.5	56.3	95.2	-
European earlier						
Upper Paleolithic						
Dolní Věstonice 13	41.6	71.5	57.1	53.1	63.6	-
Dolní Věstonice 14	-	-	-	-	-	58.8
Dolní Věstonice 15	54.9	57.3	53.6	-	48.2	40.7
Euroamericans						
males - right	± 5.4	± 14.2	± 9.8	± 8.1	± 8.5	± 7.9

The Mladeč 17 more caudal right rib (probably 9 or 10) has a convex articular facet, a large pit dorsally between the head and the articular facet, a rounded shaft between the articular facet and the angle, and then a modest intercostal crest and sulcus distal of the angle.

The Mladeč 18 left twelfth rib appears to be relatively robust with rounded margins. In addition to its smooth proximodistal spiral, it is caudally convex proximally and then cranially convex distally.

There are no notable features on the Mladeč 15, 19, and 20a to 20e rib pieces.

The available rib diameters at the neck, articular facet and angle are provided in Table 6. Comparisons of the index of the minimum to maximum diameters (generally the breadth versus the height, except for rib 2) are provided in Table 7. For each of Mladeč 14 and 17, comparisons are made to the adjacent ribs given uncertainties in rib number. Although it has long been stated that Neandertals have very round ribs compared to recent humans (Schaaffhausen, 1858; Boule, 1911–13), recent analyses (e.g., Heim, 1976; Arensburg, 1991; Franciscus and Churchill, 2002) have documented considerable within-sample variation in this feature. However, Franciscus and Churchill (2002) have argued that Neandertal ribs are distinctive mostly in the robusticity of their more caudal ribs, and this is supported by the data in Table 7, particularly for the eleventh rib. In this, only Kebara 2 among the Neandertals has a relatively thin eleventh rib, although Dolní Věstonice 13 has relatively robust ones. The Mladeč 18 twelfth (or eleventh) rib is one of the thinnest of these Late Pleistocene specimens exceeded in this feature only by Dolní Věstonice 15 and matched by some recent Euroamericans. However, the Mladeč 16 and 17 ribs are also relatively thin for Late Pleistocene humans. Moreover, the Mladeč 14 second or third rib falls in the middle of variable samples.

The Mladeč 13 clavicle

Mladeč 13 was originally identified as a proximal rib fragment, but reconsideration suggests that it is the distal portion of an immature right clavicle (see chap. 8, Plate IX, Fig. b). Its maximum preserved length is 60.7 mm. Its fragmentary condition provides little morphological information, reflected in difficulties in determining its identification.

The Mladeč 23 and 24 humeri

Preservation and maturity

The Mladeč sample preserves portions of two right humeri, Mladeč 23 and Mladeč 24. The former retains the proximal epiphysis and proximal third of the diaphysis, whereas the latter retains most of the diaphysis (see chap. 8, Plate XIII).

Mladeč 23 is an almost mature right proximal humerus, broken distally at the level of the deltoid tuberosity, approximately where the tuberosity begins its superoinferior course from the lateral to the anterior (ventral) aspects of the diaphysis. The proximal shaft is complete distal to the level of the surgical neck. The proximal epiphysis, however, has endured some damage. The lesser tubercle lacks only the most anterior projection, and the intertubercular sulcus is completely preserved, but nothing remains of the greater tubercle. The damage associated with the loss of the greater tubercle has exposed cancellous bone from the lateral surgical neck to the superior margin of the humeral head. Posteriorly, a band (ca. 10 mm wide) of mostly cortical bone is missing along the posterior aspect of the anatomical neck. While preservation of the bone is excellent, the bone surface is obscured by encrusting matrix on the medial head and shaft, and slight surface erosion is visible on the anteromedial border of the shaft.

Mladeč 24 is a virtually complete right humeral diaphysis, preserved from slightly proximal of the level of the surgical neck to the distal epiphyseodiaphyseal region. Nothing remains of the

humeral head, anatomical neck, or greater and lesser tubercles, but the insertion for *M. pectoralis major* is visible slightly inferior to the level of the lesser tubercle, as are the insertions for *M. latissimus dorsi* and *M. teres major*. Distally, the complete olecranon fossa is preserved, and a lateral portion of the trochlea remains attached to the inferior aspect of the olecranon fossa. The bulk of the trochlea, the capitulum, and the medial and lateral epicondyles are missing. On the anterior surface, the coronoid fossa is completely preserved with a small shelf of bone directly inferior of it, where a fragment of the trochlea remains attached. The radial fossa is also preserved, but it is broken along its inferior margin. Overall, the specimen exhibits good preservation, although surface matrix is found on the proximal shaft and in the olecranon, radial and coronoid fossae and surrounding areas. In the mid-distal diaphysis there is a fossilization break which has been reassembled with minimal separation of the two pieces; in 1998 the join was opened, a sample of bone was taken from the middle of the cortical bone for accelerator mass spectrometry radiocarbon dating of the specimen, the adjoining surfaces cleaned of matrix, and the two pieces reassembled. Dating of the specimen failed due to contamination and low carbon yield.

The Mladeč 23 humerus exhibits radiographically an indication of its proximal (head) epiphyseal line, extending from the medial side about two-thirds of the distance laterally, even though externally it is not apparent on the cortical bone anteriorly and medially or on the exposed trabeculae posteriorly and laterally. This provides a general adolescent (13 to 20 years) age-at-death for Mladeč 23, although the degree of fusion suggests an age toward the higher end of that range. The Mladeč 24 humerus exhibits no trace externally or radiographically of the distal epiphyseal fusion line, indicating a late adolescent or adult status for it.

Mladeč 24 length estimation

Since it is necessary to scale detailed measurements of the humerus to a measure of overall size whenever possible, the anatomical lengths of the more complete Mladeč 24 humerus were estimated; the Mladeč 23 humerus is insufficiently preserved to allow an adequate estimation of its original length. In order to do this, the bone was placed on a metric grid and the locations of the middle of the proximal medial diaphyseal curvature (for the medial deviation of the head), the proximal end of the *M. pectoralis major* tuberosity, the posteroproximal trochlea and the distal coronoid fossa were located. The average of each pair of proximal or distal landmarks was noted, and the distance between them determined (296.5 mm for Mladeč 24). The same measurements were taken on a geographically mixed sample of recent human humeri, and least squares regressions for maximum length, articular length and biomechanical length were determined (see notes to Table 8). The resultant values for Mladeč 24 are provided in Table 8; the standard errors of the estimates for Mladeč 24 are between 3.0 and 3.5 mm, all of which are less than 1% of the predicted lengths.

This approach only assumes that the relative overall dimensions of the epiphyses are similar to those of the recent human sample; given the apparently modest dimension of at least one aspect of the distal epiphysis (see olecranon fossa discussion below), this assumption appears to be reasonable. If the dimensions of the epiphyses have been underestimated, then the errors will be conservative since they will tend to make diaphyseal and epiphyseal aspects of the Mladeč 24 humerus appear more robust than they originally were.

Morphology

The Mladeč 23 humeral head is evenly rounded with the mediolateral diameter probably (given damage) greater than the anteroposterior diameter (see Table 8). The head-neck angle is 142°. The lesser

Table 8. Osteometric dimensions of the Mladeč 23 and 24 right humeri (in mm and degrees). Estimated values are in parentheses

	Mladeč 23	Mladeč 24
Maximum length ¹	–	(373.5)
Articular length ²	–	(366.0)
Biomechanical length ³	–	(366.5)
Head mediolateral diameter (M-9)	44.1	–
Head anteroposterior diameter (M-10)	(40.0)	–
Head mediolateral arc ³	63.0	–
Head depth	17.5	–
Head-neck angle (M-17)	(142°)	–
Surgical neck maximum diameter	27.0	22.6
Surgical neck minimum diameter	22.0	19.9
Surgical neck circumference	78.0	69.0
Lesser tubercle length	22.0	–
Lesser tubercle breadth	12.5	–
Intertubercular sulcus depth (S-23) ⁵	(3.8)	–
Intertubercular sulcus breadth (S-24)	7.9	–
Midshaft maximum diameter (M-5)	–	21.9
Midshaft minimum diameter (M-6)	–	15.5
Midshaft circumference (M-7a)	–	61.0
Deltoid diameter (M-6a)	19.7	21.3
Deltoid circumference	–	63.0
Distal minimum circumference (M-7)	–	59.0
Distal diaphyseal AP diameter	–	18.5
Distal diaphyseal ML diameter	–	16.7
Maximum deltoid tuberosity breadth ⁶	10.8	9.0
Pectoralis major breadth ⁶	7.9	4.7
Latissimus dorsi / teres major breadth ⁶	6.3	–
Supraolecranon AP diameter	–	14.6
Supraolecranon ML diameter	–	28.8
Medial pillar thickness (S-12)	–	7.5
Lateral pillar thickness (S-13)	–	(16.0)
Olecranon fossa breadth (M-14)	–	28.0
Olecranon fossa depth (M-15)	–	11.6
Coronoid fossa breadth	–	16.2
Septal aperture	–	absent
Maximum preserved length	147.2	313.0

¹ Maximum length estimated from the mean distance between the proximal medial diaphyseal curvature and the proximal pectoralis major tuberosity proximally and the posteroproximal trochlea and the distal coronoid fossa distally (PresLen = 296.5 mm), using a least squares regression based on recent humans (MaxLen = 1.30 × PresLen – 14.1, $r^2 = 0.945$, N = 29). $SE_{est} = 3.4$ mm.

² Articular length estimated from the mean distance between the proximal medial diaphyseal curvature and the proximal pectoralis major tuberosity proximally and the posteroproximal trochlea and the distal coronoid fossa distally (Pres Len = 296.5 mm), using a least squares regression based on recent humans (ArtLen = 1.22 × PresLen + 2.0, $r^2 = 0.949$, N = 29). $SE_{est} = 3.1$ mm.

³ Biomechanical length (proximal head to distal lateral trochlear margin) estimated from the mean distance between the proximal medial diaphyseal curvature and the proximal pectoralis major tuberosity proximally and the posteroproximal trochlea and the distal coronoid fossa distally (Pres Len = 296.5 mm), using a least squares regression based on recent humans (BiomLen = 1.25 × PresLen – 4.9, $r^2 = 0.950$, N = 29). $SE_{est} = 3.1$ mm.

⁴ Maximum arcs (AP and ML relative to head) of the subchondral bone (Vandermeersch and Trinkaus, 1995).

⁵ Measurement definitions from Senut (1981).

⁶ Maximum distinct breadth of the muscular insertion rugosity.

tubercle is obliquely oriented with a peak distally; there is a large muscle tendon facet (for *M. subscapularis*) on it with a broad sulcus between it and the head articular margin.

The Mladeč 23 proximal anterior diaphysis exhibits a broad (maximum width 15.6 mm) area of mildly rugose surface bone for the combined attachments of *M. pectoralis major*, *M. latissimus dorsi* and *M. teres major*. It is possible to largely discern the attachment for *M. pectoralis major* from that for the other two muscles, and the maximum breadths of these attachments are in Table 8. The preserved portion of the deltoid tuberosity is a broad, roughened area that is minimally raised from the adjacent diaphyseal surface and exhibits minimal rugosity.

On the Mladeč 24 proximal diaphysis, there is a clear but narrow and minimally rugose insertion for *M. pectoralis major*. However, the attachments for *M. latissimus dorsi* and *M. teres major* cannot be discerned; although the region for their insertions is partly obscured with matrix, it is unlikely that their attachments were more than minimally developed. The deltoid tuberosity is discernible as a gentle swelling rather than as a distinct tuberosity. One can discern longitudinal striations on the tuberosity, but there is none of the rugosity frequently associated with the osteological insertion of the deltoid muscle. Distally, the supracondylar crests are minimally present.

The size of the *M. pectoralis major* tuberosity in particular, as reflected in its breadth relative to humeral length, is one of the features that have been shown to largely separate the Neandertals and early modern humans (Trinkaus, 2000). As illustrated in Fig. 1, the relative *M. pectoralis major* breadths of the Neandertals are above those of all early modern humans. Among the Neandertals, only those of La Ferrassie 1 and Lezetxiki 1 approach the early modern human distribution. It is not possible to appropriately compare the Mladeč 23 *M. pectoralis major* breadth, since humeral length is not available for it; however its breadth of 7.9 mm is in the middle of the early modern human distribution and among the Neandertals only the La Ferrassie 2 and Lezetxiki 1 humeri have lower absolute values. The Mladeč 24 breadth of 4.7 mm, however, is among the smaller of the early modern human values, and it is the lowest value relative to humeral length of any of the Late Pleistocene specimens for which data are available. Only the Dolní Věstonice 14 humerus approaches it.

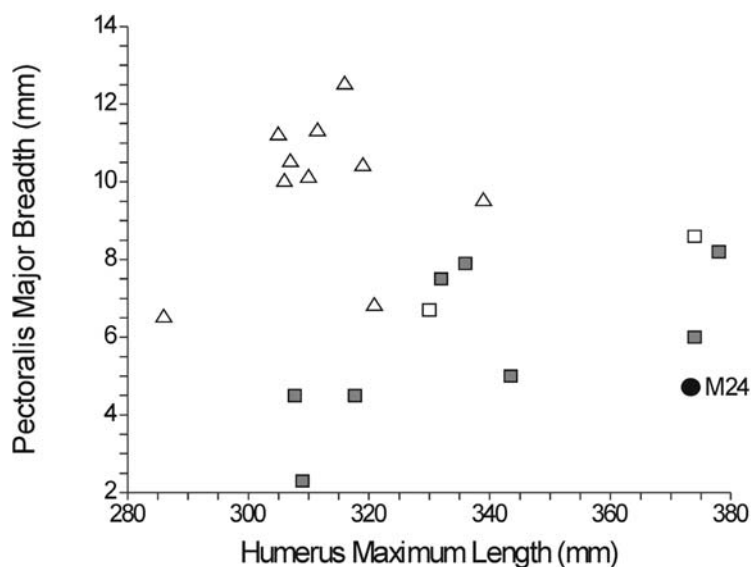


Fig. 1. *M. pectoralis major* tuberosity breadth versus humeral length for Mladeč 24 (black circle – M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

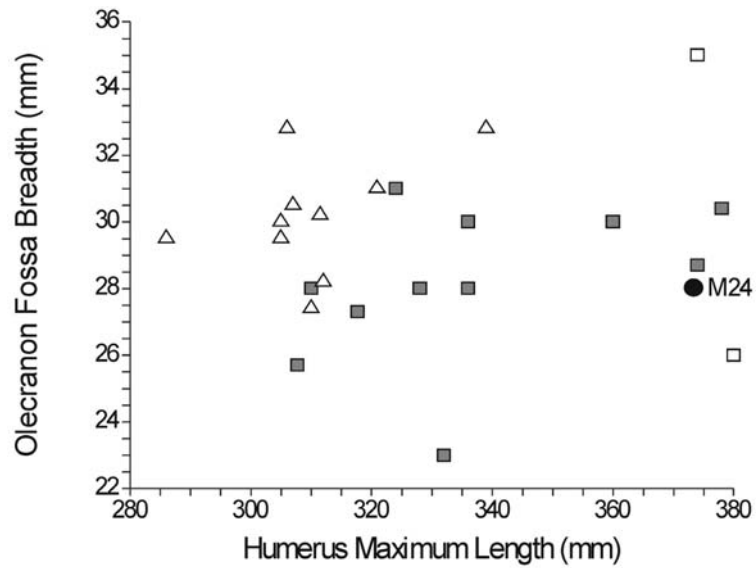


Fig. 2. Olecranon fossa breadth versus humeral length for Mladeč 24 (black circle - M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

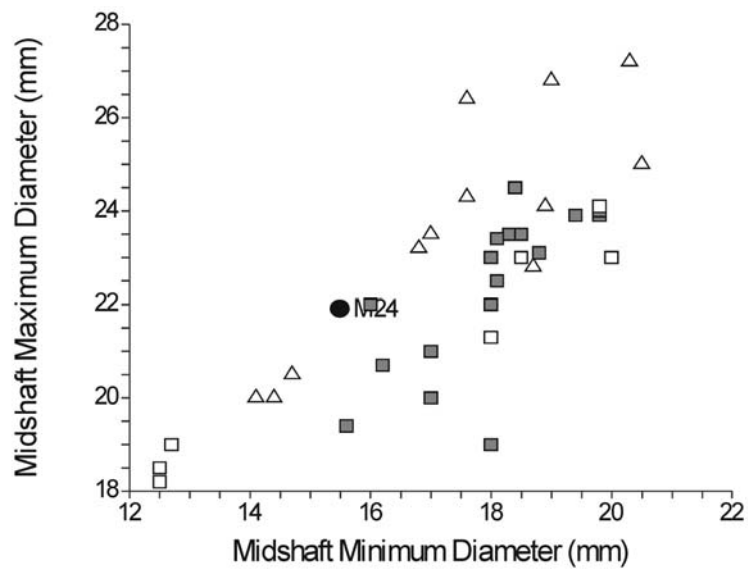


Fig. 3. Humeral midshaft maximum versus minimum subperiosteal diameters, for Mladeč 24 (black circle - M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

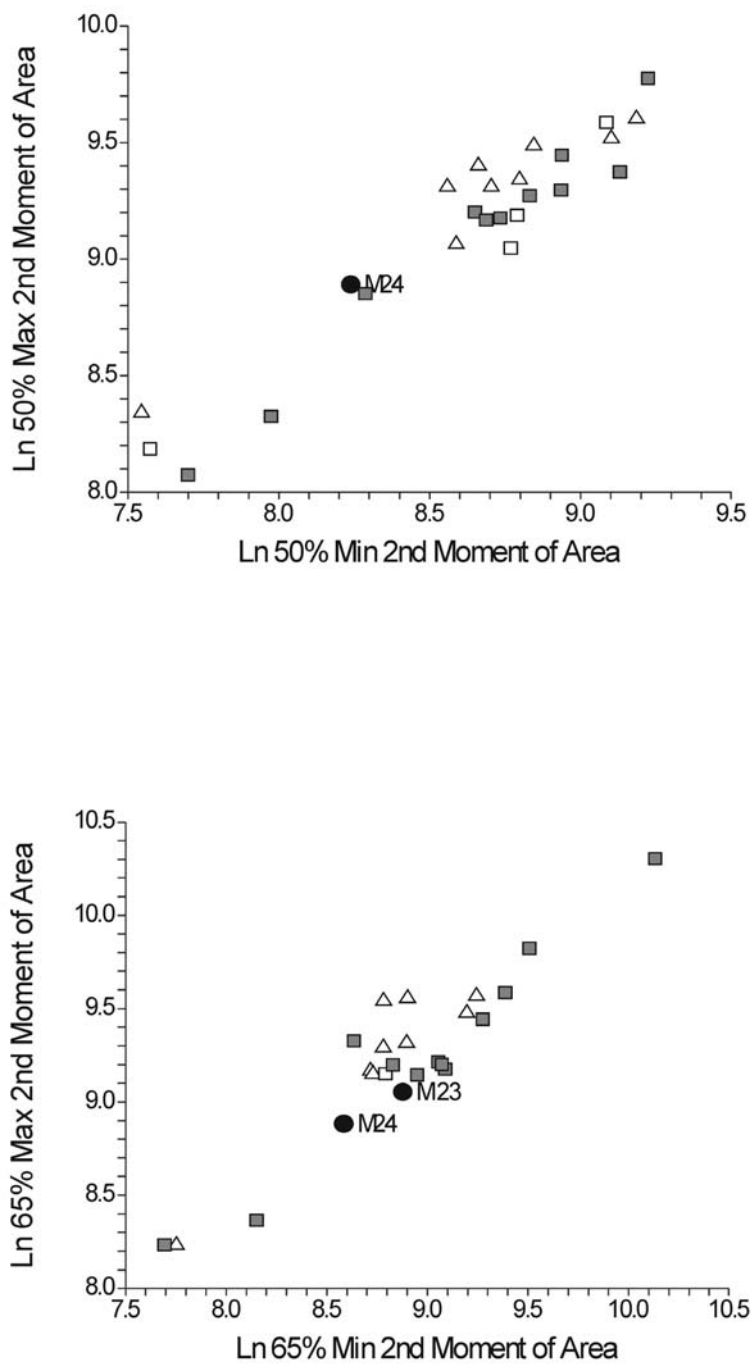


Fig. 4. Maximum versus minimum second moments of area of the humeral mid-shaft (50%) and mid-proximal shaft (65%), for Mladeč 23 and 24 (black circles – M23 and M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

The other measure of muscular hypertrophy available on the Mladeč humeri is an indirect one, the breadth of the olecranon fossa (as reflecting olecranon breadth and hence *M. triceps brachii* tendon size) relative to humeral length. The Neandertals again have higher relative values than the early modern humans, although the degree of overlap is greater than with the *M. pectoralis major* tuberosity breadth (Table 10; Fig. 2). The Mladeč 24 humerus is among the most gracile of the available specimens. It is close to that of Dolní Věstonice 14 and only Dolní Věstonice 16 and Skhul 5 have lower relative values.

The diaphyseal shape has been assessed using midshaft maximum and minimum external diameters, to maximize sample size, and using 50% (midshaft) and 65% (mid-proximal diaphysis) maximum versus minimum second moments of area. The latter provide more accurate measurements of diaphyseal cortical bone distribution and permit the inclusion of the Mladeč 23 humerus (for the 65% section), but available comparative data are more limited.

The midshaft subperiosteal diameter comparison (Fig. 3) shows a general trend, with the Neandertals and the smaller Qafzeh-Skhul specimens having more ellipsoid diaphyseal proportions and the other early modern humans having rounder (or, more accurately, less ellipsoid) midshafts. Since a more ellipsoid shaft would provide for greater rigidity to bending in the plane of the maximum diameter, this appears to suggest greater robusticity of the Neandertal and some Qafzeh-Skhul humeri. In this, Mladeč 24 is the most ellipsoid of the earlier Upper Paleolithic specimens; although it is close to the middle of the Neandertal range of variation, it is not significantly different from either early modern human sample (Table 10).

The second moments of area comparisons provide less separation of the Late Pleistocene samples, although they continue the general pattern of more ellipsoid humeral diaphyses among the Neandertals (Fig. 4; Table 10). In the 50% cross section, Mladeč 24 remains in the middle of the Neandertals but close to other early modern humans, whereas in the 65% cross section, both of the Mladeč humeri are among the early modern humans but Mladeč 24 remains close to the Neandertal distribution (Fig. 4; Table 10).

Diaphyseal robusticity

These aspects of muscular hypertrophy and diaphyseal shape can be, for Mladeč 24 in particular, associated with an assessment of diaphyseal robusticity using especially cross sectional geometry (Table 9). Relative cortical area at the mid-distal (35%) diaphysis provides little separation of the comparative samples, and Mladeč 24 falls in the middle of the Late Pleistocene distribution (Table 10; Fig. 5). The more proximal diaphyseal sections provide some separation of the late archaic and early modern human samples despite considerable overlap and the high relative val-

Table 9. Cross-sectional geometric properties of the Mladeč 23 and 24 humeri. Areas in mm², second moments of area in mm⁴. 0% is distal

	Mladeč 23 65%	Mladeč 24 35%	Mladeč 24 50%	Mladeč 24 65%
Total area (TA)	350.8	263.4	271.9	294.0
Cortical area (CA)	193.1	201.9	181.1	201.5
Medullary area (MA)	157.7	61.5	90.8	92.5
AP 2nd moment of area (I_x)	8337	6350	6240	6366
ML 2nd moment of area (I_y)	7387	4516	4802	6188
Max 2nd moment of area (I_{max})	8525	6753	7248	7184
Min 2nd moment of area (I_{min})	7199	4113	3794	5370
Polar moment of area (J)	15724	10866	11042	12554

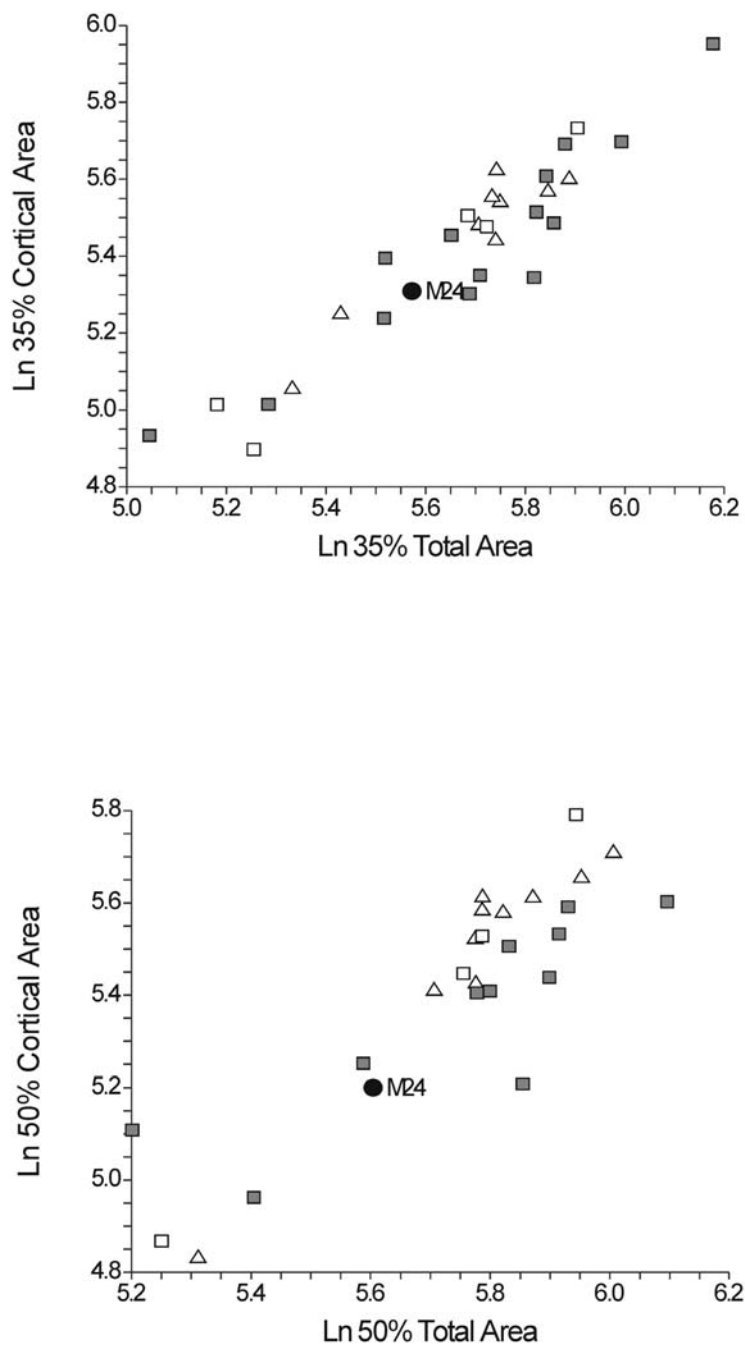


Fig. 5. Cortical area versus total subperiosteal area for the mid-distal (35%) and midshaft (50%) humerus for Mladeč 24 (black circles – M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

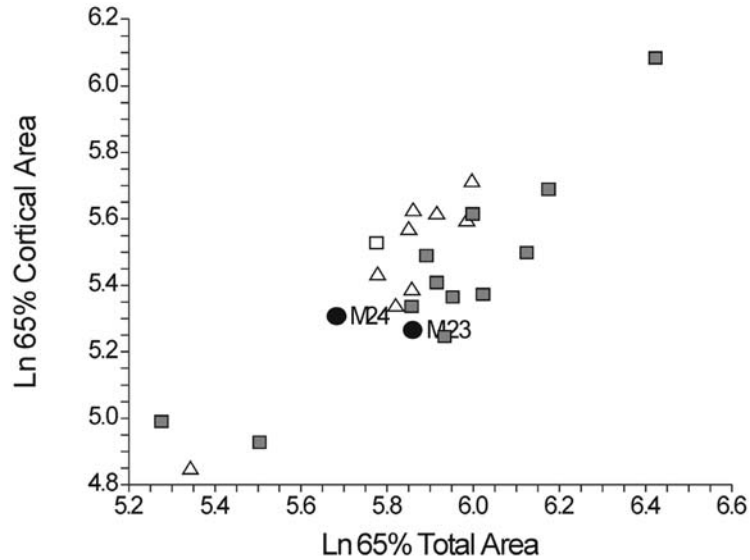


Fig. 6. Cortical area versus total subperiosteal area for the mid-proximal (65%) humerus for Mladeč 23 and 24 (black circles – M23 and M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

ues of the very small Nahal-Ein-Gev 1 specimen (Fig. 6). In the 50% comparisons, Mladeč 24 is among the earlier Upper Paleolithic specimens but close to the Middle Paleolithic ones, and in the 65% section Mladeč 24 has moderately higher relative cortical area whereas Mladeč 23 remains with the majority of the earlier Upper Paleolithic specimens and distinct from the Neandertals (Fig. 6).

It is debatable to what extent relative cortical area reflects diaphyseal robusticity rather than the life history of endosteal resorption versus subperiosteal deposition of the humerus in question. Comparisons of diaphyseal measures of bone quantity to bone length, however, provide better assess-

Table 10. Mladeč 23 and 24 humeral metric comparisons using linear residuals from the reduced major axis line through the pooled comparative sample. The P-value derives from the ANOVA comparison across the three reference samples, and the Mladeč values are Z-scores [(Mladeč values – sample mean)/standard deviation]. Z-scores are provided only relative to samples ≥ 5 . I_{max} and I_{min} : maximum and minimum second moments of area; CA and TA: cortical and total subperiosteal areas; J: polar moment of area.* $P < 0.05$ with a multiple comparison correction ($\alpha/9$)

	P-Value	Neandertals		Qafzeh-Skhul	Earlier Upper Paleolithic	
		Mladeč 23	Mladeč 24	Mladeč 24	Mladeč 23	Mladeč 24
Olec. br. / Length	<0.001*	-	5.04	-	-	1.44
Midshaft Max. / Min.	0.004*	-	0.26	1.18	-	1.73
50% I_{max} / I_{min}	0.011	-	0.19	-	-	1.74
65% I_{max} / I_{min}	0.069	2.01	1.40	-	0.73	0.20
35% CA / TA	0.372	-	0.55	0.46	-	0.10
50% CA / TA	0.045	-	1.33	-	-	0.59
65% CA / TA	0.013	2.38	0.08	-	0.44	1.05
Distal circ. / Length	0.001*	-	3.43	-	-	3.35
J / Length	<0.001*	-	3.66	0.40	-	2.54

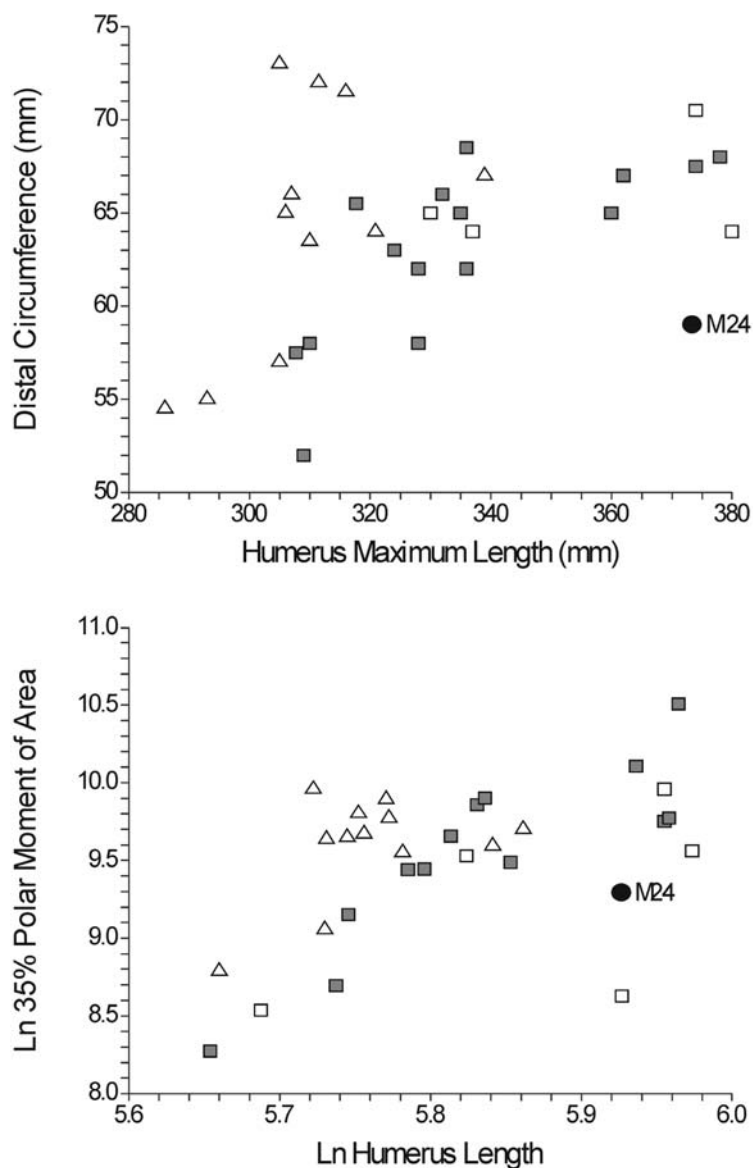


Fig. 7. Measures of humeral robusticity for Mladeč 24. Distal minimum circumference (above) and mid-distal (35%) polar moment of area (below) for Mladeč 24 (black circle – M24), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares).

ments of the bone's robusticity. Previous assessments of humeral diaphyseal scaling (e.g., Ruff et al., 1993; Trinkaus and Churchill, 1999; Ruff, 2000a) have varied as to whether humeral length alone or humeral length combined with body mass should be used to scale humeral robusticity. However, since a number of recent humans with fully functional upper limbs are incapable of supporting their body weights on their upper limbs (in either suspensory or supportive modes) (Trinkaus, personal experience), body weight should not necessarily be used to scale humeral robusticity. Therefore, meas-

ures of human humeral diaphyseal size are scaled here solely against an estimate of beam length, humeral length.

To maximize sample size, initially distal minimum diaphyseal circumference relative to humeral length was compared (Table 10; Fig 7). Several Neandertals provide high values, several early modern humans have more gracile humeri, and the two samples are significantly different (Table 10); there is nonetheless some overlap between the samples. However, regardless of the degree of Neandertal to early modern human similarity or difference in relative distal circumference, none of them is as gracile as the Mladeč 24 humerus. The Mladeč 24 humerus is approached only by the Skhul 5 and, to a lesser extent, the Dolní Věstonice 3 humeri.

The patterns of sample tendencies hold for the more appropriate comparison of 35% polar moment of area to humeral length (Fig. 7). The reference samples are significantly different, Mladeč 24 remains very gracile compared to the Neandertal and earlier Upper Paleolithic samples, although in this comparison it is close to the values for Dolní Věstonice 14, Pavlov 1 and Skhul 4 and above the low value for Skhul 2. Mladeč 24 is completely separate from even the most gracile Neandertal humeri.

The interpretation of the relative gracility of the Mladeč 24 humerus depends in part on the appropriate scaling employed for humeral diaphysis. As discussed above, it is most appropriate to use humeral length alone, as beam length, to scale human humeral diaphyseal and articular dimensions. If humeral length alone is employed, then Mladeč 24 is clearly a very gracile humerus, among the most gracile humeri known from the Middle Paleolithic and earlier Upper Paleolithic, suggesting relatively light habitual loads on the upper limb. If, however, it were argued that some percentage of body mass should be combined with humeral length, then the relatively small dimensions of the Mladeč 24 diaphysis could be the product of a very linear body (low mass relative to arm length), or a combination of a linear body and a gracile bone.

The Mladeč 25c ulna

Preservation and maturity

The Mladeč 25c right ulna preserves most of the proximal end of the bone plus some of the adjacent diaphysis (chap. 8, Plate XIV). For the portions preserved, most of the bone is intact. The primary damage is to the volar margins of the olecranon and coronoid processes, although the coronoid damage is mostly abrasion to the margin with little bone loss. The proximal olecranon epiphysis appears to have been fully fused at the time of death, but it has been abraded and gives the superficial appearance of the olecranon metaphysis. This indicates an age-at-death of at least ca. 15 years (Scheuer and Black, 2000).

Morphology

The Mladeč 25c ulna is a large and rugose bone (Tables 11 and 12). The various muscular and ligamentous attachments are strongly marked on the bone, and the diaphyseal crests appear to have been fully formed. The proximal diaphysis is triangular in cross section, and there is a strong development of a posterolateral sulcus. The proximal end of the interosseus crest is thick (4.0 mm) and prominent. There is a strong marking for the *M. brachialis* insertion with a distinct concavity formed on the distal coronoid process for it. However, the supinator crest is poorly developed.

The abrasion of the coronoid process and particularly erosion of the olecranon process prevent metrical assessment of the trochlear notch orientation. However, it is evident in lateral view from the

Table 11. Osteometric dimensions of the Mladeč 25c right proximal ulna (in mm and degrees). Estimated values are in parentheses

Proximal shaft AP diameter (M-14)	24.5
Proximal shaft ML diameter (M-13)	24.0
Olecranon breadth (M-6)	(25.0)
Olecranon thickness (MCH-7) ¹	21.3
Olecranon length (M-8; MCH-12)	(20.5)
Coronoid height (MCH-8)	43.0
Tuberosity position (MCH-11)	33.0
Proximal trochlear angle ²	19°
Radial facet height	(20.0)
Radial facet breadth	(17.0)
Anterior breadth of coronoid-radial half (M-9)	14.0
Posterior breadth of coronoid-radial half (M-10)	16.6
Radial breadth of the coronoid ³	10.7
Ulnar breadth of the coronoid ³	18.3
Maximum preserved length	114.2

¹ Measurement definition from McHenry et al. (1976).

² Taken in the coronal plane of the bone.

³ From the mid-coronoid crest to the radial or ulnar margin.

Table 12. Cross-sectional geometric properties of the Mladeč 25a ulna, Mladeč 25a, 25b and 26 radii, and Mladeč 31 metacarpal 3. Areas in mm², second moments of area in mm⁴. 0% is distal. Proximodistal positions are based on the morphology and are therefore approximate

	Mladeč 25c	Mladeč 25a	Mladeč 25b	Mladeč 25b	Mladeč 26	Mladeč 26	Mladeč 31
	80%	80%	35%	50%	35%	50%	50%
Total area (TA)	246.6	180.0	144.1	163.4	114.1	110.2	55.9
Cortical area (CA)	172.4	117.0	116.0	139.0	97.0	85.9	48.5
Medullary area (MA)	74.2	63.0	28.1	24.4	17.1	24.3	7.4
AP 2nd moment of area (I_x)	4097	2531	1443	1724	1040	858	220
ML 2nd moment of area (I_y)	4985	2049	1774	2608	994	1004	276
Max 2nd moment of area (I_{max})	5057	2592	1775	2610	1096	1039	284
Min 2nd moment of area (I_{min})	4025	1988	1442	1723	938	824	212
Polar moment of area (J)	9083	4580	3217	4332	2034	1863	496

large size of the coronoid process and the modest development of what is preserved of the volar olecranon that the orientation of the trochlear notch was predominantly volar and proximal. In this, it contrasts with the more strictly volar orientation of the trochlear notch seen in Neandertals and archaic *Homo* generally (Trinkaus, 1983; Churchill et al., 1996).

The trochlear notch also turns strongly laterally relative to the diaphysis, or vice versa. The angle between the midline crest of the trochlear notch and the midline of the proximal diaphysis is ca. 19°.

The coronoid process is notable primarily for its strong medial flare, indicating a large medial portion to the humeral trochlea. As an indication of the degree of medial flare, the distance from the mid-trochlear notch crest to the radial side is 10.7 mm, whereas it is 18.3 mm to the medial side. The radial facet is large and broad, and in terms of curvature fits well with the head of the Mladeč 25a right radius.

The Mladeč 25a, 25b and 26 radii

Preservation and maturity

The radial remains from Mladeč include a proximal right radius with the head, the neck, the tuberosity, and a small portion of the proximal diaphysis to the beginning of the interosseus crest (Mladeč 25a), a right midshaft section from the proximal interosseus crest to the beginning of the flare for the distal epiphysis (Mladeč 25b), and a smaller left radial midshaft section (Mladeč 26) (chap. 8, Plate XIV). The last has its proximal break dorsally near the maximum development of the interosseus crest but closer to midshaft elsewhere, and distally it is broken near the minimum circumference.

The first two specimens, Mladeč 25a and 25b, are very similar in diaphyseal size, both are right, and they could very well belong to the same bone. If Mladeč 25a derives from the same elbow as the Mladeč 25c ulna, then the three pieces could derive from the same forearm. Mladeč 26 is clearly smaller (Tables 12 and 13), and it is therefore unlikely to be from the left arm of the same individual. If they are assumed to be from the same individual, their distal minimum circumferences provide an asymmetry value $[(\text{right} - \text{left}) / (\text{right} + \text{left}) / 2]$ of 15.0. A sample of 14 earlier Upper Paleolithic paired radii provides a median of 4.2 and a maximum value of 12.2 (Barma Grande 2), small Neandertal and Qafzeh-Skhul samples provide ranges of 0.0 to 8.7 ($N = 4$) and 2.4 to 3.1 ($N = 3$) respectively, and a robust recent human sample (Ohba, 1935) has a median of 2.7, a 95% value of 10.2, and a maximum outlier of 16.0. It is therefore possible, but unlikely, that the Mladeč 25b and 26 derive from the same individual.

The Mladeč 25a proximal radius gives the appearance of having a partially, but largely, fused head epiphysis. However, close inspection of the purported epiphyseal fusion line indicates that it is a postmortem break and not a fusion line. This is indicated by the exposed trabeculae within the break, rather than a metaphyseal surface, and by its location within the head subchondral bone rather than between the head and the neck. This indicates an age-at-death of at least ca. 15 years (Scheuer and Black, 2000).

Morphology

The Mladeč 25a proximal radius is notable especially for its absolutely large head, neck and tuberosity (Tables 12 to 14). The sagittal diameter of the head (25.2 mm) is at the upper end of the range of variation for earlier Upper Paleolithic humans, being approached only by that of Paviland 1 (24.6 mm); among Middle Paleolithic humans, only Skhul 4 (24.8 mm) and Shanidar 3 (25.0 mm) come close. In concert with the large size of its head, the sagittal neck diameter is also large; its diameter of 15.6 mm is above those of all earlier Upper Paleolithic specimens except Cro-Magnon 4303 and 4305a (16.3 and 15.5 mm, respectively), and among Middle Paleolithic specimens it is exceeded only by that of Skhul 4 (16.3 mm).

The combination of head and neck diameters provides it with an index of 161.5, which is close to the mean of a variable earlier Upper Paleolithic sample (Table 14) and relatively low for a Neandertal specimen. Given the shift, albeit non-significant, for an increase in relative head diameter between Neandertals and early modern humans (Table 14), Mladeč 25a clusters with the early modern humans and only a minority of the Neandertals. In the context of this, the Mladeč 25a neck anteroposterior to mediolateral diameter proportions are similar to those of the comparative samples, which differ little among themselves.

Since Neandertals have long radial necks relative to radial length (Trinkaus, 2000), reflecting the mechanical advantage of *M. biceps brachii* for elbow flexion, an index was devised using radial head diameter as a surrogate for overall radial size, given the similarities in the radial head to length proportions of later Pleistocene and recent humans (Trinkaus, 1983). The resultant indices reinforce the

Table 13. Dimensions of the Mladeč 25a right proximal radius, 25b right radial midshaft and 26 left radial midshaft (in mm and degrees).

	Mladeč 25a	Mladeč 25b	Mladeč 26
Head AP diameter (M-5[1])	25.2	–	–
Head depth (mid-proximal fossa)	3.4	–	–
Prox. ulnar prox.-dist. dia.: lat. surf. ¹	11.0	–	–
Prox. ulnar prox.-dist. dia.: maximum ¹	12.5	–	–
Neck AP diameter (M-5[2])	15.6	–	–
Neck ML diameter (M-4[2])	14.2	–	–
Neck circumference (M-5[4])	51.0	–	–
Head-neck length (M-1a)	38.2 ²	–	–
Neck-shaft angle (M-7)	(14°)	–	–
Tuberosity length (S-1)	29.4	–	–
Tuberosity breadth (S-4)	17.8	–	–
Tuberosity projection (S-8)	19.0	–	–
Shaft diameter at tuberosity	16.2	–	–
Tuberosity position ³	2	–	–
Proximal AP diameter ⁴	13.7	–	–
Proximal ML diameter ⁴	14.6	–	–
Proximal circumference ⁴	48.0	–	–
Midshaft AP diameter (M-5a) ⁵	–	13.6	11.7
Midshaft ML diameter (M-4a)	–	17.1	14.1
Distal minimum circumference (M-3)	–	43.0	37.0
Maximum preserved length	82.0	127.0	93.8

¹ The lateral surface measurement includes only the proximodistally flat portion of the surface, whereas the maximum dimension extends to the plane of the proximal head.

² This is the distance to the proximodistal middle of the tuberosity; the measurement to the most prominent point on the tuberosity provides a head-neck length of 36.0 mm.

³ Position 2 indicates that the interosseus crest is in line with the dorsal third of the tuberosity (Trinkaus and Churchill, 1988).

⁴ Diameters and circumference taken at the midpoint between the tuberosity and the proximal extent of the interosseus crest.

⁵ The positions of midshaft estimated based on interosseus crest morphology.

pattern of greater *M. biceps brachii* power for Neandertals in general, although the differences between the Late Pleistocene samples are non-significant. The Mladeč 25a value, however, is well above the comparative sample means, exceeded only by those for Dolní Věstonice 14, La Ferrassie 2, and Shanidar 6 and 8. The three Neandertals with high values are all small females with small radial heads; however, both Dolní Věstonice 14 and especially Mladeč 25a have rather large radial heads, emphasizing their combinations of long radial necks and especially large radial tuberosities.

The estimated Mladeč 25a neck-shaft angle is close to the Neandertal mean value and about a standard deviation above the earlier Upper Paleolithic mean. Among the latter sample, it is exceeded by Cro-Magnon 4303 and Paviland 1, and it therefore remains within the earlier Upper Paleolithic distribution.

The Mladeč 25a radial tuberosity is large and prominent, especially on its dorsal margin. It is moderately rotated anteriorly, such that its dorsal third is in line with the interosseus crest (position 2 of Trinkaus and Churchill, 1988). This arrangement is found in all three comparative samples, but there is a highly significant shift between Neandertals and earlier Upper Paleolithic humans in their frequency distributions of radial tuberosity orientation. The Neandertals have mainly the more directly medial orientation, including the initial Upper Paleolithic Vindija 13.8 radius but not the Saint Cé-

Table 14. Comparative osteometrics for the Mladeč radii. For comparative samples with $N > 4$, the mean, standard deviation and N are provided. For continuous variables, the ANOVA P -value is provided between the comparative samples for head diameter and neck-shaft angle; for indices and tuberosity position, the Kruskal-Wallis P -value between these samples is provided. * $P < 0.05$ with a multiple comparison correction ($\alpha/7$)

	Mladeč 25	Mladeč 26	Neandertals	Qafzeh-Skhul	Earlier Upper Paleolithic	Comparative P -value
Head AP diameter (mm)	25.2	–	21.6 ± 2.4 (13)	20.2, 22.0, 24.8	23.1 ± 1.4 (14)	0.160
Head/neck AP index	161.5	–	178.2 ± 13.4 (13)	152.3, 165.6, 184.9	166.0 ± 16.5 (8)	0.297
Neck AP/ML index	109.9	–	114.4 ± 7.6 (14)	90.2, 115.1, 119.5	110.6 ± 8.1 (11)	0.349
Tuberosity/ head index ¹	107.7	–	99.3 ± 8.2 (12)	93.5, 99.4	94.0 ± 8.1 (12)	0.228
Neck-shaft angle	14°	–	14.4° ± 1.1° (12)	–	11.1° ± 3.1° (8)	0.003*
Tuberosity position	2	–	1: 3.6% 2: 28.6% 3: 67.9% (14)	1: 25.0% 2: 50.0% 3: 25.0% (4)	1: 21.2% 2: 78.8% 3: 0.0% (26)	<0.001*
Midshaft AP/ML index	79.5	83.0	77.1 ± 3.3 (13)	78.9, 92.5, 92.9	79.1 ± 5.4 (12)	0.091

¹ Tuberosity / head index = (tuberosity length x tuberosity breadth x head-neck length)^{1/3} / head AP diameter (x 100).

saire 1 specimen. All of the earlier Upper Paleolithic ones are anteromedial to some degree (Table 14); the Qafzeh-Skhul sample is intermediate. The position of the Mladeč 25a tuberosity is not diagnostic of one group or the other, even though it is found more frequently among the early modern humans.

Both the Mladeč 25b and 26 diaphyses are tear-dropped shaped with small sulci on either side of the interosseus crest; there are no concavities elsewhere on the diaphyses. As such, they contrast with some early modern human radial diaphyses and are within the range of overlap between Neandertal and early modern humans in radial diaphyseal cross-sectional shape. There is little difference between the comparative samples in relative anteroposterior versus mediolateral midshaft proportions (except for a couple of high values in the Qafzeh-Skhul sample), and the two Mladeč radial diaphyses fall comfortably within the distributions (Table 14).

The Mladeč 31 metacarpal bone

Preservation and age-at-death

The Mladeč 31 metacarpal bone presents most of a right immature third metacarpal (chap. 8, Plate XVI). The shaft is complete, the base is largely covered with carbonate crust and sustained abrasion to the palmar surface and the styloid process, and the distal metaphysis is preserved dorsally and

palmar-ulnarly. The maximum preserved length is 69.1 mm. The complete absence of head epiphysis fusion indicates an age-at-death less than 14 to 16 years (Scheuer and Black, 2000).

Morphology

The diaphysis presents very weakly marked lines for the dorsal interosseus muscles. They are gentle angles proximally and become flat distally. The extent of the projection of the styloid process is unknown, but the capitate facet curves clearly up onto the base of the styloid process, suggesting that it was projecting beyond the plane of the capitate facet. The capitate facet is turned about 10° ulnarly relative to the perpendicular to the diaphyseal axis. The adjacent metacarpal facets are partially obscured by matrix. However, the metacarpal 2 facet is large and dorsopalmarly concave. Palmarly it is 7.0 mm proximodistally, and dorsally it is ca. 5.0 mm proximodistally. Ulnarly, there are two facets for the metacarpal 4, one dorsal and one palmar with a clear sulcus between them.

Base and midshaft dimensions are provided in Tables 12 and 15. Articular length (mid capitate surface to the most distal point on the head) was estimated using a least squares regression based on recent human mature third metacarpals from the preserved length (65 mm) from the mid-capitate facet to the dorsal epiphyseal margin ($\text{ArtLen} = 1.15 \times \text{PresLen} - 0.75$; $r^2 = 0.952$, $N = 34$). The resultant value is 74.0 mm. On the basis of this, a robusticity index (geometric mean of the midshaft diameters/articular length) was computed as 11.3 for Mladeč 31. This value is relatively low compared to other Late Pleistocene sample values, which do not differ significantly between them (Kruskal-Wallis $P = 0.135$) (Table 16). Among the earlier Upper Paleolithic specimens, it is approached only by the value of 11.5 for the female Dolní Věstonice 3. The modest value for Mladeč 31 may be influenced by its relatively long articular length, which is 3.3 standard deviations from the Neandertal mean but only 1.5 standard deviations from the earlier Upper Paleolithic mean length. However, the similarly long Barma Grande 2 third metacarpals (75.4 mm) have an average robusticity index of 13.9, suggesting that either Mladeč 31 is simply gracile or the immature status of the bone is affecting its degree of diaphyseal hypertrophy.

Table 15. Osteometric measurements of the Mladeč 31 metacarpal 3 (in mm and degrees)

Proximal dorsal articular breadth	12.7
Proximal palmar articular breadth	8.4
Horizontal base angle (ulnar deviation)	80°
Midshaft height	8.1
Midshaft breadth	8.6

Table 16. Osteometric comparisons for the Mladeč 31 and 90 third metacarpals. Mean and standard deviation (N) are provided for samples greater than five; individual values provided for smaller samples. Robusticity index = (geometric mean of midshaft diameters / articular length) x 100

	Articular length (mm)	Robusticity index
Mladeč 31	74.0	11.3
Mladeč 90	77.8	12.8
Neandertals	61.9 ± 3.7 (6)	13.3 ± 1.0 (6)
Qafzeh-Skhul	63.1, 65.6	13.7, 16.7
Earlier Upper Paleolithic	67.0 ± 4.7 (8)	13.0 ± 0.9 (7)

The Mladeč 88 to 91 hand remains

Preservation

Since they derive from Chamber E, rather than Chamber D, and may therefore not be associated with, or the same age as, the other Mladeč postcranial remains, the Mladeč 88 to 91 hand bone (see chap. 8, Plate XVIII) are described here, separately from the Mladeč 31 metacarpal bone. Measurements are in Table 17.

Mladeč 90 is a right metacarpal 3, which is complete except for the radial half of the head and the adjoining shaft. Its preserved length equals its anatomical maximum length of 81.9 mm. The articular surfaces are normal, and there is no evidence of abnormalities. The Mladeč 91 metacarpal bone is from the right fourth ray. Both articular ends and the associated metaphyseal areas are missing, and thus it cannot be determined if this is an adult specimen. However, the flares for both epiphyses and the complete diaphysis are present. The total preserved length is 44.5 mm.

The Mladeč 88 phalanx is a partial proximal hand phalanx, which lacks part of the distal shaft and all of the head. Other damage includes postmortem chipping on the marginal ridges, damage to the dorsal left base, and slight damage to the dorsal right surface adjacent to the metacarpal facet. Total length of the preserved specimen is 45 mm. It probably derives from the second ray, based on the relatively broad expansion of the base for the interosseus muscles. Given the greater expansion of the base on the right side (presumably for the first dorsal interosseus muscle), the specimen is probably left.

The Mladeč 89 proximal hand phalanx is complete except for some minor postmortem chipping along the well-developed palmar marginal ridges and slightly more damage on the dorsal aspect of the proximal articular rim. There are no abnormalities. Preserved maximum length is 49 mm. The specimen is most likely from the third digit, given the largely, but not entirely, symmetrical development of the radial and ulnar proximal tubercles and its relatively broad shaft. The moderately greater right basal tubercle suggests that it is left.

The Mladeč 88, 89 and 90 bones are generally similar in relative overall size and musculoligamentous markings, and they may derive from the same individual. The Mladeč 91 metacarpal 4 is smaller and more gracile and therefore probably represents a second individual. An assessment of the possible association of the first three hand bones can be made by comparing the lengths

Table 17. Osteometric measurements of the Mladeč 88 to 91 metacarpals and proximal phalanges (in mm). Estimated values are in parentheses

	Mladeč 90 Metacarpal 3	Mladeč 91 Metacarpal 4	Mladeč 88 Proximal Phalanx 2	Mladeč 89 Proximal Phalanx 3
Articular length	77.8	–	–	47.5
Midshaft height	10.5	7.8	8.8	8.1
Midshaft breadth	9.4	7.3	10.9	10.0
Proximal max. height	19.6	–	14.1	(13.0)
Proximal max. breadth	15.9	–	18.2	16.9
Proximal artic. height	–	–	12.0	11.2
Proximal artic. breadth	15.9	–	14.5	13.4
Styloid projection	4.1	–	–	–
Distal height	16.4	–	–	9.1
Distal maximum breadth	–	–	–	13.0
Distal articular breadth	–	–	–	12.0

of the Mladeč 89 and 90 third ray proximal phalanx and metacarpal. The resultant index is 61.1; this value is low for a recent European sample (68.1 ± 2.3 , $N = 38$), being 3.04 standard deviations from the recent human mean. Yet, it is only close to the lower limit of a European Gravettian sample (65.8 ± 3.6 , $N = 11$); it is 1.31 standard deviations below that mean, matched by the value of 61.0 for Dolní Věstonice 13, and above the index of 59.6 for Paglicci 25. A small Neandertal sample has similar values (66.0 ± 2.6 , $N = 5$), and the Qafzeh 9 index (71.6) is near the top of the Late Pleistocene range. It may be that the Mladeč remains, like Neandertals (Villemeur, 1994) and apparently also earlier Upper Paleolithic humans, have more abbreviated ulnar proximal phalanges than at least recent Europeans. Consequently, the combination of Mladeč 89 and 90 based on their lengths would be moderately unusual for a recent human, but well within the ranges of variation of Late Pleistocene humans. The hypothesis that these three bones represent one individual is thus not rejected.

Morphology

As with the Mladeč 31 metacarpal, the Mladeč 90 bone is long. Its articular length of 77.8 mm is 2.3 standard deviations above an earlier Upper Paleolithic mean (Table 16) and 4.3 standard deviations from a Neandertal mean. It is therefore slightly longer than those of Mladeč 31 and even Barma Grande 2. Its diaphysis has a relatively smooth dorsal surface, but the palmar crest is strongly marked. A robusticity index, between the geometric mean of the midshaft diameters and the articular length, is 12.8, which is very close to the earlier Upper Paleolithic mean and within one standard deviation of a Neandertal sample. Therefore, despite its length, it is not particularly gracile.

Proximally, Mladeč 90 has a minimally transversely concave capitate facet and a moderately projecting styloid process. The ratio of its styloid projection from the mid-carpal surface (4.1 mm) to its articular length of 77.8 mm is 5.27. This index is similar to the values of a Neandertal sample (4.94 ± 1.83 , $N = 8$) and well within the range of variation of a small earlier Upper Paleolithic sample (4.09 ± 1.22 , $N = 5$); the Qafzeh specimens have very small styloid processes (Qafzeh 9: 1.49 mm). Neandertal third metacarpals have relatively small styloid processes compared to recent humans (recent Euroamericans: 7.76 ± 1.71 mm, $N = 30$; see Niewoehner et al., 1997); it is apparent from these comparisons that early modern humans share this archaic pattern. Mladeč 90 is similar to both of these Late Pleistocene samples.

The Mladeč 91 fourth metacarpal retains essentially only its diaphysis, which has weakly developed dorsal interosseus crests and a sharp palmar crest. There is little else of note on it.

The Mladeč 88 and 89 proximal hand phalanges are notable for the degree of hypertrophy of the palmar crests for the flexor tendon sheaths. They are prominent on both bones, but especially on the Mladeč 88 proximal phalanx 2. Both of their bases turn slightly palmarly, and the head of Mladeč 89 is deviated slightly radially (assuming that it is left). The completeness of the Mladeč 89 phalanx permits a robusticity index (geometric mean of the midshaft diameters/articular length) comparison. The value is 18.9 for Mladeč 89, which is close to those of Qafzeh 3 and 9 (19.2 and 19.6) and an earlier Upper Paleolithic mean (19.4 ± 1.3 , $N = 7$). It is, however, 2.13 standard deviations below the mean of a Neandertal sample (22.1 ± 1.5 , $N = 9$) and below the range of that sample. Given the similarities of third ray proximal phalanx to metacarpal length proportions across these samples, this suggests a decrease in phalangeal robusticity between these late archaic and early modern human samples (Kruskal-Wallis P -value without Mladeč 89 = 0.002; $P = 0.001$ with Mladeč 89 in the earlier Upper Paleolithic sample).

The Mladeč 21 and 22 pelvic remains

Preservation, age and sex

The Mladeč 21 and 22 pelvic remains consist of two partial os coxae (innominate bones). Mladeč 21 is a mature partial left ilium and ischium, and Mladeč 22 is an immature partial right ischium. They derive from two individuals, based on size, morphology and developmental status.

Mladeč 21 is a partially preserved adult left os coxae (chap. 8, Plate XII). It retains the posterior half of the acetabulum, including most of the lunate articular surface (except for the anterosuperior portion) and the acetabular notch. The proximal portion of the ischial body and tuberosity, the greater sciatic notch, and the sacroiliac surface are present and undistorted.

The acetabulum is broken away superiorly and anteriorly, and the adjacent iliopectineal line and the entire pubis are missing. An ischial segment extends from the inferior rim of the acetabulum for about 40 mm and includes a 29.5 mm segment of ischial tuberosity. The superior and posterolateral borders of the ischial tuberosity are the only ones remaining. A segment of the obturator foramen rim is preserved from the inferior extent of the acetabular rim to the most superior extent of the root of the ischiopubic ramus. The posterior surface of the ischium is not preserved, except for the inferior base of the ischial spine. The lesser sciatic notch is not preserved; however, a wide greater sciatic notch is present and the medial (internal) aspect of the ilium preserves the arcuate buttress and line extending toward the sacroiliac articular surface. Inferior to the sacroiliac articular surface lies a deep and wide preauricular sulcus. The edges of the preauricular sulcus and the entire sacroiliac articular surface are obscured by the encrusting matrix, which adheres to most of this specimen. The posterior inferior iliac spine and the base of the iliac tubercle are present, but the posterior superior iliac spine and all of the iliac crest are missing in addition to the entire ilium anterosuperior of the level of the arcuate line and sacroiliac articular surface.

Although nothing remains of the iliac crest, it is apparent that Mladeč 21 had attained an adult skeletal age. No traces of epiphyseal lines occur in the acetabulum, indicating that the primary elements of the os coxae are completely fused, and the ischial tuberosity is fused to the body of the ischium. According to recent human standards, fusion of the ischial tuberosity occurs approximately between 19 and 20 years of age (Johnston and Zimmer, 1989; Scheuer and Black, 2000). Therefore, it is unlikely that the age of Mladeč 21 is younger than this.

Two features strongly suggest that Mladeč 21 is a female based on the sexually dimorphic characteristics of modern human pelves (Brůžek, 2002). First, the greater sciatic notch of Mladeč 21 is wide and open (e.g., the distance from the posterior inferior iliac spine to the ischial spine is relatively great) and, second, there is a wide, deep preauricular sulcus. The first is documented by measurements (Table 18), in which the subtense from the chord between the posterior inferior iliac spine and the dorsal ischium is only 25.5% of that chord, and the point of the maximum subtense is 72.3% of the distance from the posterior inferior iliac spine to the ischium. The precise form of the Mladeč 21 preauricular sulcus is obscured by encrustations, but it appears to be relatively shallow superiorly and then becomes a deeper groove that rounds inferiorly adjacent to the posterior inferior iliac spine. Its form may occur in males or females as a result of tension on the sacroiliac ligaments (a paraglenoid sulcus), but the depth of the sulcus suggests the bony resorption through pregnancy that is diagnostic of its being female. However, the degree of openness of the greater sciatic notch would be very unusual in a male pelvis.

Mladeč 22 is a right os coxae preserving a mostly complete acetabulum, most of the ischial body, and an anteroinferior segment of the ilium. The acetabulum is complete except for the anterosuperior-most segment of the lunate articular surface and the anterior-most margin of the acetabular notch. The rim of the acetabulum is well preserved except for its posterosuperior margin, which is

abraded. The specimen is broken anterior to the acetabulum, and nothing remains of the iliopubic eminence, the pubic body and symphysis, or the ischiopubic ramus.

Inferior to the acetabulum, the ischial body is nearly complete and lacks only a small postero-medial portion including the tip of the ischial spine, although the lesser sciatic notch is visible just below it. The ischial tuberosity metaphysis is well preserved with only slight surface abrasion to the rims, but none of the epiphysis remains. The posterior surface of the obturator foramen rim and the root of the ischiopubic ramus are present.

Superior to the acetabulum, a small portion of the ilium is present including the anterior inferior iliac spine. The ilium extends cranially from the superior rim of the acetabulum for 55 mm. A well-developed iliopsoas groove separates the anterior inferior iliac spine from the arcuate buttress on the medial surface of the bone. The preserved segment of arcuate buttress and line is 44 mm long. Posterior to the preserved segment of arcuate buttress and line and superior to the anterior inferior iliac spine, nothing remains of the ilium.

The subadult age of Mladeč 22 is apparent in its epiphyseal union status. The ilium, ischium and pubis have undergone complete fusion, and there are no signs of epiphyseal lines in the acetabulum. The ridges and furrows present on the Mladeč 22 ischium indicate that the ischial tuberosity epiphysis had not united with the ischial body. According to recent human standards (Johnston and Zimmer, 1989), the age of Mladeč 22 would be between 13 to 15 (based on the fused primary elements of the os coxae) and 19 to 20 years of age (based on the unfused ischial tuberosity epiphysis). Unlike Mladeč 21, there are no morphological indicators of sex preserved on the Mladeč 22 specimen. However, the large size of the acetabulum, ischial body and anterior inferior iliac spine strongly suggest that this specimen is male.

Morphology

Despite the series of measurements that are possible on the Mladeč 21 and 22 os coxae (Table 18), there is little Late Pleistocene comparative data available for these measurements. Moreover, the partially encrusted state of the bones obscures many of the finer surface details.

Overall size is best indicated by the acetabular heights of these two specimens. To provide a comparative sample, acetabular height was measured (or taken from the literature) for thirteen earlier Upper Paleolithic specimens, three Qafzeh-Skhul specimens, and four Neandertals. To maximize the sample size, acetabular height was predicted for an additional fourteen earlier Upper Paleolithic specimens, two Qafzeh-Skhul individuals, and five Neandertals from their sagittal femoral head diameters. This was done using a least squares regression based on the pooled Late Pleistocene sample of associated femoral heads and acetabulae ($\text{AcetHt} = 1.30 \times \text{FemHd} - 6.5$, $r^2 = 0.932$, $N = 13$). The resultant samples (Table 19) provide a modest difference across the three pooled-sex comparative samples (ANOVA $P = 0.079$), which is in agreement with the slightly higher predicted body masses for the Neandertals (Ruff et al., 1997).

The articular height of Mladeč 21 (ca. 53 mm) falls very close to the pooled sex means of the two early modern human samples, being slightly below them. It is slightly above the mean for the earlier Upper Paleolithic female sample, and at the top of the very small Middle Paleolithic female range, being matched by La Ferrassie 2. However, it is exceeded by the predicted values (55.4 mm each) for the Předmostí 4 and 10 Gravettian female remains.

The higher value of 59.8 mm for Mladeč 22 is slightly above all of the male comparative means for acetabular height, but it is within one standard deviation of the Neandertal and earlier Upper Paleolithic mean values and is only relatively high compared to the Qafzeh-Skhul sample. Among earlier Upper Paleolithic males, it is matched by the value predicted for Sungir 1 (59.9 mm) and exceeded by the predicted value of Barma Grande 2 (61.8 mm) and the measured diameter of Fanciulli 4 (65.3 mm). Moreover, the Neandertal and earlier Upper Paleolithic male means are not significantly

Table 18. Osteometric dimensions of the Mladeč 21 left os coxae and the Mladeč 22 right os coxae (in mm). Values in parentheses are estimated

	Mladeč 21	Mladeč 22
Acetabulum height (articular)	(53.0)	59.8
Acetabulum height (capsule)	–	61.0
Acetabulum depth (articular)	–	27.5
Acetabulum depth (capsule)	–	30.5
Lunate surface superior minimum diameter	–	28.0
Lunate surface lateral minimum diameter	20.0	22.9
Lunate surface lateral maximum diameter	(23.0)	–
Lunate surface inferior minimum diameter	22.0	22.7
Lunate surface inferior maximum diameter	23.2	26.1
Acetabulum center to closest point on auricular surface	(70.0)	–
Acetabulum center to tip of anterior inferior iliac spine	–	62.6
Minimum inferior iliac thickness	22.2	–
Iliac arcuate line chord ¹	56.6	–
Iliac arcuate line subtense	9.1	–
Greater sciatic notch: dorsal ischium to post. inf. iliac spine	47.0	–
Greater sciatic notch: superior notch to post. inf. iliac spine	34.0	–
Greater sciatic notch: notch chord to superior notch	12.0	–
Acetabulum center to ischial tuberosity angle	(65.5)	77.0
Acetabulum center to ischial tuberosity center	–	63.0
Acetabular rim to closest point on ischial tuberosity	10.5	14.7
Ischial tuberosity breadth	(28.0)	(29.3)
Ischial spine to posterior inferior iliac spine	(71.0)	–
Acetabulosciatic breadth	34.5	36.0
Auricular surface breadth	(53.0)	–
Maximum preserved dimension	199.0	160.3

¹ Chord distance and maximum subtense along the iliac arcuate line from the anterior auricular surface to the point opposite the anterior inferior iliac spine (Ruff, 1995).

Table 19. Comparative acetabular height measurements. Mean and standard deviation (N) for samples greater than four; individual measurements for smaller samples

	Pooled sex	Male	Female
Neandertals	58.6 ± 3.5 (9)	59.3 ± 2.9 (8)	53.0
Qafzeh-Skhul	54.7 ± 2.4 (5)	54.1, 55.3, 56.3, 57.2	50.8
Earlier Upper Paleolithic	54.8 ± 4.7 (27)	57.8 ± 3.2 (15)	51.5 ± 3.4 (10)

Male earlier Upper Paleolithic versus Neandertal P = 0.279

different (t-test P = 0.279). However, the acetabular height for Mladeč 22 would be unusual for a Late Pleistocene female, since it is 2.44 standard deviations from the earlier Upper Paleolithic female mean; this supports its diagnosis as male.

Consequently, even though the acetabular heights of Mladeč 21 and 22 are moderately large, they are by no means unusual for either a Neandertal or an earlier Upper Paleolithic individual

of the same sex. These acetabular dimensions, contra Wolpoff (1989), do not serve to align the Mladeč 21 and 22 with either the late archaic or the early modern human Late Pleistocene European samples.

The *M. obturator internus* sulcus is not preserved on Mladeč 21, but the ischial tuberosity is strongly rotated ventrally. The Mladeč 22 *M. obturator internus* groove is not evident, but the ischial spine is at the same vertical level as the superior margin of the superior ischial tuberosity metaphysis. Its ischial tuberosity is also strongly rotated ventrally.

The Mladeč 22 anterior inferior iliac spine is prominent and vertically straight, with only a slight internal concavity. The adjacent area of the acetabular rim for the insertion of the reflected head of *M. rectus femoris* is crushed and provides no evidence of its original configuration.

The break of the Mladeč 22 right ilium exposes the base of the iliac pillar (or acetabulocrystal buttress), which has a total internal-external thickness of 14.1 mm and internal and external cortical thicknesses of 2.3 mm and 3.8 mm, respectively. These values are very close to the mean values for a recent European sample (2.4 ± 0.5 mm and 3.9 ± 0.6 mm, respectively, $N = 23$) provided by Stringer (1986). Comparative Late Pleistocene data are unavailable, but radiographic observations and inspection of fossilization breaks of both Neandertal and earlier Upper Paleolithic ilia indicate that they generally have iliac cortical thicknesses similar to those of recent humans.

On the dorsal surface of the posterior Mladeč 21 ilium, there is a tubercle opposite the auricular surface, which extends as a raised crest to the area of the iliac tuberosity.

The Mladeč 27 and 28 femora

Preservation and maturity

Mladeč 27 is a well preserved right femoral diaphysis (chap. 8, Plate XV). Proximally, the distal base of the lesser trochanter is observable, but the head, neck, greater trochanter, intertrochanteric region and lesser trochanter are absent. Much of the popliteal surface is visible at the distal metaphysis, but nothing remains of the condyles, epicondyles or patellar articular surface. The most distal extent is posterolateral, just proximal of the capsular attachment above the dorsal lateral condyle. The entire length of the diaphysis is complete and in excellent condition, but much of the bone is covered by matrix that is quite thick and, in some areas, globular in form. Despite this encrustation, all of the major muscle attachment sites are visible, and the original subperiosteal contour can be discerned without difficulty. There are no rejoined breaks in the bone and no evidence of distortion. There are no indications as to the maturity of the specimen, since all epiphyses/metaphyses are absent, but the size and general morphology of the diaphysis (see below) suggest minimally a late adolescent age and probably a fully mature status.

The Mladeč 28 femur is less complete but less encrusted (chap. 8, Plate XIV). The specimen consists of a 198 mm long proximal segment of an adult left femur. Unlike the other fossil remains in the Mladeč sample, no matrix adheres to this specimen. The head is absent, as are most of the anterior, superior and posterior aspects of the medial femoral neck. The inferior contour of the lateral neck is preserved and extends uninterrupted into the medial surface of the proximal shaft. Superiorly, a short (ca. 10 mm) portion of the lateral neck is preserved along with the adjacent greater trochanter and trochanteric fossa. The greater trochanter, however, is not completely preserved, since much of the lateral and posterior surfaces are broken away.

The intertrochanteric crest is missing and only the base of the lesser trochanter is preserved. This leaves a band of exposed trabecular bone extending superiorly and laterally from the lesser trochanter to the anterosuperior margin of the lateral greater trochanter and continuing medially

across the anterior surface of the bone to the femoral neck. There is slight loss of cortical bone on the third trochanter, and the diaphysis is preserved for 102 mm below the distal base of the lesser trochanter.

The distal break is within the proximal half of the diaphysis, clearly proximal of midshaft. The specimen therefore does not provide midshaft measurements, and those provided by Szombathy (1925) are inaccurate. The cortical bone and medullary canal are visible at the distal fracture, which is flat and horizontally disposed anteriorly, thus forming a right angle with the anterior surface of the diaphysis. The fracture is somewhat more irregular posteriorly and exhibits a slight posteroinferior level.

The full maturity of Mladeč 28 is indicated by the complete obliteration of the epiphyseal fusion lines for the trochanteric epiphyses.

Femoral length estimation

The Mladeč 27 femur is sufficiently complete to provide a reasonable estimate of its original biomechanical and interarticular lengths (see notes to Table 20). The distance between the distal margin of the lesser trochanter and the posterolateral supracondylar margin is 322 mm. This value may slightly

Table 20. Osteometric dimensions of the Mladeč 27 right femur, Mladeč 28 left femur and Mladeč 102 immature left femur (in mm)

	Mladeč 27	Mladeč 28	Mladeč 102
Maximum length (M-1) ¹	485.7	-	-
Bicondylar length (M-2) ²	483.3	-	-
Biomechanical length ³	454.7	-	-
Proximal sagittal diameter (M-10)	25.5	23.5	12.6
Proximal transverse diameter (M-9)	30.0	33.8	15.4
Proximal circumference	89.0	89.0	-
Midshaft sagittal diameter (M-6)	28.3	-	(13.4) ⁴
Midshaft transverse diameter (M-7)	24.0	-	(14.0) ⁴
Midshaft circumference (M-8)	83.0	-	-
Gluteal tuberosity breadth	8.0	12.5	-
Hypotrochanteric fossa	absent	absent	-
Third trochanter	-	present	-
Anterior curvature chord	301.0	-	-
Anterior curvature subtense	12.0	-	-
Anterior curvature position (to proximal)	123.0	-	-
Maximum preserved length	338.0	198.0	53.0

¹ Maximum length estimated from the bicondylar length using a least squares regression based on recent humans ($\text{MaxLen} = 0.98 \times \text{BicLen} + 9.9$, $r^2 = 0.996$, $N = 50$).

² Bicondylar length estimated from the biomechanical length using a least squares regression based on earlier Upper Paleolithic humans ($\text{BicLen} = 1.02 \times \text{BiomLen} + 21.0$, $r^2 = 0.992$, $N = 13$).

³ Biomechanical length (average distance parallel to the diaphyseal axis between each distal condyle and the proximal neck just medial of the greater trochanter) estimated from the distance between the distal lesser trochanter and the lateral supracondylar margin ($\text{BiomLen} = 1.23 \times \text{PresLen} + 57.3$, $r^2 = 0.945$, $N = 50$), $\text{SEest} = 1.2$ mm.

⁴ The Mladeč 102 "midshaft" diameters may be taken slightly proximal of midshaft. This is unlikely to greatly affect the values, given the near circularity of immature femora and the absence of a pilaster. Contrary to previous assessments, the Mladeč 28 femur is not sufficiently preserved toward midshaft to provide reliable midshaft diameters.

underestimate the length of the bone, since the distal landmark may be 1–2 mm from the actual supracondylar margin; any such underestimation is minimal, and it is conservative in the comparisons below, since it will tend to accentuate, trivially, the perceived robusticity of the diaphysis. This value was used to estimate biomechanical length using a least squares regression based on recent human femora, from which bicondylar and maximum length were then estimated (see Table 20).

The length of the Mladeč 28 femur cannot be reliably estimated for more than general size comparisons. However, it is possible to locate the 80% diaphyseal cross section morphologically near the middle of the proximal posterolateral gluteal buttress. This position is 87 mm distal of the proximal end of the biomechanical length (on the superior neck just medial of the greater trochanter), which provides a very approximate biomechanical length of 435 mm (and a bicondylar length of 465 mm). Note that placing the 80% section 5 mm more distal would increase the estimated biomechanical length to 460 mm (and the bicondylar length to 490 mm). The differences in these length estimates have little effect on the positions and the biomechanical implications of the 80% and 65% diaphyseal cross sections compared below, but they are sufficient to provide a general indication of the original length of the Mladeč 28 femur; it was probably close to that of Mladeč 27.

Length comparisons

The estimated bicondylar length of Mladeč 27 of ca. 483 mm places it well above the female values for all three of the comparative samples, and it is 2.33 standard deviations above the mean of the earlier Upper Paleolithic female mean (Table 21). However, it falls well within the male ranges of variation of both the earlier Upper Paleolithic and the Qafzeh-Skhul samples. It remains just over two standard deviations (2.04) from the Neandertal male mean; it is approximately the same as the high outlier in femoral length among the Neandertals, Amud 1. The roughly estimated values for the original length of the Mladeč 28 femur would make it either a reasonably average early modern human male in size or a relatively large female.

Table 21. Comparisons of femoral bicondylar lengths. Mean and standard deviation (N) for samples greater than four; individual measurements for smaller samples

	Pooled sex	Males	Females
Neandertals	436.8 ± 26.1 (12)	445.0 ± 18.8 (10)	384.0, 407.0
Qafzeh-Skhul	474.0 ± 29.9 (7)	475.0, 486.0, 490.0, 515.0	417.8, 464.8, 469.5
Earlier Upper Paleolithic	456.7 ± 33.6 (25)	478.6 ± 21.1 (13)	428.3 ± 23.6 (10)

Body mass estimation for Mladeč 27

The appropriate scaling of weight-bearing limbs for assessments of diaphyseal robusticity and muscle hypertrophy requires an estimation of body mass for each specimen, since the baseline load on the diaphysis or muscle is body mass times the beam length around which the load is operating. For this reason, measures of cortical area, which reflect resistance to axial loading, should be compared to body mass, and measures of muscle hypertrophy or diaphyseal bending strength should be compared to body mass times bone length (Ruff et al., 1993; Trinkaus and Ruff, 2000).

Such considerations of the effects of body mass are especially important for comparisons across samples which vary in body proportions, as did the Neandertals and early modern humans of the northwestern Old World (Trinkaus, 1981; Ruff, 1994; Holliday, 1997; 2000). In cases in which there is significant variation in body shape and relative limb length, comparisons using only bone length

will overestimate hypertrophy for stockier individuals and underestimate skeletal hypertrophy for linear individuals. In fact, although earlier analyses using only bone length for size standardization “documented” a significant reduction in femoral robusticity with the emergence of modern humans (e.g., Twisselmann, 1961; Trinkaus, 1976), assessments combining the effects of differential body mass to lower limb bone length proportions (e.g., Ruff et al., 1993; Trinkaus and Ruff, 1999a, b; Trinkaus et al., 1999b; Trinkaus and Rhoads, 1999; see Trinkaus, 2000; Ruff et al., 2000) have shown that there was little change in femoral (or tibial) diaphyseal, muscular or articular hypertrophy through the Late Pleistocene.

Body mass for the comparative samples was estimated following Ruff et al. (1997) in which body mass was predicted from recent human samples using estimated stature and bi-iliac breadth. Stature was estimated using ecogeographically appropriate, and sex-specific when known, formulae from Trotter and Gleser (1952); male and female estimates were averaged for individuals of unknown sex. Bi-iliac breadth was measured when available (see Holliday, 1995). Otherwise, it was estimated from either a pooled-sex sample from the same group when available (for the earlier Upper Paleolithic sample) or from the most complete specimen providing limb length and bi-iliac breadth (Kebara 2 for the Neandertals and Skhul 4 for the Qafzeh-Skhul sample).

To provide a body mass estimate for Mladeč 27, whose body proportions are unknown and whose inferred body proportions could provide information on its morphological affinities (Holliday, 1997), it was modeled as an average Neandertal, Qafzeh-Skhul individual and earlier Upper Paleolithic individual. The resultant values for body mass are 69.4 kg for the earlier Upper Paleolithic model, 69.7 kg for the Qafzeh-Skhul one, and 83.5 kg for the Neandertal one. Since the Qafzeh-Skhul model provides almost the same value as the earlier Upper Paleolithic one, it was not included in the comparisons. Consequently, in the comparisons of femoral properties of Mladeč 27 that involve body mass estimation, two data points are provided, one for it with stocky Neandertal body proportions and one with it having earlier Upper Paleolithic linear body proportions.

Morphology

A portion of the Mladeč 28 anterolateral greater trochanteric region is preserved, and the *M. gluteus minimus* insertion is moderately rugose. The medial aspect of the greater trochanter exhibits a well-developed trochanteric fossa for the insertion of *M. obturator externus* and *internus*. The anterior surface of the proximal shaft is smoothly concave.

On the posterolateral surface of Mladeč 28, lateral to the preserved base of the lesser trochanter, there is a well-developed and distinct gluteal tuberosity, for the insertion of *M. gluteus maximus*. At the superior extent of the gluteal tuberosity, there is an oval protuberance of bone, a well-developed third trochanter (*sensu* Hrdlička, 1937), which marks the superior extent of the gluteal tuberosity. From the third trochanter, a gluteal ridge extends mediolaterally for a distance of ca. 81 mm until it merges with the lateral margin of the *linea aspera*. The gluteal tuberosity is broad (see below) but not at all rugose, in contrast to those seen on most Neandertal femora and the Cro-Magnon ones. It is bordered laterally by a prominent, but blunt, proximolateral gluteal buttress, or flange. There is a clear sulcus between the gluteal tuberosity and the full lateral extent of the gluteal buttress, and the buttress is separated from the anterior diaphyseal convexity by a broad and shallow sulcus. The pectineal area is smooth, and there is a faint spiral line anteriorly, that is evident only adjacent to the lesser trochanter.

The Mladeč 27 proximolateral femoral diaphysis exhibits far less development of the gluteal buttress and a more modest gluteal tuberosity. There is no anterior sulcus between the buttress and the anterior diaphysis, and the posterior one is modest. Its gluteal tuberosity is partially ob-

scured by matrix, but it is clearly modest in size (see below) and rugosity. There is a clear pectineal crest and a faint but apparent spiral line. These two femora from Mladeč contrast strongly in their subtrochanteric configurations, in terms of both diaphyseal cross-sectional shape (reflecting in large part the relative development of the gluteal buttress) and gluteal tuberosity size.

The relative development of the gluteal buttress is reflected in the cross-sectional diaphyseal proportions at the subtrochanteric (or mERIC) level (Table 20). In the comparison of the external diaphyseal diameters [through the mERIC index (Tables 20 and 24) and graphically (Fig. 8)], there is a general pattern in which the earlier Upper Paleolithic specimens have proportionately greater mediolateral diameters than most of the Neandertals, and the Qafzeh-Skhul specimens fall generally with the rounder diaphyses of the Neandertals (the high outlier is Skhul 5). In this comparison, the measurements are normally taken such that the “mediolateral diameter” is the maximum external diameter of the cross section across the gluteal buttress; as a result of the variable but ubiquitous anteversion (or torsion) of the femoral head and neck of these femora (Twiesselmann, 1961; Sládek et al., 2000), the “mediolateral diameter” is actually slightly anteromedial to posterolateral on most specimens. The “anteroposterior diameter” is then taken perpendicular to the mediolateral one.

The proportions of the subtrochanteric region were also compared using second moments of area at the 80% level (Tables 22 and 23; Fig. 8). However, it is not appropriate to simply compare maximum versus minimum diameters at this level, since there are several Neandertal and early modern human femora in which the maximum second moment of area is oriented largely anteroposteriorly, whereas in most of the earlier Upper Paleolithic femora the maximum second moment of area is predominantly mediolateral (similar to the maximum external diameter). Consequently, even though they do not take into account the effects of anteversion on the proximal femoral diaphysis, anteroposterior and mediolateral second moments of area (oriented with respect to the midshaft and distal femur) are compared in Fig. 8. The resultant distribution provides less separation of the reference samples, although all of the Neandertals and all of the Qafzeh-Skhul specimens except Qafzeh 8 are along the upper (rounder with less of a gluteal buttress) half of the earlier Upper Paleolithic distribution. Mladeč 27 falls in at the edge of the Neandertal distribution and close to the early Upper Paleolithic mean (Table 25). Mladeč 28 is also close to the middle of the earlier Upper Paleolithic distribution, very distinct from the Neandertals and separate from most of the Qafzeh-Skhul specimens (Table 25). It is probable that, should the 80% second moment of area be oriented with respect to the anteversion angles of these femora, which is possible for neither the Mladeč femora nor many of the other Late Pleistocene femora given damage to their necks, that a greater separation of the Middle and Upper Paleolithic samples, and of Mladeč 27 and 28, similar to that seen in the external diameters, would be evident.

Table 22. Cross-sectional geometric properties of the Mladeč 27 femur. Areas in mm², second moments of area in mm⁴. 0% is distal

	20%	35%	50%	65%	80%
Total area (TA)	879.8	562.3	497.7	504.3	597.3
Cortical area (CA)	311.4	309.5	390.7	397.0	389.8
Medullary area (MA)	568.4	252.8	107.0	107.3	207.5
AP 2nd moment of area (I_x)	32413	25065	23588	20056	21088
ML 2nd moment of area (I_y)	40825	15758	15493	18636	29263
Max 2nd moment of area (I_{max})	41359	25077	24169	20676	29325
Min 2nd moment of area (I_{min})	31880	15746	14912	18015	21027
Polar moment of area (J)	73239	40823	39081	38692	50352

Table 23. Cross-sectional geometric properties of the Mladeč 28 and 102 femora and the Mladeč 32 metatarsal 3. Areas in mm², second moments of area in mm⁴. 0% is distal

	Mladeč 28 65%	Mladeč 28 80%	Mladeč 102 50% ¹	Mladeč 102 80%	Mladeč 32 50%
Total area (TA)	495.5	574.4	135.6	148.9	71.0
Cortical area (CA)	409.3	426.9	101.4	106.3	60.4
Medullary area (MA)	86.2	147.5	34.2	42.6	10.6
AP 2nd moment of area (I_x)	16469	21049	1375	1292	381
ML 2nd moment of area (I_y)	21937	32743	1398	2019	452
Max 2nd moment of area (I_{max})	22443	37190	1541	2021	499
Min 2nd moment of area (I_{min})	15963	16602	1232	1289	334
Polar moment of area (J)	38406	53792	2773	3310	833

¹ The midshaft cross-section of Mladeč 102 may be slightly proximal of midshaft.

Table 24. Diaphyseal indices for the Mladeč and comparative sample femora. Mean and standard deviation (N) for samples greater than four; individual measurements for smaller samples

	Meric index	Pilastric index
Mladeč 27	85.0	117.9
Mladeč 28	69.5	--
Neandertals	82.0 ± 3.3 (13)	103.3 ± 9.2 (13)
Qafzeh-Skhul	80.6, 83.8, 86.1, 103.5	124.2 ± 11.9 (8)
Earlier Upper Paleolithic	73.4 ± 5.7 (25)	116.6 ± 11.2 (23)
Kruskal-Wallis P-values	<0.001	0.001

Table 25. Mladeč 27 and 28 femoral metric comparisons using linear residuals from the reduced major axis line through the pooled comparative sample. The P-value derives from the ANOVA comparison across the three reference samples, and the Mladeč values are Z-scores [(Mladeč values – sample mean) / standard deviation]. Z-scores are provided only relative to samples > 5. I_x , I_y , I_{max} and I_{min} : anteroposterior, mediolateral, maximum and minimum second moments of area; CA and TA: cortical and total subperiosteal areas; J: polar moment of area; Z_p : polar section modulus; BMxLen.: estimated body mass times length. For the gluteal tuberosity breadth and polar section modulus comparisons, values are provided for Mladeč 27 modeled with the body proportions of an earlier Upper Paleolithic human (UP) and of a Neandertal (N). * P < 0.05 with a multiple comparison correction ($\alpha/12$)

	P-value	Neandertals		Qafzeh-Skhul		Earlier Upper Paleolithic	
		Mladeč 27	Mladeč 28	Mladeč 27	Mladeč 28	Mladeč 27	Mladeč 28
Proximal AP/ML	<0.001*	1.03	3.74	–	–	1.66	0.59
80% I_x/I_y	0.034	2.60	4.06	0.78	1.17	0.06	0.44
Gluteal Br./BMxLen.	0.060	1.41 (UP) 2.47 (N)	–	–	–	0.90 (UP) 2.32 (N)	–
Midshaft AP/ML	<0.001*	2.63	–	0.27	–	0.27	–
50% I_x/I_y	<0.001*	3.70	–	0.18	–	0.20	–
65% I_x/I_y	<0.001*	3.58	0.16	0.57	5.21	0.24	1.97
50% CA/TA	0.656	0.78	–	0.95	–	0.61	–
65% CA/TA	0.923	0.62	0.07	0.25	0.10	0.50	0.13
80% CA/TA	0.559	0.71	0.39	1.50	0.12	1.41	0.14
PseudoJ/Length	<0.001*	4.48	–	2.78	–	2.70	–
50% J/Length	<0.001*	5.10	–	2.05	–	1.97	–
50% Z_p /BMxLen	0.553	2.27 (UP) 4.03 (N)	–	1.89 (UP) 3.41 (N)	–	1.78 (UP) 3.78 (N)	–

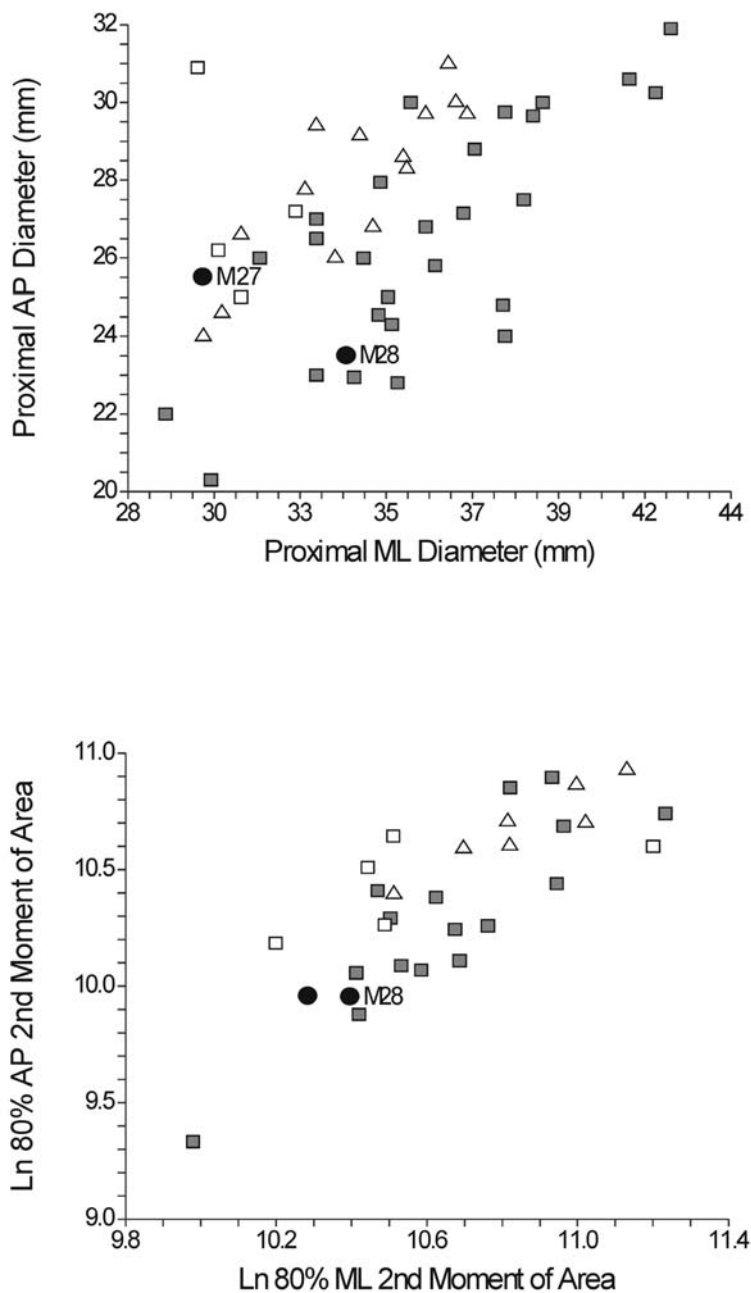


Fig. 8. Subtrochanteric femoral diaphyseal proportions. Anteroposterior versus posterior subperiosteal diameters (above) and anteroposterior versus mediolateral second moments of area (below) for Mladeč 27 and 28 (black circles – M27 and M28), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares). In the second moment of area comparison, Mladeč 27 is the value to the left

Table 26. Comparisons of femoral osteometric values. Mean and standard deviation (N) for samples greater than four; individual measurements for smaller samples

	Gluteal tuberosity breadth (mm)	Neck-shaft angle (°)	Anterior curvature subtense (mm)
Neandertals	12.9 ± 2.0 (10)	121.0° ± 4.7° (9)	15.5 ± 3.4 (6)
Qafzeh-Skhul	6.6, 8.5, 9.5, 11.4	133.2° ± 2.6° (6)	10.0, 17.0, 21.0
Earlier Upper Paleolithic	9.7 ± 2.1 (12)	121.5° ± 8.0° (16)	14.1 ± 3.1 (10)
ANOVA P-values	0.001	0.002	0.631

In the comparison of the gluteal tuberosity size, measured as the breadth of the tuberosity given difficulties in discerning the distal end of the tuberosity in many femora, the Mladeč femora are also dichotomous. There is a significant difference across the Late Pleistocene samples (Table 26; ANOVA $P = 0.001$), with the Neandertals having generally broader tuberosities. The tuberosity breadth of 12.5 mm of Mladeč 28 is at the top of the early modern human range of variation, being matched only by that of Cro-Magnon 4322/4323A, but it is in the middle of the Neandertal range of variation. In contrast, the value of 8.0 mm for Mladeč 27 is below the means of all of the samples, and only the female Dolní Věstonice 3 and Qafzeh 9 have narrower tuberosity breadths. It is not possible to scale the Mladeč 28 gluteal tuberosity breadth to body size, but this can be done for Mladeč 27. Despite the significant difference in absolute tuberosity breadths across the Late Pleistocene samples (Table 26), scaling them to body mass times femoral length (Table 25; Fig. 9) provides only a modest separation of the samples; it is principally the small individuals in both samples that have proportionately large tuberosities. The earlier Upper Paleolithic body mass for Mladeč 27 places it within the ranges of variation of Late Pleistocene humans, if in a relatively gracile position, whereas the Neandertal body mass would make it the most gracile of the known Middle or earlier Upper Paleolithic specimens and significantly different from the reference samples (Table 25).

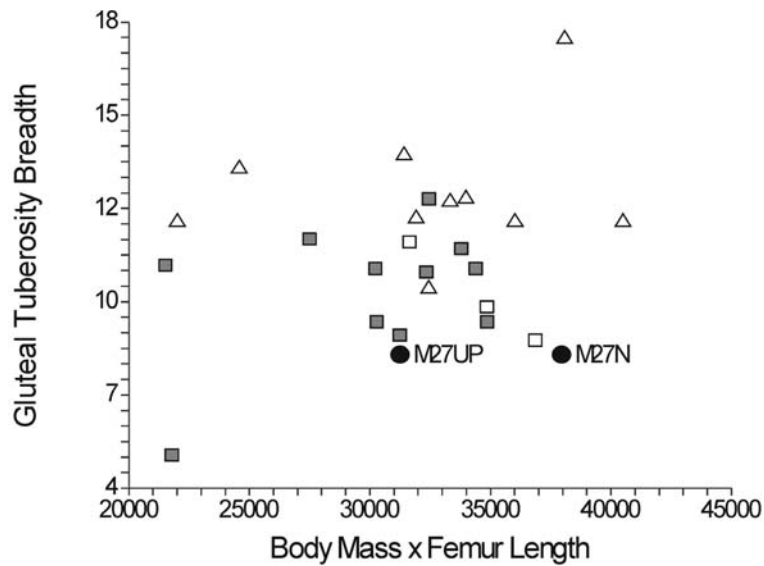


Fig. 9. Gluteal tuberosity breadth versus body mass times femoral length for Mladeč 24 (black circles), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares). The left value for Mladeč 27 (M27UP) is based on a body mass estimate using earlier Upper Paleolithic body proportions, whereas the right value for Mladeč 24 (M27N) employed a body mass estimate based on Neandertal body proportions

It is possible to estimate the neck-shaft angle of Mladeč 28 at about 123° to 125°, despite the damage to the head and neck region. This value is unexceptional for a Neandertal or an earlier Upper Paleolithic human, falling minimally above the essentially identical means for the two samples (Table 26). It is, however, well below the mean of the Qafzeh-Skhul sample, whose femoral neck-shaft angles are anomalously high for a Pleistocene human sample, being closest to those of recent urban human populations (Trinkaus, 1993; Anderson and Trinkaus, 1998). The three Late Pleistocene samples are significantly different (ANOVA $P = 0.002$), but this difference is driven entirely by the Qafzeh-Skhul sample, since the Neandertal and earlier Upper Paleolithic angles are very close (t-test $P = 0.836$).

The midshaft of Mladeč 27 is dominated by a clear pilaster and its associated *linea aspera*. The *linea aspera* has a single narrow angle, reaching a maximum breadth of 3.0 mm. Laterally along the pilaster the bone is flat, and there is no sulcus adjacent to the *linea aspera*. Medially, there is a small ridge which is ca. 6.2 mm anteromedial from the *linea aspera* at midshaft, which parallels the *linea aspera*, only to blend in with it distally. The Mladeč 28 *linea aspera*, where preserved proximally, is smooth and relatively narrow, being 3.4 mm wide by the distal break, or moderately proximal of midshaft.

The cross-sectional shape of the Mladeč 27 femur at midshaft can be quantified by both its external diameters [the pilastric index and a graph of the data (Table 24 and Fig. 10)] and using anteroposterior versus mediolateral second moments of area (Table 22; Fig. 10). In the external diameters, but especially in the second moments of area, the Neandertals and the early modern humans show little overlap and are highly significantly different (Table 25). The low earlier Upper Paleolithic values are several Gravettian specimens from Pavlov and Předmostí; the highest Neandertal value is the late Saint Césaire 1 (see Trinkaus et al., 1999a), and the slightly lower Neandertal ones are the slightly older Neandertal 1 and Rochers-de-Villeneuve 1. In both comparisons, Mladeč 27 falls clearly with the early modern humans and significantly distinct from the Neandertals.

It is not possible to compare the Mladeč 28 diaphysis to other femora using the midshaft; however, it preserves the mid-proximal diaphysis, and it is possible to estimate the position of the 65% diaphyseal cross-section (Table 23). This was done by using morphological criteria to locate the 80% (subtrochanteric section), measuring the distance from the proximal neck to the 80% section (ca. 20% of biomechanical length), and then placing the 65% section 15% of that estimated biomechanical length distal of the 80% one. Its position is unlikely to be more than a few millimeters proximal or distal of the original position. The resultant plot of the 65% anteroposterior versus mediolateral second moments of area (Fig. 11) provides a high degree of separation of the Neandertal and early modern human samples (Table 25). The one high Neandertal value is Spy 2, and the one low earlier Upper Paleolithic value is Dolní Věstonice 41, an isolated short shaft section whose location of the 65% section may be too proximal (Trinkaus et al., 2000). Therefore, even though the pilaster (when present) is not fully developed in this mid-proximal section of the femoral diaphysis, there is sufficient development of it in these early modern human femora to provide separation between the Neandertals and the early modern humans. The Mladeč 27 position is consistent with the midshaft comparisons in falling in the middle of the pilastric early modern human femora. Mladeč 28, however, is in line with the Neandertal distribution and largely separate from the earlier Upper Paleolithic sample and small errors in the location of the section could not account for its diaphyseal mechanical proportions. However, its cross-sectional shape indicates the beginning of a pilaster, in that the posteromedial and especially posterolateral diaphyseal surfaces adjacent to the *linea aspera* exhibit some degree of flattening. Moreover, it is not known how it would compare to some of the now-lost non-pilastric Gravettian Předmostí femora.

The Mladeč 27 femur is sufficiently complete to assess its anterior diaphyseal curvature. Its point of maximum curvature is located slightly proximal of midshaft, 41% of the distance from the prox-

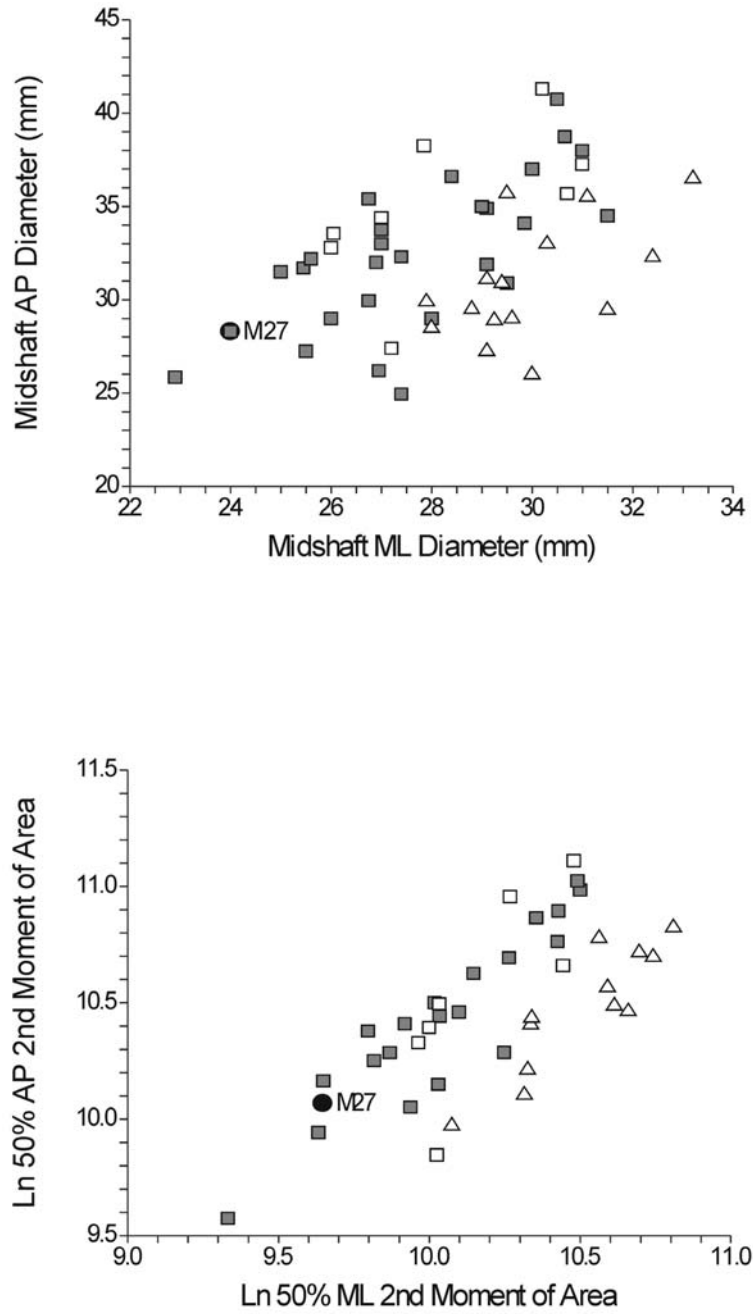


Fig. 10. Midshaft femoral proportions. Anteroposterior versus mediolateral subperiosteal diameters (above) and second moments of area (below) for Mladeč 27 (black circle – M27), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares). The value for Mladeč 27 in the subperiosteal diameter comparison is partly obscured by identical values for Willendorf 2

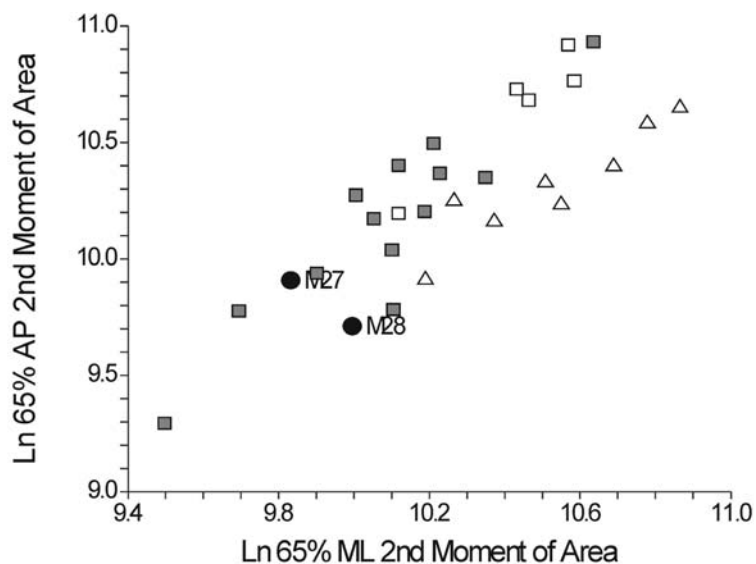


Fig. 11. Mid-proximal (65%) anteroposterior versus mediolateral second moments of area for Mladeč 27 and 28 (black circles – M27 and M28), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

imal end of the chord. Since it is the absolute subtense, rather than the subtense scaled to any measure of bone length, which is of relevance (Shackelford and Trinkaus, 2002), comparisons are made solely to the absolute subtenses of the comparative samples. The value of 12 mm for Mladeč 27 is slightly below the means for those samples but well within their ranges of variation (Table 26). In this, it is at the top of a later Upper Paleolithic sample and those of more recent humans (Shackelford and Trinkaus, 2002).

Diaphyseal robusticity

Even though it is commonly considered a reflection of overall robusticity, the relative proportion of the diaphyseal cross section made up of cortical bone (or percent cortical area) is a better reflection of differential endosteal resorption versus subperiosteal deposition through the life cycle than of the relative strength of the diaphysis (Ruff and Hayes, 1983; Ruff et al., 1994). The relative cortical to total subperiosteal areas of the Mladeč femora (Figs. 12 and 13) align them with the Late Pleistocene comparative samples, which are little different despite a couple of outliers in the distributions (Table 25). In the 65% and especially the 80% sections, the Mladeč 27 femur has a moderately lower percent cortical area than Mladeč 28, but both of them are within the Late Pleistocene distributions.

Given the absence of a reliable length estimate and midshaft, it is not possible to assess the overall robusticity of the Mladeč 28 femur. It is possible, however, to assess it indirectly for the Mladeč 27 femur using several approaches.

Initially, to maximize sample size (and to be able to include the Předmostí femora), a “pseudo polar moment of area” was calculated, by modeling the midshaft as a solid ellipse and using the external diameters to calculate second moments of area. Given the similarities across the samples in percent cortical area, modeling them as solid beams is not likely to distort the data greatly, although treating the highly pilastric femoral diaphyses as ellipses does increase their relative

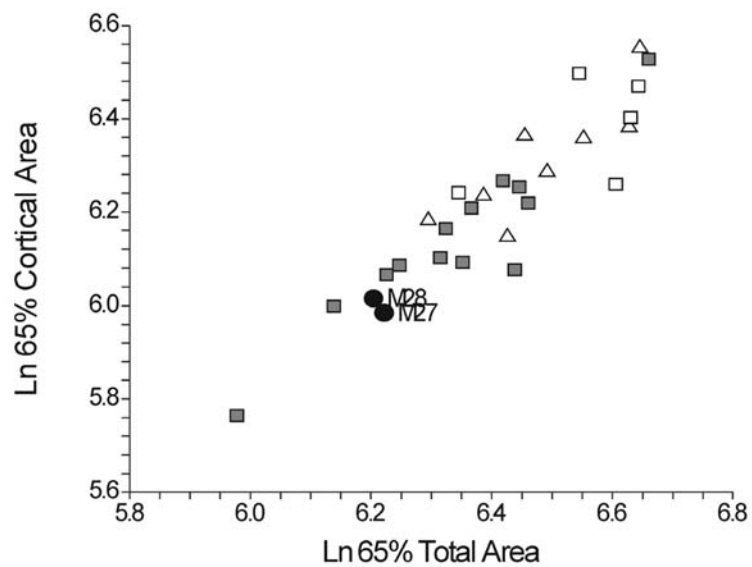
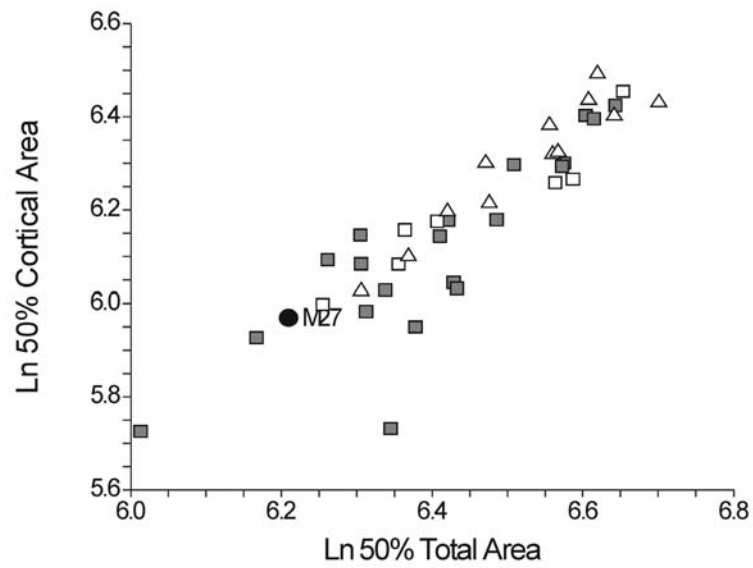


Fig. 12. Comparisons of femoral midshaft (50%) and mid-proximal (65%) diaphyseal cortical versus total subperiosteal area for Mladeč 27 and 28 (black circles - M27 and M28), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

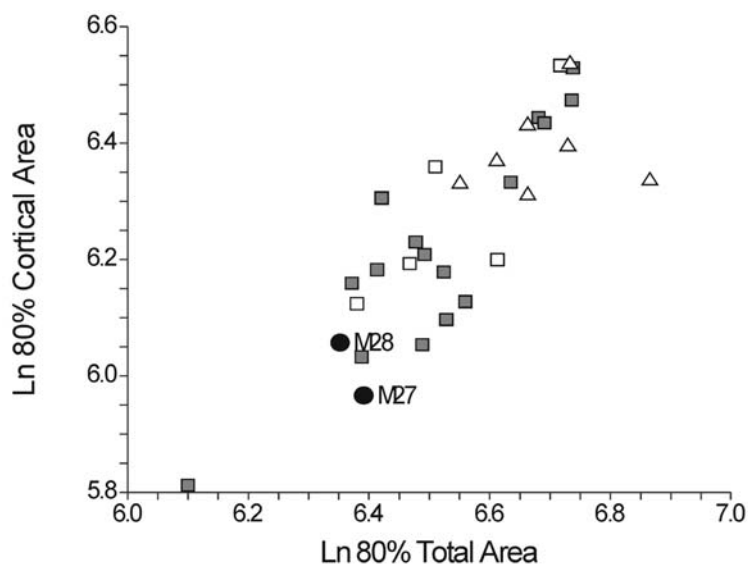


Fig. 13. Comparisons of femoral subtrochanteric (80%) diaphyseal cortical versus total subperiosteal area for Mladeč 27 and 28 (black circles – M27 and M28), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

values. The resultant plot of it to femoral length (Fig. 14) provides a significant degree of separation between the Neandertals and early modern humans, with the latter appearing more gracile (Table 25). Mladeč 27 falls at the gracile end of the early modern human distribution. A similar result is obtained when the cross-sectionally measured polar moment of area is compared to femoral length (Fig. 14). However, both of these comparisons ignore the effects of body proportions on femoral robusticity and largely reflect the stockier proportions of the Neandertals compared to early modern humans.

To correct for variance in body proportions, the midshaft diaphyseal strength was plotted against femoral length time body mass (Fig. 15). The result is little separation of any of the Late Pleistocene samples, as has been previously documented (Ruff et al., 1993; Trinkaus and Ruff, 1999a; Trinkaus, 2000; see Table 25). The two models of Mladeč 27 body proportions provide contrasting results. The earlier Upper Paleolithic model places it at the gracile margin of the Late Pleistocene distribution, relatively gracile but close to several early modern human specimens. The Neandertal model for its proportions makes it exceptionally gracile for a Late Pleistocene human, being about four standard deviations from the Neandertal and earlier Upper Paleolithic samples. Given its similarity to other early modern human femora in its midshaft anteroposterior to mediolateral proportions [which reflect mobility patterns (Ruff, 2000b)] and relative cortical area, it is unlikely that Mladeč 27 was an abnormally gracile early modern human. More likely, as suggested by its relative gluteal tuberosity breadth, it was moderately gracile for a Late Pleistocene human and had the linear body proportions of a European early modern human.

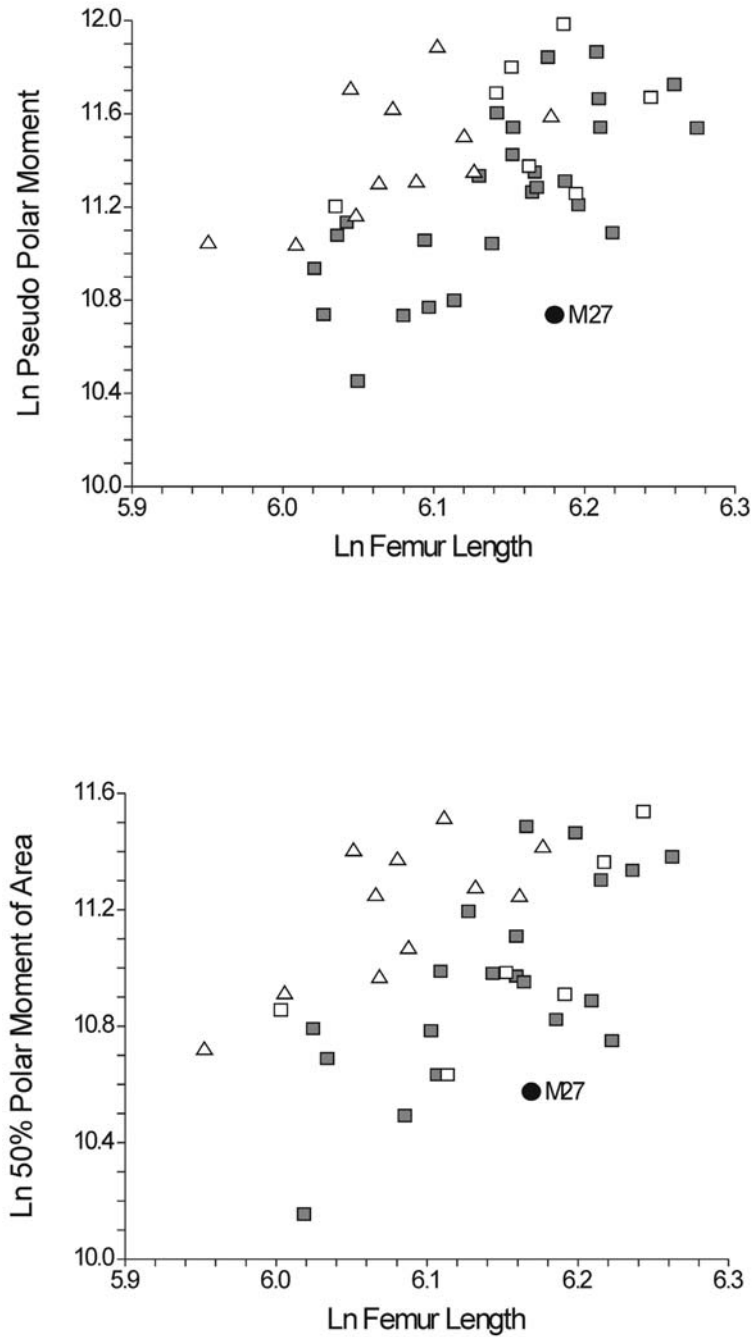


Fig. 14. Comparisons of femoral midshaft dimensions versus length, using an estimate of strength using external diameters (above) and cross-sectional geometry (the polar moment of area) (below), for Mladeč 27 (black circle – M27), earlier Upper Paleolithic humans (gray squares), Neandertals (open triangles) and Qafzeh-Skhul humans (open squares)

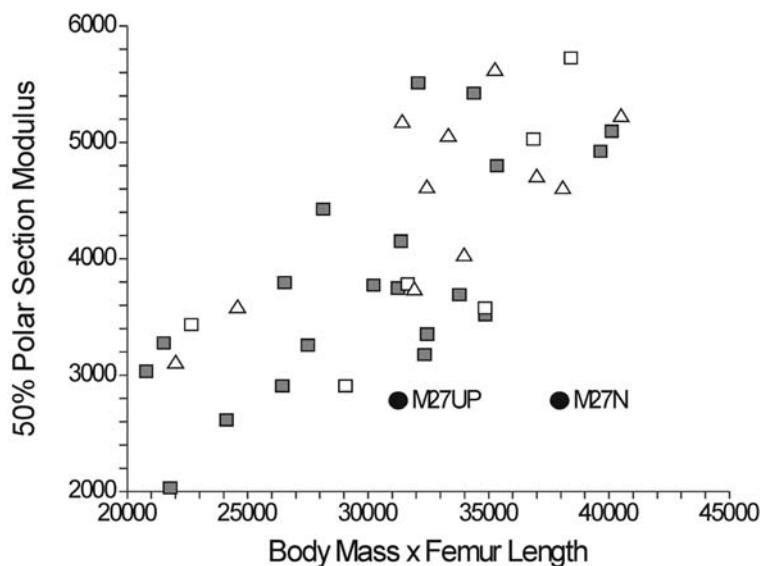


Fig. 15. Femoral robusticity of Mladeč 27, comparing the midshaft polar section modulus to body mass times femoral length. The left value for Mladeč 27 (M27UP) is based on a body mass estimate using earlier Upper Paleolithic body proportions, whereas the right value for Mladeč 27 (M27N) employed a body mass estimate based on Neandertal body proportions

The Mladeč 102 immature femur

Preservation

Curated with the Mladeč human remains in the Naturhistorisches Museum Wien is a previously undescribed proximal immature human femoral diaphyseal section (chapter 8, Plate XVIII). It exhibits the same bone preservation and carbonate encrustation as the other Mladeč remains and therefore is considered to be part of the sample. It also exhibits the museum catalog number of 5459 present on the other Mladeč human remains and in the same style of handwriting. It is given the number of Mladeč 102, adding on to the comprehensive catalog list of the Mladeč human remains. It may be the specimen listed by Szombathy in 1922 as the fourth radial fragment (Table 1).

Mladeč 102 is a left juvenile femur from the middle of the gluteal buttress to the proximal *linea aspera*, 53 mm long. The shaft is complete for the distal 38.3 mm, but proximally the gluteal buttress is partially absent and crushed inwards. There is carbonate concretion anteriorly and posterolaterally, the latter obscuring the gluteal tuberosity. The age-at-death of the specimen cannot be determined precisely, but it resembles the size and degree of diaphyseal development seen in earlier juvenile (ca. 3–6 year old) human femora. It could derive from the same individual as the Mladeč 3 cranium or be from a slightly older individual.

Morphology

There is little of note on this small specimen (Tables 20 and 23). The proximal diaphysis provides a meric index of 81.8. This value is in the middle of the variation of other Late Pleistocene juvenile specimens, including the Neandertal Cova Negra 3 (82.9) and La Ferrassie 6 (77.0) spe-

cimens, the Qafzeh 10 (88.4) and Skhul 1 (83.3) femora, and the earlier Upper Paleolithic Lagar Velho 1 (83.0) skeleton. The distal break, which is probably slightly proximal of midshaft, provides a pilastric index of 95.7. This value is similarly within the ranges of variation of Late Pleistocene juvenile femora, since the Neandertal Cova Negra 3, La Ferrassie 6 and Roc de Marsal 1 provides indices of 93.5, 93.9 and 96.2 respectively, the younger Dederiyeh 1 and 2 Neandertal femora provide indices of 98.1 and 103.0, and the Skhul 1 (112.9), Qafzeh 10 (105.6) and Skhul 8 (94.7) femora span most of the range. The earlier Upper Paleolithic Lagar Velho 1 and the east Asian Yamashita-cho 1 early modern human juveniles have indices of 94.5 and 100.6 respectively.

The Mladeč 29 tibia

Preservation and maturity

This specimen is the lateral portion of a right distal tibial epiphysis (chap. 8, Plate XVI). The fibular notch is preserved, as well as the lateral aspects of the anterior and posterior epiphyseal surfaces. The preserved anterior breadth of the specimen is 22 mm; the preserved posterior breadth is 18 mm. The specimen has been broken since its recovery, since Szombathy's (1925) description indicates that it was a complete right distal tibial epiphysis. This is confirmed by his illustration of the specimen, description of the medial malleolus and malleolar articular surface, and his reported distal epiphyseal breadth of 58 mm (Szombathy, 1925, 26). Most of the specimen is covered by surface matrix except for the medial broken edge, where the internal trabeculae are clearly visible and undistorted.

The proximal surface of the bone, although covered by a thin layer of matrix, is clearly that of an unfused epiphysis. This is confirmed by the presence of a thin layer of cortical bone along the proximal edge of the current break through the bone. Given the fusion of this epiphysis in later adolescence (15 to 18 years) (Scheuer and Black, 2000), this bone therefore represents at most an individual about 16 years old at death.

Morphology

The Mladeč 29 tibial epiphysis is notable for two features, its large size and its squatting facet.

To provide a measure of its size (Table 27), the "area" of the distal articular facet for the talar trochlea was computed using the formula for a trapezoid as 1040 mm². This is the largest value known among Late Pleistocene late archaic and early modern humans [data from Holliday (1995)

Table 27. Osteometric dimensions of the Mladeč 29 right distal tibia (in mm)

Distal epiphyseal breadth (M-6) ¹	58.0
Distal epiphyseal sagittal length (M-7)	43.5
Distal articular breadth ¹	32.0
Medial articular depth ¹	30.0
Lateral talar articulation sagittal depth	34.5
Distal fibular articulation sagittal length	27.9
Lateral squatting facet height	≥ 9.4
Lateral squatting facet breadth	> 15.5

¹ Dimension not preserved on specimen, and measurement is taken from Szombathy (1925). It is presumed to have been broken after Szombathy's analysis.

and Sládek et al. (2000)], although Barma Grande 2 (948.6 mm²), Caviglione 1 (904.8 mm²) and Fanciuilli 4 (956.8 mm²) are close. It is well above the means of the three references samples: Neanderthals (765.2 ± 115.7 mm², N = 6), Qafzeh-Skhul (738.2 ± 84.8 mm², N = 4) and earlier Upper Paleolithic (806.7 ± 102.1 mm², N = 14). That makes it, respectively, 2.38, 3.56 and 2.29 standard deviations above those sample means.

This large talar trochlear facet is accompanied by a prominent lateral squatting facet, which extends vertically up to the epiphyseal cartilage margin. Its medial margin was lost in the recent breakage. Similar squatting facets are commonly found on other Late Pleistocene distal tibiae (Trinkaus, 1975a; Sládek et al., 2000).

The Mladeč 30 talus

Preservation

Mladeč 30 is a large left talus and represents one of the most complete specimens in the Mladeč postcranial sample (chap. 8, Plate XVI). The specimen is nearly completely preserved, lacking only the anteroinferior corner of the lateral malleolar surface and adjacent posterior calcaneal surface. Minor surface abrasion occurs elsewhere on the bone, including the inferomedial border of the head and much of the medial neck, the anterior-most portion of the posterior calcaneal facet, and the medial margin of the medial talar tubercle. Most of the specimen is covered by a thin layer of matrix, except for portions of the trochlea and the lateral malleolar articular surface.

Comparison of talar trochlear articular surface size and curvature suggests that Mladeč 30 may derive from the same individual as the Mladeč 29 distal tibia, even though they derive from opposite sides. The complete fusion of the posterior tubercles suggests an age-at-death greater than 10 to 13 years (Scheuer and Black, 2000).

Morphology

Given its completeness, the Mladeč 30 talus provides a largely complete set of osteometrics and discrete trait observations, with only those requiring reconstruction of the lateral tips of the lateral malleolar surface and posterior calcaneal facet having estimation (Tables 28 and 29). The talus is notable primarily for its large size, since all of its overall and trochlear dimensions are well above the means of the Late Pleistocene comparative samples (Table 30). However, they all remain within two standard deviations of those means, and its length is within one standard deviation of the mean of the earlier Upper Paleolithic sample. In fact, its length is matched or exceeded by those of Barma Grande 2, Cro-Magnon 4377, Fanciuilli 4 and Veneri 1.

Despite its large overall size, its head-neck length is average for a Late Pleistocene human, being below the mean of the earlier Upper Paleolithic sample. To assess its relative head-neck length, which is an indirect measure of relative trochlear size (Rhoads and Trinkaus, 1977), it was compared to talar length. The resultant index (33.3) is below the means of the comparative samples (Table 31) but well within their ranges of variation. There is a trend for the earlier Upper Paleolithic tali to have longer necks relative to Middle Paleolithic specimens, and the difference approaches significance. The same pattern is evident in the comparison of trochlear size to talar length (Table 31), in which Mladeč 30, in this comparison, is more than two standard deviations from the earlier Upper Paleolithic sample but similar to the two Middle Paleolithic samples. The Mladeč 30 talus therefore exhibits the relative expansion of the trochlea seen in the earlier Late Pleistocene samples, as noted by Wolpoff (1989), but it is equally close to the Neanderthals and

Table 28. Osteometric dimensions of the Mladeč 30 left talus (in mm and degrees). Estimated values are in parentheses

Length (M-1)	57.0
Medial maximum length	57.4
Lateral maximum length	62.0
Maximum height	34.5
Maximum articular height (to trochlear margins) (M-3b)	30.0
Minimum articular height (to trochlear sulcus)	28.2
Articular breadth (M-2b)	(53.0) ¹
Trochlear length (M-4)	38.7
Anterior trochlear breadth	35.5
Middle trochlear breadth (M-5)	34.0
Posterior trochlear breadth	26.2
Trochlear height (M-6)	10.8
Lateral malleolar breadth (M-7a)	(10.0) ¹
Lateral malleolar height	(29.5) ¹
Lateral malleolar oblique height (M-7)	(30.0) ¹
Medial malleolar breadth	9.0
Head-neck length (M-8)	19.0
Head length (M-9)	37.2
Head breadth (M-10)	26.5
Posterior calcaneal length (M-12)	37.0
Posterior calcaneal breadth (M-13)	27.0
Trochlear angle ²	8°
Neck angle (M-16)	26°
Trochlear torsion angle (M-17)	35°
Basal torsion angle (M-17a)	35°
Posterior calcaneal angle (M-15)	34°
Subtalar angle ³	44°

¹ The lateral tip of the lateral malleolar process is absent, and it was necessary to model it in plasticine using the adjacent contours of the lateral malleolar surface and the posterior calcaneal surface. These measurements are dependent in part on that restoration.

² The angle between the two dorsal trochlear margins (Trinkaus, 1975b).

³ The angle between the proximo-distal trochlear axis and the "subtalar" line across the posterior and medial calcaneal surfaces (Trinkaus, 1975b).

Table 29. Discrete traits of the Mladeč 30 left talus. See Barnett (1954) and Trinkaus (1975a) for definitions

Anterior extension of medial malleolar surface	present (minimal)
Anterior extension of medial trochlea	absent
Anterior extension of lateral trochlea	present
Lateral squatting facet	present
Sulcus tali margin rounding	present
Sulcus tali facet	present
Anterior-medial calcaneal facet fusion	complete

Table 30. Osteometric comparisons of the Mladeč 30 talus to Late Pleistocene comparative samples. Mean and standard deviation (N) provided. All in millimeters. ANOVA P-values provided for the comparative samples

	Length	Articular breadth	Trochlear length	Trochlear breadth	Head-neck length
Mladeč 30	57.0	(53.0)	38.7	34.0	19.0
Neandertals	52.0 ± 3.2 (11)	49.2 ± 2.4 (11)	35.9 ± 2.3 (11)	28.4 ± 1.8 (11)	18.8 ± 2.1 (11)
Qafzeh-Skhul	52.6 ± 4.2 (6)	44.7 ± 4.1 (7)	34.5 ± 1.9 (7)	28.7 ± 2.7 (7)	18.1 ± 3.2 (6)
Earlier Upper Paleolithic	53.2 ± 4.3 (23)	46.2 ± 5.6 (13)	34.4 ± 2.8 (23)	29.3 ± 2.7 (20)	19.9 ± 2.5 (15)
ANOVA P-value	0.715	0.095	0.238	0.599	0.311

Table 31. Comparative talar proportions. Mean and standard deviation (N) and ANOVA P-values for the comparative samples provided

	Head-neck length/Length	Trochlea/Length	Neck Angle	Torsion Angle
Mladeč 30	33.3	63.6	26°	35°
Neandertals	36.1 ± 3.1 (11)	61.6 ± 2.0 (11)	26.0° ± 4.0° (11)	40.4° ± 4.8° (11)
Qafzeh-Skhul	34.2 ± 3.7 (6)	60.7 ± 4.2 (6)	25.8° ± 2.3° (6)	38.4° ± 9.0° (5)
Earlier Upper Paleolithic	38.2 ± 3.8 (16)	59.7 ± 1.8 (21)	24.2° ± 3.9° (20)	34.6° ± 2.4 (8)
ANOVA P-value	0.058	0.099	0.369	0.841

the Middle Paleolithic early modern humans in this respect. Interestingly, the one other European Aurignacian talus, that from Fontana Nuova, provides indices of 37.6 and 56.7 which contrast with those of Mladeč 30.

The angular orientations of the Mladeč 30 articulations are similar to those of other Late Pleistocene humans and recent human samples (Table 31; Trinkaus, 1975b). The articular discrete traits of the Mladeč 30 specimen mostly suggest frequent hyperdorsiflexion of the talocrural articulation, presumably through the assumption of a squatting position (Trinkaus, 1975a). The one exception to this is the minimal anterior extension of the medial malleolar surface, contrasting with the ubiquitous anterior extension of this facet among Late Pleistocene human tali. The anterior and medial calcaneal surfaces are completely fused, and they have a projection into the middle of the sulcus tali. This results in a narrow sulcus tali, minimally 4.9 mm wide. Finally, the lateral posterior tubercle is much more strongly developed than the medial one, and it borders a broad sulcus for the *M. flexor hallucis longus* tendon (ca. 8.5 mm wide).

The Mladeč 32 metatarsal 3

Preservation and age-at-death

The Mladeč 32 left metatarsal 3 is a complete immature bone, lacking only the unfused head epiphysis (chap. 8, Plate XVI). There is a thin layer of carbonate crust over the entire bone, and there was minor crushing to the plantar base. Since metatarsal heads normally fuse between the ages of 12 and 16 years (Scheuer and Black, 2000), this bone likely represents an individual no older than the middle of the second decade of life.

Morphology

The Mladeč 32 metatarsal 3 has a triangular diaphysis with rounded angles. There is a strong twist to the bone, which provides the torsion angle of 11° between the base and the head metaphysis, indicating a well-formed pedal arch. The base has a large triangular facet for the lateral cuneiform bone. The metatarsal 2 facets are double, with a 6 mm gap between them (Table 32). There is a single and larger metatarsal 4 facet. The plantar tubercle for the short plantar ligaments is moderately large.

Using a least squares regression based on mature recent human third metatarsals, the articular length of the bone has been estimated to be 80.9 mm ($\text{ArtLen} = 0.99 \times \text{PresLen} + 8.5$, $r^2 = 0.964$, $N = 44$). This value, as with the Mladeč 31 metacarpal 3, is large for a Late Pleistocene human, being approached by Barma Grande 2 (79.8 mm), Skhul 4 (80.3 mm) and Veneri 1 (79.8 mm) (Table 33). Its robusticity index (geometric mean of the midshaft diameters/articular length) was computed as 12.0. This value is similar to other Late Pleistocene sample values, which do not differ significantly between them (Table 33).

Table 32. Osteometric dimensions of the Mladeč 32 left metatarsal 3 (in mm). Values in parentheses are estimated

Midshaft height	10.8
Midshaft breadth	8.7
Proximal maximum height	22.1
Proximal articular height	17.8
Dorsal (maximum) proximal articular breadth	14.0
Plantar (minimum) proximal articular breadth	7.2
Metatarsal 2 dorsal facet height	7.2
Metatarsal 2 dorsal facet breadth	10.7
Metatarsal 2 plantar facet breadth	(7.7)
Metatarsal 4 facet height	9.9
Metatarsal 4 facet breadth	14.3
Plantar tuberosity proximodistal length	17.0
Preserved length	73.4

Table 33. Osteometric comparisons for the Mladeč 32 third metatarsal. Mean and standard deviation (N) are provided for samples greater than five; individual values provided for smaller samples. ANOVA P-value for the comparative samples provided for length and Kruskal-Wallis P-value provided for the index

	Articular length (mm)	Robusticity index
Mladeč 32	80.9	12.0
Neandertals	68.3 ± 3.9 (6)	12.3 ± 0.9 (6)
Qafzeh-Skhul	67.6, 73.7, 80.3	11.3, 12.5, 14.3
Earlier Upper Paleolithic	72.1 ± 6.4 (10)	11.8 ± 0.8 (10)
Comparative P-values	0.324	0.322

Paleopathology of the Mladeč postcranial elements

The Mladeč postcranial remains in the Naturhistorisches Museum Wien exhibit no macroscopic evidence of lesions externally. It is possible that there are minor ones obscured by the ubiquitous carbonate encrustations, but they are likely to be very minor if present. There is also no evidence of transverse (Harris) lines radiographically on the Mladeč 23 proximal humerus, the Mladeč 24 distal humerus, the Mladeč 25a proximal radius, the Mladeč 31 metacarpal or the Mladeč 32 metatarsal. Although they are (probably) not from the same individuals, this absence of transverse lines is in agreement with the absence of dental enamel hypoplasias on Mladeč 1 and 2 maxillary teeth and the Mladeč 8, 9 and 10 posterior teeth; there are minor pits on the Mladeč 8 and 9 maxillary canines. The hand remains from Chamber E also lack pathological lesions.

Associations by individual

The Mladeč postcranial remains from Chamber D therefore include the remains of both mature individuals and immature individuals. It is likely that these do not each represent separate individuals but can be associated based on size, morphology, and age-at-death. The following associations are considered to be reasonable, but they remain hypothetical in the absence of DNA fingerprinting of the remains.

The Mladeč 102 femoral diaphysis, as that of a younger juvenile, may come from the same individual as the Mladeč 3 cranial remains, depending largely on the age estimations for each.

There is a series of immature remains, whose ages-at-death provide a range between 13 and 16 years. These include three rib pieces with unfused head epiphyses (Mladeč 12, 14 and 17; age-at-death < 20–25 years), the Mladeč 23 proximal humerus (age-at-death 16–20 years), the Mladeč 31 metacarpal 3 (age-at-death < 14–16 years), the Mladeč 22 os coxae (between 13–15 years and 19–20 years), the Mladeč 29 distal tibia (age-at-death < ca. 15 years), and the Mladeč 32 metatarsal 3 (age-at-death < 12–16 years). In addition, the Mladeč 30 talus has an age-at-death greater than 10–13 years, and it is a good match morphologically and dimensionally for the Mladeč 29 distal tibia. The Mladeč 24 humerus, whose epiphyseal line is fused where preserved, may be developmentally too old to be included within this individual and, in any case, would duplicate the Mladeč 23 humerus. In addition, the Mladeč 25a and 25c proximal radius and ulna, which appear on the basis of size and morphology to derive from the same arm, have a minimum age of ca. 15 years based on complete fusion of their proximal epiphyses.

It is therefore possible that these remains represent a single individual, although one would have to argue for a relatively late fusion of the metacarpal 3 head, distal tibial and metatarsal 3 head epiphyses and a relatively early fusion of the proximal humeral, radial and ulnar epiphyses. It is more likely that more than one individual is represented by these remains, and that the mid-adolescent remains are restricted to those that show clear immature status (the ribs, the metacarpal 3, the os coxae, the distal tibia and the metatarsal 3). The remainder of the immature pieces (the proximal humerus and possibly the immature ribs), perhaps joined by other late adolescent or skeletally mature remains, represent an additional individual.

Most of these adolescent or possibly adolescent remains are moderately (but not exceptionally) large in size compared to other earlier Upper Paleolithic Europeans. These include especially the Mladeč 25a and 25c radius and ulna, the Mladeč 31 metacarpal, the Mladeč 22 os coxae, the Mladeč 29 and 30 tibia and talus, and the Mladeč 32 metatarsal. It is therefore likely that these remains all derive from large, mid-adolescent and late adolescent individuals. The two more complete crania from Chamber D of the Mladeč Cave, Mladeč 1 and 2, are late adolescent in age based on dental attrition (especially the absence of distal interproximal facets on the Mladeč 1 M²s), and it is possible

that one of them is the same individual as the late adolescent or young adult postcrania. However, these crania have been considered to be female (chap. 10), since they contrast with the marked cranial superstructures of Mladeč 5 and 6 and the large palate of Mladeč 8, whereas the late adolescent based on these postcrania is likely, on the basis of size, to be male. Therefore, either there is greater variation in male cranial superstructure development than has been assumed for the Mladeč sample [such as is seen in the Dolní Věstonice 11/12, 13, 14 and 16 and Pavlov 1 males (Vlček, 1991; Franciscus and Vlček, 2005)], or the Mladeč 1 and 2 cranial remains do indeed represent different individuals than these apparently male postcrania. The additional Mladeč Chamber D skull remains, the Mladeč 8 maxilla and the Mladeč 9 and 10 isolated teeth, are fully mature.

The remainder of the Mladeč postcrania are either undiagnostic as to age (beyond being adolescent or adult) and could belong to these Mladeč adolescents (e.g., additional rib fragments, the Mladeč 27 femoral diaphysis), clearly belong to other individuals based on duplication of elements, size and/or morphology (e.g., Mladeč 24 humerus, Mladeč 21 os coxae, Mladeč 26 radius), and/or they are fully mature (Mladeč 11 vertebra, Mladeč 24 humerus, Mladeč 21 os coxae, Mladeč 28 femur). There are no reliable criteria available to assess whether these mature remains might be associated with each other or with the mature craniodental remains from Chamber D.

As noted above, it is likely that three of the Chamber E hand remains, Mladeč 88 to 90, derive from one mature individual.

Morphological affinities of the Mladeč human postcranial remains

The basic morphological pattern of the Mladeč human postcranial elements is that of relatively robust early modern humans. There is a suite of characteristics in the remains that align them principally with the early modern human remains known from the earlier portion of the Upper Paleolithic (generally between 20,000 and 28,000 years BP) of Europe. These characteristics include (1) the tapering of the lower cervical spinous process, (2) the relative thinness of several of the rib remains, (3) the modest *M. pectoralis major* tuberosities, (4) the small size of the olecranon fossa, (5) the gracility of the humeral diaphysis, (6) the more proximal orientation of the ulnar trochlear notch, (7) the proximal phalangeal robusticity, (8) the smooth gluteal tuberosities, and (9) the modest femoral hypertrophy that is best seen as a reflection of linear body proportions in the context of robust Late Pleistocene femora.

At the same time, there are several features which are either intermediate or variable between late archaic and early modern humans. The ventral height of the Mladeč 11 vertebral body appears relatively low, similar to those of the Neandertals, but it is also matched by those of Skhul 5. The more anterior radial tuberosity position is closely aligned with early modern humans, but it overlaps the Neandertal range of variation. The metacarpal 3 robusticity is variable. The marked gluteal buttress/flange of Mladeč 28 is proportionately and morphologically similar to those of earlier Upper Paleolithic humans and distinct from those of the Neandertals, but the Mladeč 27 rounder subtrochanteric femur is close to the Neandertals in proportions; however, in this feature Mladeč 27 is also close to the Qafzeh-Skhul sample. The gluteal tuberosity of Mladeč 27 is very modest similar to those of many earlier Upper Paleolithic humans, but the one of Mladeč 28 (which cannot be scaled to body size) is one of the largest known for early modern humans and, in absolute terms, most similar to those of the Neandertals. The femoral midshaft of Mladeč 27 exhibits a distinctively modern human pilaster, whereas the mid-proximal shaft (to the extent preserved) of Mladeč 28 is broader, mechanically similar to Neandertal femora, and has only a suggestion of the proximal formation of a pilaster. And finally, the relative trochlear size of the Mladeč 30 talus separates it from earlier Upper Paleolithic humans and places it among the Neandertals, but it is also indistinguishable from the Qafzeh-Skhul sample.

Consequently, although there are several features which might be taken to provide evidence of morphological affinities of the Mladeč postcranial remains to those of the Neandertals, most of them are variable within the small Mladeč sample and/or they align the Mladeč remains as much with the Middle Paleolithic Qafzeh-Skhul early modern humans as with the Neandertals. It becomes difficult to assess whether the “archaic” features of the Mladeč human postcrania are the result of some degree of Neandertal ancestry, affinities to Middle Paleolithic early modern humans, or aspects of robusticity reflecting earlier Upper Paleolithic human behavioral patterns in Europe.

It should be emphasized that these conclusions do not necessarily mean that the Mladeč sample provides no evidence of Neandertal ancestry for Central European early modern human samples (see Smith and Trinkaus, 1991; Frayer, 1993; Wolpoff et al., 2001). It only means that it is difficult to use those portions of the postcranial remains preserved for these early Upper Paleolithic humans to substantiate such a hypothesis.

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