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The Sunghir 3 Upper Paleolithic Juvenile: Pathology versus Persistence in the Paleolithic

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ABSTRACT The Mid Upper Paleolithic Sunghir 3 late juvenile early modern human, from the most elaborate burial in the Pleistocene, had pathologically foreshortened and anteriorly bowed femora and, based on her dental enamel hypoplasias and transverse lines, sustained severe and persistent systemic stress throughout her decade of life. Her modest femoral and tibial asymmetry and her femoral bicondylar angles indicate non-pathological patterns of posture and locomotion. The levels of rigidity for her weight-bearing tibiae and the non-dominant left arm reflect normal weight-bearing and manipulation. These indicators are combined with an elevated level of right humeral strength, leading to pronounced humeral diaphyseal asymmetry, combined with elevated muscular insertion asymmetry. In combination with marked upper limb muscle markings and normal levels of bone formation, these reflections of her robustness indicate that she was fully mobile and participated actively in the tasks of her social group. There is no indication of the skeletal hypotrophy/atrophy that would be associated with less than full participation in the mobility and subsistence of her social group. As such, Sunghir 3 joins a growing list of developmentally or degeneratively pathological Late Pleistocene humans who nonetheless remained mobile and active.

Key words: femur; tibia; humerus; robustness; asymmetry; Russia

Introduction

It has become increasingly apparent, through paleopathological analyses of Pleistocene *Homo* remains, that there were frequent cases of long-term survival of serious abnormalities among these mobile foraging populations (Wu *et al.*, 2011, and references therein). These lesions include developmental abnormalities, degenerative adult conditions, and substantial trauma affecting craniofacial and/or appendicular anatomy. The best documented cases are from the Late Pleistocene, in which there is commonly preservation of substantial portions of the skeleton, but instances are known throughout the Pleistocene. There have been differential diagnoses of these abnormalities (e.g. Trinkaus, 1983; Montgomery *et al.*, 1994; Oliva, 1996; Tillier *et al.*, 2001; Lebel & Trinkaus, 2002; Formicola & Buzhilova, 2004; Trinkaus *et al.*, 2006; Gracia *et al.*, 2009; Bonmatí *et al.*, 2010; Shang & Trinkaus, 2010), considerations of whether the conditions required social caring for long-term survival (e.g. Lebel & Trinkaus, 2002; Lordkipanidze *et al.*, 2005), and thoughts on whether mortuary practices were affected by their unusual conditions (e.g. Formicola, 2007; Trinkaus & Buzhilova, 2010). In these cases, however, it is only occasionally evident whether the pathological condition adversely affected the ability of the individual to participate in the subsistence and other survival activities of its foraging population.

One of the Pleistocene humans who exhibits substantial abnormalities and was apparently subject to persistently high levels of systemic stress is the late juvenile from Sunghir, Russia (Sunghir 3). Although her femoral deformities and non-specific stress indicators have been described in detail and differentially diagnosed (Buzhilova, 2000; Formicola & Buzhilova, 2004; Guatelli-Steinberg *et al.*, 2012), there has been little consideration of the degree to which she achieved and maintained the level of skeletal robustness, and hence physical activity, that was characteristic of earlier Upper Paleolithic human populations. It is in this

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context that we reassess, using humeral, femoral, and tibial properties, the degree to which Sunghir 3 may have participated in the mobility levels and subsistence activities of her social group.

The Sunghir 3 juvenile

The Sunghir 3 partial skeleton was discovered in 1969 at the Sunghir site in northern Russia (56° 08′ N, 40° 25′ E) in a double burial of two late juvenile – early adolescent individuals, buried head-to-head (Figure 1; Bader, 1998). They were clothed in perishable material that was elaborately decorated with red ochre and ≥10,000 mammoth ivory beads; the beads and pigment then covered the skeletons following decomposition. The bodies were accompanied by spears of straightened ivory alongside of the two bodies and several mobilary art objects. The older individual (Sunghir 2) had hundreds of arctic fox canines with him, and next to his left arm was the ochre-filled femoral diaphysis of an adult human (Sunghir 4). Direct AMS radiocarbon dates on Sunghir 2 and/or 3 range from ~26 to ~30 ka ^{14}C BP (31–34 ka cal BP) (Kuzmin *et al.*, 2004; Dobrovolskaya *et al.*, 2012; Marom *et al.*, 2012). The burial is the most elaborate Pleistocene human burial currently known, approached only by that of the adult Sunghir 1.

It was quickly realized that the younger of the individuals, Sunghir 3, a 9–11 year old probable female as determined by recent DNA analyses (Mednikova *et al.*, 2000; Poltoraus *et al.*, 2000; Formicola & Buzhilova, 2004; Guatelli-Steinberg *et al.*, 2012), was both culturally and biologically unusual (Bukhman, 1984; Buzhilova, 2000, 2005; Mednikova, 2000; Formicola & Buzhilova, 2004; Guatelli-Steinberg *et al.*, 2012). Most of her skeleton appeared to be non-pathological, but her bilaterally symmetrical femora exhibit a pronounced and even anterior bowing of the diaphyses (Figure 2). This bowing is accompanied by marked development of the pilaster (Figures 2 and 3), probably as a biomechanical compensation for increased anteroposterior bending strains from the anterior bowing, yet her femoral and other long bone relative cortical thicknesses appear to be normal (Mednikova, 2000). The femora are also reduced in length relative to her tibiae; her crural index of ~91.6 exceeds those of the slightly older Sunghir 2 (86.8) and the adult Sunghir 1 (84.7), and it is 3.2 standard deviations from the mean of an Upper Paleolithic adult sample (84.8 ± 2.1, $N = 39$). It also exceeds similarly aged recent humans (between 9.0 and 11.9 years) by four standard deviations (Cowgill *et al.*, 2012). Her

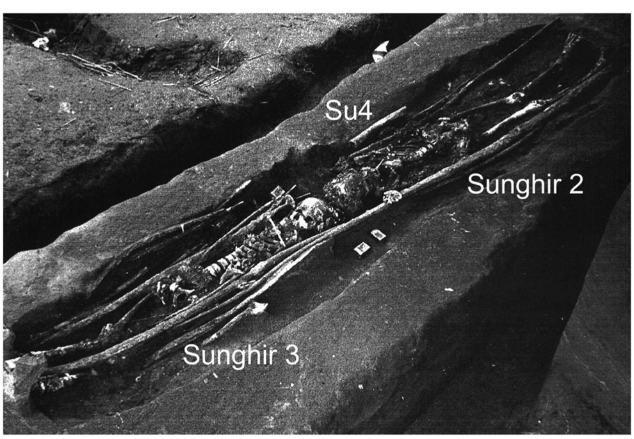

Figure 1. The Sunghir 2, 3, and 4 human remains as exposed during excavation in 1969. Su4: the Sunghir 4 femoral diaphysis next to Sunghir 2. From Bader (1998) with permission.

Figure 2. Medial (left) and anterior (right) views of the Sunghir 3 left femur. Scale: 10 cm. This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

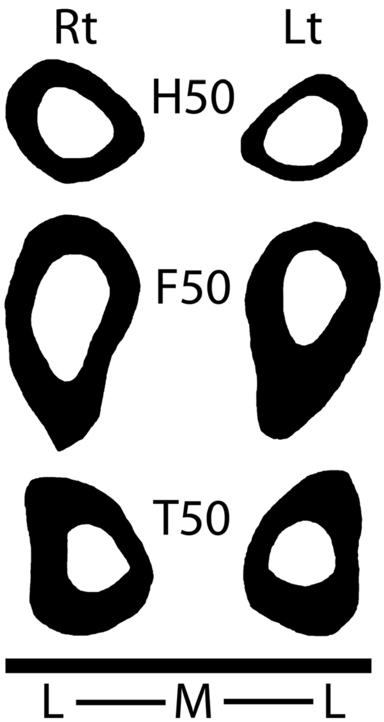

Figure 3. Reconstructed cross-sections of the Sunghir 3 midshaft humeral (H50), femoral (F50), and tibial (T50) diaphyses. Sections are viewed from distal, anterior is above and lateral is to the outside. Scale bar: 5 cm.

humeral–femoral index of ~78 is also much higher than those of Sunghir 1 and 2 (72.5 and ~72.3, respectively), an Upper Paleolithic sample mean (71.9 ± 3.1, $N = 41$), and those of most recent humans (Trinkaus, 1981).

Her dentition exhibits pronounced and persistent dental enamel hypoplasias, and multiple transverse lines are evident in the femora and to a lesser extent the tibiae (Buzhilova, 2000; Guatelli-Steinberg *et al.*, 2012). In particular, the pronounced dental enamel hypoplasias exhibit slow recovery from the periods of developmental stress, and the transverse lines indicate that the stress episodes persisted until shortly before her death at the end of the first decade of life.

The etiology of the femoral bowing has been difficult to determine, but a prenatal developmental abnormality of the femoral cartilaginous anlage, possibly linked to maternal physiology during pregnancy, appears most likely (Formicola & Buzhilova, 2004). The non-specific developmental lesions may reflect frequent stress in the population (less pronounced dental hypoplasias are present on Sunghir 2) and/or persistent frailty as a result of the congenital abnormality (Guatelli-Steinberg *et al.*, 2012).

The remainder of the very complete Sunghir 3 skeleton, including the other primary long bones, appears superficially normal, with expected patterns of diaphyseal proportions and cortical thicknesses (Mednikova, 2000) and bone tissue formation (Bukhman, 1984; Kozlovskaya, 2000). However, it has not been possible previously to assess the degree to which Sunghir 3 may have been an age-appropriate participant in the activities of her social group. Therefore, given the superficially non-pathological nature of the largely complete Sunghir 3 tibiae (Figure 4) and humeri (Figure 5), and the responsiveness of diaphyseal bone to habitual levels of loading, especially during development (Pearson & Lieberman, 2004; Ruff *et al.*, 2006), we have assessed the extent to which the upper and lower limbs of Sunghir 3 conform to the level and patterns of skeletal hypertrophy to be expected in a late juvenile among Late Pleistocene human hunter–gatherers. Of particular relevance to this assessment is the observation that, during development, diaphyseal bone will hypertrophy to normal levels of robustness only under conditions and levels of loading common to the individual's population (Ruff, 2003).

Figure 4. Anterior views of the Sunghir 3 right and left tibiae (left and center) and lateral view of the left tibia (right). Scale: 10 cm. This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

Figure 5. Anterior views of the Sunghir 3 humeri. Scale: 10 cm. This figure is available in colour online at wileyonlinelibrary.com/journal/oa.

Materials and methods

The Sunghir 3 tibial and humeral diaphyseal properties are compared principally to those of late juvenile to early adolescent early and recent modern humans. An age range of 8 to 15 years is employed, since it should be sufficient to bracket the age-at-death of Sunghir 3 (9–11 years) without introducing the non-linearity of developmental cross-sectional parameters.

For the Late Pleistocene, the comparative sample includes Sunghir 2 and the few available early modern humans between the ages of 8 and 15 years postnatal [from the sites of Arene Candide, Barma Grande, Pataud, Taforalt, and El Wad for the tibia and from Pataud and El Wad for the humerus; the data are from Cowgill (2008) and Holt (1999)]. These fossil specimens are compared to samples of recent human humeri ($N = 120$) and tibiae ($N = 155$) between the ages of 8 and 15 years. These recent human remains derive from Point Hope (Alaska, USA), Indian Knoll (Kentucky, USA), northern California Amerindians (California, USA), Mistihalj (Bosnia), Kulubnarti (Nubia), Lisbon (Portugal), and Johannesburg (South Africa) (Cowgill, 2008, 2010). The recent human remains are pooled into two samples, one from pre-industrial archeological sites and the other (the last two samples) of 20th century documented children from mechanized urban settings. Ages for six of the seven samples (all except the documented Lisbon sample) were assessed from lateral mandibular radiographs using recent Euroamerican standards for dental crown and root formation (Smith, 1991; Liversidge & Molleson, 2004). When an associated dentition was not available for an individual, within sample least squares regressions based on bone lengths were employed (Cowgill, 2008). All specimens with abnormalities other than minor non-specific stress indicators were excluded.

To provide a broader context for humeral asymmetry, midshaft data are included for mature humeri of early modern humans from the Upper Paleolithic sites of Cap Blanc, Chancelade, Dolní Věstonice, Ein Gev, Grotte des Enfants, Laugerie Basse, Minatogawa, Nazlet Khater, Ohalo, Paglicci, Pataud, Pavlov, Romanelli, Romito, St. Germain-la-Rivière, and Tianyuan (Kimura & Takahashi, 1992; Churchill, 1994; Trinkaus *et al.*, 1994; Sládek *et al.*, 2000; Crevecoeur, 2008; Shang & Trinkaus, 2010). Recent human adult data from the sites providing immature observations are supplemented with data from Yoshiko and Ikawasu (Japan), Aleutian Islands (Alaska, USA), Pottery Mound (New Mexico, USA), and Euroamericans (New Mexico and Missouri, USA), the last being a 20th century documented sample (Churchill, 1994; Trinkaus *et al.*, 1994).

The primary data consist of humeral and tibial linear osteometrics and midshaft (50% of length) cross-sectional geometric parameters, including total subperiosteal and cortical areas, perpendicular maximum and minimum second moments of area, and the polar moment of area (see Tables 1 and 2 for Sunghir 3). Cross-sections were reconstructed for most of the fossil specimens and recent human bones using polysiloxane dental putty (Cuttersil Putty Plus®, Heraeus-Kulzer) to transfer the subperiosteal contour, and then parallax-corrected cortical thicknesses from biplanar radiography to interpolate the endosteal contour (O'Neill & Ruff, 2004). They were then enlarged ~10× and digitized on a Summagraphics® 1812 tablet, and the cross-sectional parameters were computed using SLCOMM/SLICE (Nagurka & Hayes, 1980; Eschman, 1992). The

Table 1. Linear osteometric dimensions of the Sunghir 3 humeri, femora, and tibiae. In millimeters except as indicated

	Right	***Left***	***Asymmetry***[a]
Humerus			
Intermetaphyseal length	239.0	--	--
Pectoralis major tuberosity breadth[b]	3.7	2.5	38.7%
Teres major/latissimus dorsi breadth[b]	8.0	6.1	27.0%
Deltoid tuberosity breadth[b]	5.0	3.0	50.0%
Epicondylar breadth	48.5	45.5	6.4%
Femur			
Anteroposterior head diameter	39.0	38.5	1.3%
Superoinferior head diameter	37.5	38.0	1.3%
Distal metaphyseal breadth	68.4	67.7	1.0%
Metaphyseal bicondylar angle	10°	11°	9.5%
Gluteal tuberosity breadth[b]	8.2	8.5	3.6%
Tibia			
Intermetaphyseal length	282.0	(282.0)	--

[a]Asymmetry is calculated as: |((Rt–Lt)/((Rt + Lt)/2))x100|. A positive value indicates a larger right dimension.
[b]The muscle insertion breadths are the maximum breadths of the distinct margins of the rugose diaphyseal surface.

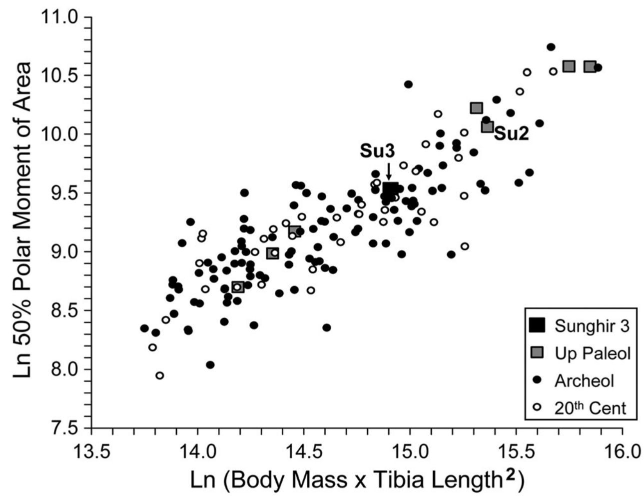

Figure 6. Bivariate plot of tibial midshaft diaphyseal polar moments of area versus estimated body mass times biomechanical length squared for recent human 8–15 year-olds, Upper Paleolithic 8–15 year-olds with Sunghir 2 (Su2) indicated, and Sunghir 3 (Su3).

Minatogawa and Nazlet Khater data are from CT scans (Kimura & Takahashi, 1992; Crevecoeur, 2008).

To scale the humeral and tibial diaphyseal rigidity, the polar moments of area are plotted against estimated body mass times maximum intermetaphyseal length squared (Cowgill, 2010; Trinkaus & Ruff, 2012) (Figures 6 and 8). Body mass was predicted for the immature individuals based on age-appropriate equations from Ruff (2007), using femoral distal metaphyseal mediolateral breadth and/or femoral head diameter as preserved; for Sunghir 3, the resultant values are 37.8 kg (±5.36) and 37.2 kg (±4.73) (averaged to 37.5 kg). Bilaterally preserved femoral and tibial measurements were averaged prior to the comparisons; given asymmetry, the humeral ones are treated separately. Asymmetry was computed as the absolute value of the percent directional asymmetry (Auerbach & Ruff, 2006): |((Rt–Lt)/((Rt + Lt)/2))x100|. In the assessment of bilateral humeral hypertrophy, the humeri were sorted into dominant versus non-dominant sides based on the midshaft polar moments of area of each individual, and the comparisons of midshaft rigidity were then done for the dominant and non-dominant humeri separately (Figure 8).

In addition to these assessments of tibial and humeral midshaft hypertrophy using cross-sectional geometry, normal locomotor anatomy development is assessed using the metaphyseal femoral bicondylar angle and femoral and tibial midshaft polar moment of area asymmetry. Upper and lower limb asymmetry are further assessed with measures of muscular insertion size on the Sunghir 3 humeri and femora.

Bivariate comparisons employ the standardized residuals (raw residuals/standard deviation of the residuals) from the reduced major axis line through the pooled recent human immature sample; the pooled residuals are normally distributed. All values are logged to correct for the substantial body size increase with development, even within the age range of 8 to 15 years. All of the comparisons employ non-parametric (Wilcoxon

Table 2. Cross-sectional geometric parameters for the Sunghir 3 humeral, femoral and tibial midshafts

	Humerus		***Femur***		***Tibia***	
	Right	Left	Right	Left	Right	Left
Total area (mm^2)	232	180	412	393	291	288
Cortical area (mm^2)	157	107	286	312	232	256
Max second moment of area (mm^4)	4851	2955	22944	20352	9140	9447
Min second moment of area (mm^4)	3092	1604	6820	6775	4703	4287
Polar moment of area (mm^4)	7943	4559	29764	27126	13843	13734
Polar moment asymmetry[a]	54.1%		9.3%		7.9%	

[a]Asymmetry is calculated as: |((Rt–Lt)/((Rt + Lt)/2))×100|. A positive value indicates a larger right dimension.

or Kruskal–Wallis) tests given the small fossil samples and/or the skewed natures of some of the distributions.

Results

Femoral development

Despite their abnormal curvature and associated pilastric compensation (Figures 2 and 3), the Sunghir 3 femora exhibit low levels of asymmetry and one distinctive reflection of a non-pathological postural/locomotor development. The asymmetry in femoral articulations is within osteometric measurement error (<2%), and the asymmetry in the gluteal tuberosity breadth appears only slightly higher given the small dimension of the feature (Table 1). There is also little asymmetry in the metaphyseal bicondylar angle.

More importantly, the bicondylar angles of the Sunghir 3 femora (10° and 11°) are in the middle of the range of variation for the articular bicondylar angle of adult Upper Paleolithic humans ($9.2° \pm 2.4°$, $N = 24$), all of which are well within recent human ranges of variation (Tardieu & Trinkaus, 1994). The Sunghir 3 metaphyseal bicondylar angles are also above the articular angle of Sunghir 1 (~7°) and the metaphyseal angle of Sunghir 2 (7°). Her angles are also among the higher values for recent human children in the same developmental age range (Tardieu & Trinkaus, 1994). In this context, a bicondylar angle greater than ~4° only develops during childhood with the assumption of normal movement of the knees under the center of gravity, usually ~4 years postnatal (Tardieu & Trinkaus, 1994). Sunghir 3, therefore, despite her femoral deformities, acquired the knee position associated with effective adult posture and locomotion (Sutherland *et al.*, 1988; Cowgill *et al.*, 2010).

Tibial hypertrophy

The Sunghir 3 tibial cross-sectional geometry is compared only to 8 to 15 year old late juvenile to early adolescent tibiae, given changes in lower limb diaphyseal shape relative to younger and older individuals (Ruff *et al.*, 1994; Cowgill, 2010). They are subperiosteally similar to those of other Late Pleistocene (and recent human) late juvenile tibiae (Figures 3 and 4). They exhibit a low level of diaphyseal cross-sectional asymmetry (Table 2), despite a slightly greater anterior curvature in the left one. In the scaled rigidity of the tibial diaphysis, the Upper Paleolithic immature tibiae and the two recent samples are insignificantly different ($P = 0.482$) (Figure 6). The Sunghir 3 scaled average tibial rigidity falls in the middle of the recent human distribution (standardized residual <0.01) and among the other Upper Paleolithic immature tibiae (0.29 ± 0.34, $N = 7$). In this context, there is a reduction in the recent urban samples in cortical to total subperiosteal area proportions, relative to the pre-industrial archeological sample ($P < 0.001$), but the Upper Paleolithic and archeological samples are similar ($P = 0.556$). Sunghir 3, with a standardized residual of 0.33 falls with the earlier samples (Upper Paleolithic: 0.29 ± 0.76, $N = 7$; Archeological: 0.34 ± 0.83, $N = 115$).

These measures of tibial hypertrophy fall well within the ranges of variation of similarly aged early and recent modern human tibiae, and especially those of the non-urban samples. They indicate that Sunghir 3 was loading her legs to a degree and in a manner commensurate with full locomotor and/or burden carrying loading. There is no indication of an underdevelopment (hypotrophy) of her tibial diaphyses, such as one might predict if her femoral deformities and persistent systemic stress prevented her from the same level of mobility evident for other Upper Paleolithic (and Sunghir 1 and 2) individuals.

Humeral asymmetry

The Sunghir 3 humeral midshafts (Figures 3 and 5) exhibit a pronounced level of asymmetry in their polar moments of area, with a value of 54.1% (Figure 7). This percent asymmetry is above those of Sunghir 2 (32.1%) and is approached by El Wad 10315 (44.7%) among the few Upper Paleolithic immature individuals preserving both humeral midshafts. However, it is matched by six (27.2%) of the mature Upper Paleolithic individuals [Dolní Věstonice 13 and 14 (58.7% and 58.3%), Grotte-des-Enfants 4 (52.2%), Laugerie Basse 4 (56.9%), Romito 4 (51.3%), and Tianyuan 1 (55.8%)]. The immature and mature fossil samples are statistically indistinguishable ($P = 0.857$), but within each age group, the fossil samples have higher asymmetry values than the archeological and 20th century recent human samples [P: 0.036 and 0.021 (immature); 0.006 and <0.001 (adult), respectively; all significant at $P < 0.05$ after a sequentially reductive multiple comparison correction].

To assess whether the marked humeral asymmetry of Sunghir 3 is due to dominant (right) arm hypertrophy or non-dominant (left) arm hypotrophy, the midshaft rigidity of each is scaled to body mass and bone length (Figure 8). In the dominant humerus, there is no difference across the Upper Paleolithic and recent

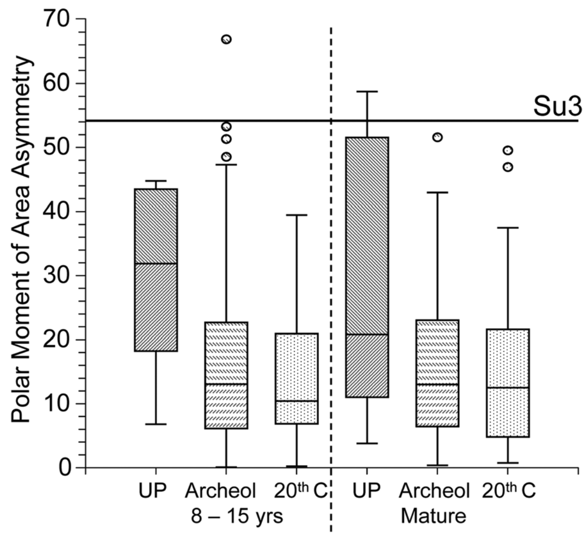

Figure 7. Box plot of the absolute values of the percent asymmetry in the humeral midshaft rigidity for Upper Paleolithic (UP) and recent 8–15 year-olds (left), and for similar samples of mature remains (right). The value for Sunghir 3 is 54.1%. Sample sizes are 5, 93, and 27, respectively, (left to right) for the immature remains, and 22, 117 and 56, respectively, for the mature samples.

human samples ($P = 0.665$), and there is only a modest and non-significant difference in the non-dominant humerus ($P = 0.136$). In the non-dominant arm, the Sunghir 3 humerus has an average robustness (standardized residual of 0.29), but in the dominant arm, it is among the more hypertrophied of the comparative sample humeri (standardized residual of 1.37). It is therefore the hypertrophy of her right humerus that accounts for the high humeral diaphyseal asymmetry.

This dominant arm hypertrophy of Sunghir 3 is also evident in the asymmetries of her humeral muscle insertion tuberosities (Table 1). Comparative data are not available for these measures for immature individuals, but it is apparent that the high asymmetry values for all three insertion sites are well above what would be expected from the measurement of otherwise symmetrical features. This insertion asymmetry is accompanied by a distinctly larger lateral supracondylar crest on the right humerus (Figure 5), in the context of only slight epicondylar breadth asymmetry (Table 1).

The level of hypertrophy of the Sunghir 3 right humerus, in the context of a degree of left humeral robustness similar to those of other early and recent modern humans, indicates that she used both of her arms actively for manipulation, and that she was accomplishing more tasks requiring elevated strength in her dominant (right) arm, as was the case for a number of other Upper Paleolithic individuals. There is no reflection of any disuse of the arms, for manipulation, lifting, or carrying.

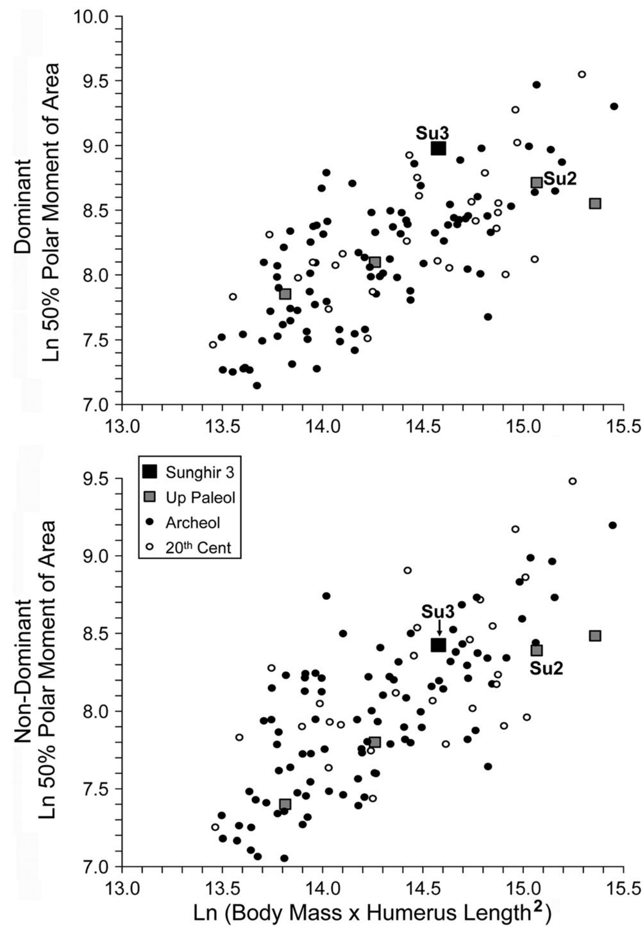

Figure 8. Bivariate plots of humeral midshaft diaphyseal polar moments of area versus estimated body mass times biomechanical length squared for recent human 8–15 year-olds, Upper Paleolithic 8–15 year-olds with Sunghir 2 (Su2) indicated, and Sunghir 3 (Su3). Dominant side humeri above and non-dominant ones below.

Discussion

It is therefore apparent that Sunghir 3 experienced non-pathological levels of activity for a Late Pleistocene late juvenile, conforming to the levels of hypertrophy evident in both immature and mature Upper Paleolithic individuals. This robustness occurred despite her femoral deformities and foreshortening and despite her indications of repeated and persistent systemic stress. The femoral bicondylar angles and low levels of asymmetry reflect non-pathological development of posture and locomotion. The tibial symmetry, cortical bone distribution, and overall rigidity indicate an individual who was loading her legs substantially more than what would occur from body mass alone at low activity levels. The humeral asymmetry data indicate that the right arm, with a normal left one, was being used for a variety of heavy duty manipulative activities. Although it is difficult to determine precisely what these activities were, they resulted in a very high level of humeral asymmetry in an immature female, rivaling the degree of asymmetry found in some adult remains. These diaphyseal comparisons combine with several indications of hypertrophied musculotendinous insertions in the upper limb, including those for triceps brachii on the left scapula, deltoideus, and teres major/latissimus dorsi on the humeri, and biceps brachii and brachialis on the radii and ulnae (Buzhilova, 2000; Buzhilova *et al.*, 2000; Buzhilova & Mednikova, 2004; Mednikova, 2005); these insertions are especially marked for the late juvenile age of Sunghir 3. Despite the femoral malformations, this individual was clearly engaged in a variety of physically demanding social/subsistence behaviors concomitant with her status as a member of a highly mobile foraging group.

Although there are other immature Pleistocene *Homo* individuals with serious abnormalities (Tillier, 1999; Tillier *et al.*, 2001; Gracia *et al.*, 2009), none of them provides evidence regarding their locomotor and/or manipulative persistence despite deformities. There are, however, several cases of adult late archaic and early modern humans with serious upper and/or lower limb abnormalities and associated evidence of functional persistence.

With respect to the loss of upper limb function, these cases include two Neandertals (Feldhofer 1 and Shanidar 1) and four Upper Paleolithic individuals (Barma Grande 2, Dolní Věstonice 15, Ohalo 2, and Obercassel 1). Feldhofer 1 had a fractured left proximal ulna, which resulted in a limited range of cubital movement, atrophy of the left humerus, and marked hypertrophy of the right humerus (Trinkaus *et al.*, 1994; Schultz, 2006). Shanidar 1 had a non-union fracture or amputation of the distal right humerus which resulted in humeral, scapular and clavicular atrophy/hypotrophy, an additional humeral fracture, and left humeral hypertrophy (Trinkaus, 1983; Trinkaus & Churchill, 1999). Barma Grande 2 exhibits marked asymmetry of the upper limb long bones, probably as a result of post-traumatic changes, with hypertrophy of the right humerus (Churchill & Formicola, 1997). Dolní Věstonice 15 sustained a right humeral distal diaphyseal deformity, left ulnar fracture and left radial deformity, resulting in right arm hypertrophy despite its abnormal curvature (Trinkaus *et al.*, 2006). Ohalo 2 experienced pathological ossification of the costosternal cartilages, associated with right humeral hypertrophy plus glenohumeral, acromioclavicular, and claviculosternal osteoarthritis (Hershkovitz *et al.*, 2005). And Obercassel 1 fractured his right ulna, which resulted in ossification of the right conoid ligaments and hypertrophy of the left humerus (Bonnet, 1919).

Sustained and healed deformities of the weight-bearing portions of the lower limb are less common in the Pleistocene fossil record. Shanidar 1 experienced a right metatarsal fracture and osteoarthritis across multiple right leg and foot articulations, resulting in an altered gait and abnormal dorsal bowing of the left tibia and fibula (Trinkaus, 1983). The Late Upper Paleolithic Vado all'Arancio 1 suffered a talocrural fracture, but remained sufficiently mobile to produce femoral and tibial diaphyseal asymmetry (Holt *et al.*, 2002). Dolní Věstonice 15 developed deformities of the femora, in association with his upper limb and other pathologies (Trinkaus *et al.*, 2006), but his tibial hypertrophy indicates that he maintained active mobility (Trinkaus *et al.*, 2001; Trinkaus, 2006). And the terminal Upper Paleolithic Romito 2 remained active into late adolescence despite pronounced chondrodystrophic dwarfism (Frayer *et al.*, 1988). Other serious lower limb abnormalities, such as the pronounced unilateral osteoarthritis of La Chapelle-aux-Saints 1 and Shanidar 3, the femoral foreshortening of Nazlet Khater 2, and the femoral and tibial muscular irregularities of Tianyuan 1, do not appear to have impeded function (Trinkaus, 1983, 1985; Crevecoeur, 2008; Shang & Trinkaus, 2010).

None of these individuals, or any of the other currently known Pleistocene *Homo* specimens, sustained injuries or deformities that would have prevented locomotion. The oldest previously noted (Trinkaus, 2011, 2012) case of a healed injury that would have prevented walking for an extended period of time (Veyrier 1) (Pittard & Sauter, 1946) has been shown to be mid-Holocene (Neolithic) in age (Stahl Gretsch, 2005). Only Vado all'Arancio 1 may have had a brief period of immobility (Holt *et al.*, 2002). The assessment of the appendicular hypertrophy of the unfortunate Sunghir 3 therefore places her among these other Late Pleistocene individuals, who not only provide evidence of long-term survival of developmental or degenerative abnormalities but also furnish evidence of substantial participation in the normal activity levels of these populations.

These considerations of the Mid Upper Paleolithic Sunghir 3 juvenile should also be placed in the context of the substantial mobility among these Interpleniglacial foragers. The adults of these populations had consistently high lower limb anteroposterior diaphyseal reinforcement for locomotion (Holt & Formicola, 2008; Trinkaus & Ruff, 2012). There are multiple indications of the long distance movement of raw materials and exotic items (Svoboda *et al.*, 1996; Féblot-Augustins, 1997; Roebroeks *et al.*, 2000). Stylistic patterns of art and body decoration are consistent over much of Eurasia (Abramova, 1995; Svoboda *et al.*, 1996; Roebroeks *et al.*, 2000; Norton & Gao, 2008), implying long distance communication. And elaborate 'red ochre' burials, although known at other time periods, are consistent across Eurasia during the Mid Upper Paleolithic (Zilhão, 2005; Formicola, 2007; Pettitt, 2011). Moreover, the harsh environmental conditions of high latitude, continental, Interpleniglacial eastern Europe in the vicinity of Sunghir (Alexeeva, 1998; Lavrushin & Spiridonova, 1998) would have necessitated considerable mobility, both residential and logistical, for survival. Any non-mobile individual is likely to have been left behind and would probably not have entered the human fossil record due to the lack of prompt burial, the ubiquitous carnivores, and therefore the rare subsequent preservation. A similar pattern has been invoked to explain the dearth of older adults in the available sample (Trinkaus, 2011).

From these considerations, now including Sunghir 3, it is apparent that these Pleistocene humans were able to survive serious impairments for extended periods of time. Yet, it also appears that only individuals who were able to remain mobile and, to some extent, contribute to the social group were able to persist, given the exigencies of a Pleistocene foraging existence.

Conclusion

Cross-sectional geometric assessment of the normal limb bones (tibiae and humeri) of the pathological Mid Upper Paleolithic Sunghir 3 late juvenile indicate that she was a physically active participant in the mobility and other activities of her social group, despite her deformed and foreshortened femora and evidence for persistent stress episodes and frailty. This diaphyseal assessment is supported by her muscle markings, bone condition, and developmental articular orientations. As such, Sunghir 3 joins a growing set of pathological Pleistocene human remains in indicating the survival and persistence of these individuals in their hunter–gatherer milieu. It also reinforces their necessity to keep up to be able to keep going.

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