



Human Palaeontology and Prehistory

The paleobiology of two adult skeletons from Baouso da Torre (Bausu da Ture) (Liguria, Italy): Implications for Gravettian lifestyle



Paléobiologie des deux squelettes adultes de Baouso da Torre (Bausu da Ture) (Ligurie, Italie) : apport à la compréhension des modes de vies durant le Gravettien

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ABSTRACT

This article presents the main skeletal characteristics of the two largely unpublished Gravettian adult skeletons from Baouso da Torre (Liguria, Italy). BT1 and BT2 were two adult tall males, who died aged respectively between 20 and 50 years, and between 20 and 30 years. Their body proportions fall within the range of variation known for the middle Upper Paleolithic, and their skeletal remains are characterized by considerable osteometric values, which fall consistently in the upper part of the Upper Paleolithic male sample variation. They show a high degree of upper limb lateralization, implying that they were likely involved in strenuous and/or repetitive unimanual tasks. They also exhibit very robust lower limbs, likely related to repeated long-distance travels in mountainous terrains. These results are in total agreement with previous hypotheses on Late Pleistocene population behavioral patterns.

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R É S U M É

Cet article présente les principales caractéristiques biologiques de deux squelettes humains gravettiens inédits provenant de Baouso da Torre (Ligurie, Italie). BT1 et BT2 étaient deux hommes adultes de grande taille, décédés respectivement entre 20 et 50 ans et entre 20 et 30 ans. Leurs proportions corporelles ne se distinguent pas de ce qui est connu pour la période. Toutefois, les dimensions de leurs ossements sont considérables et se situent systématiquement dans la partie supérieure de l'intervalle de variation de l'échantillon masculin du Paléolithique supérieur. Ces sujets présentent un haut degré d'asymétrie pour les membres supérieurs, impliquant qu'ils étaient probablement engagés fréquemment dans des activités physiques unimanuelles répétitives ou intenses. Ils présentent également une robustesse importante du membre inférieur, probablement associée à des déplacements de

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longues distances en terrain accidenté. Les résultats de cette étude sont en totale adéquation avec les hypothèses précédemment formulées sur les modes de vie des populations humaines de la fin du Pléistocène.

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1. Introduction

In the last two decades, studies on European Upper Paleolithic skeletal remains have permitted a renewed appreciation of the nature and variation of human skeletal biology and adaptations during this time period (e.g., Brewster et al., 2014; Formicola, 2003; Holliday, 1999; Holt and Formicola, 2008; Trinkaus et al., 2014). From those studies, two main considerations have started to emerge. First, Upper Paleolithic people differed in some ways from recent humans. Second, it seems clear that “the Last Glacial Maximum (LGM) [was] a critical phase in the biological and cultural evolution of Upper Paleolithic populations.” (Holt and Formicola, 2008, p. 70). This sentence written eight years ago is echoed nicely in recent studies of ancient DNA that infer a population expansion from southeastern European or western Asian refugia after the LGM (Fu et al., 2016; Posth et al., 2016). However, while population dispersals may account for some of the biological differences between the pre- and post-LGM groups in Europe (especially craniofacial dimensions and stature), other variations are likely related to behavioral changes.

The analysis of activity-related skeletal morphologies (see Knüsel, 2000) has been demonstrated to be an excellent tool to test hypotheses about micro-evolutionary processes and changing behavioral strategies in past populations, including Upper Paleolithic groups (Churchill, 1994; Churchill et al., 2000; Holt, 1999, 2003; Sparacello et al., 2014, n.d., 2017; Trinkaus, 2015; Villotte, 2011; Villotte et al., 2010). In European Upper Paleolithic groups, upper limb asymmetry (in terms of cross sectional bone geometry, external measurements, and activity related enthesopathies) is high, especially in males, which has led to suggestions that spear throwing (with or without a spear thrower) may have been a common male activity (Churchill and Rhodes, 2009; Sparacello et al., 2017; Villotte and Knüsel, 2014; Villotte et al., 2010; but see Churchill et al., 2000). Lower limb biomechanical traits are indicative of high levels of mobility (Holt, 1999, 2003; Sparacello et al., 2014, n.d.; Villotte, 2011). Although a decline in mobility from the middle Upper Paleolithic (MUP) to the late Upper Paleolithic (LUP) was proposed based on femoral traits (Holt, 1999, 2003; Villotte, 2011), recent studies suggest a scenario of high mobility levels throughout the Late Pleistocene (Sparacello et al., n.d.; Trinkaus, 2015).

The aim of this article is to present the main skeletal characteristics of the two largely unpublished adult skeletons from Baouso da Torre (also called Bausu da Ture (e.g., Holt and Formicola, 2008)). The only descriptions of these specimens are in the original studies done by Rivière (1887) and Verneau (1906), and none of the skeletons has been reevaluated in a comprehensive study since then. We discuss our results against the background of their

Upper Paleolithic contemporaries, in order to understand whether their biological and biomechanical profiles conform or deviate significantly from the picture provided by our current understanding of Late Pleistocene population diversity and behavioral patterns.

2. Material and methods

2.1. BT1 and BT2 skeletons

The Baouso da Torre cave is part of the Grimaldi, or Balzi Rossi complex of caves and rock shelters, one of the most important European Paleolithic sites on the Mediterranean coast, just at the border between Italy and France (Formicola and Holt, 2015). The skeletons of two adult (BT1 and BT2) and one adolescent (BT3) individuals were discovered in 1873 in this cave (Rivière, 1887). BT1 and BT3¹ were subsequently lost and re-discovered in 2008 by Dominique Henry-Gambier in the collections of the Musée lorrain (Villotte and Henry-Gambier, 2010). The collagen content from BT1, BT2, and BT3 – as well as from a pendant closely associated with BT2 – was too low to obtain reliable radiocarbon dates (Villotte and Henry-Gambier, 2010; unpublished data). However, the archaeological context indicates that an Upper Paleolithic date is secure and that it is likely that the burials were contemporaneous with the Gravettian occupations (Henry-Gambier, 2001; Henry-Gambier, 2008; Mussi, 1986, 2001).

The BT1 partial skeleton preserved very limited portions of the skull and dentition, the girdles, and the axial skeleton. Remaining bones – mainly from limbs – are usually sub-complete, although their surface is not altered. The BT2 skeleton is more complete but presents some reconstruction (with plaster and wax), and the surfaces are sometimes covered by concretion, glue, consolidants, or ochre, making their evaluation difficult. Almost all the bones of BT1 and BT2 are reddish, and some display clear traces of ochre. For BT2, this ochre is sometimes represented by a thick layer of several millimeters, especially on the occipital, the left parietal, the humerus, and the scapula.

No prehistoric anthropogenic marks were found on any bone. Both femora and the left humerus of BT1 display rodent gnaw marks. Rodent and carnivore marks are also visible on the BT2 skeleton: on both femora (carnivore) and on the tibiae and right fibula (carnivore marks on the extremities, rodent marks on the diaphyses).

¹ The study of BT3, which is not presented here, is still in progress. The detailed analysis of this immature individual is problematic due to the rediscovery, in recent times, of more bones/fragments of bones belonging to this skeleton, which need to be reunited with the original material before proceeding with the study (Villotte, in prep.).

2.2. The comparative sample

The comparative data is presented in detail in the [Supplementary Information \(SI 1\)](#). It consists of European Late Pleistocene humans, mostly mature individuals and a few late adolescents, chronologically divided in middle Upper Paleolithic (from about 30,000 years ago to the end of the Last Glacial Maximum) and late Upper Paleolithic (from the end of the Last Glacial maximum to the end of the Pleistocene). Osteometric and cross-sectional data derive from personal research of the authors and from the literature (See [SI 1](#)). Some individuals (Oberkassel 1, Barma Grande 2, Barma del Cavaglione 1, Vado all' Arancio 1) show marked limb abnormalities or trauma, and those skeletal elements were not included in the comparative sample.

2.3. Methods

The linear measurements follow the Martin system (M-#) ([Bräuer, 1988](#)), completed by measurements defined in [Sládek et al. \(2000\)](#) and [Murail et al. \(2005\)](#). Non-metric variations were recorded following [Hauser and De Stefano \(1989\)](#) for the skull, [Scott and Turner \(2000\)](#) for the dentition, and [Finnegan \(1978\)](#) for the infracranial skeleton. Dental wear was recorded following [Smith \(1984\)](#). “Traditional” robusticity indices computed from external measurements (i.e. diaphyseal thickness standardized to bone length) were calculated following [Bräuer \(1988\)](#). Biomechanical robusticity (i.e. diaphyseal rigidity scaled by body size) was estimated via cross-sectional geometry (CSG, see [Ruff et al., 2006a](#)). The biomechanical competence of long bones was calculated at specified percentages of bone length (mechanical length, as indicated in [Ruff, 2002](#)), using the polar moment of area as a measure of overall bending and torsional rigidity. Results were scaled by body size using bone mechanical length and estimated body mass ([Ruff, 2000](#)). The details of the methods used for CSG are provided in the [SI 2](#). Bilateral asymmetry for CSG properties and measurements of the upper limbs was computed as: $[100 \times (\text{maximum value} - \text{minimum value}) / \text{minimum value}]$, and expressed as a percentage ([Trinkaus et al., 1994](#)).

3. Results and discussion

A comprehensive skeletal inventory, as well as the morphological description of the BT1 and BT2 skeletal and dental elements, is available in the [SI 3](#). The cranial and infracranial measurements and the non-metric variations are reported in the [SI 4](#).

3.1. Sex and age assessments

The pelvis of BT1 is very badly preserved, and cannot be used for the sex assessment. However, all measurements of its appendicular skeleton are in the upper range of variation of Upper Paleolithic males (see below) and a secondary sex diagnosis based on discriminant function analysis indicates that BT1 is very likely a male ([Villotte et al., 2011a](#)). On the five morphological structures of the coxal bone used for the sex assessment in [Brůžek \(2002\)](#),

three (preauricular surface aspects, sciatic notch aspects, and morphology of the composite arch) can be scored on the BT2 left coxal bone and all indicate a male morphology (see [SI 4](#)). The probability of BT2 being a male or female has also been calculated by comparing measurements of its left coxal bone to those from a worldwide database ([Murail et al., 2005](#)). The posterior probability of BT2 being a male is 0.99 based on seven measurements (See [SI 4](#)).

Age-at-death of BT1 cannot be estimated using the pubic symphysis and the auricular surface of the ilium, since the first is missing and the latter heavily damaged. Skeletal maturity was reached (e.g., the iliac crest is fused) indicating a fully adult individual. In addition, the very limited preserved part of the auricular surface of the ilium shows no degenerative changes, no skeletal sign of degenerative processes related to senescence is present on any bone, and teeth are not heavily worn. Moreover, the metaphyseal line between the head and the diaphysis of the second right metacarpal is still macroscopically and radiologically visible. Based on those criteria, BT1 should be considered as a young adult/adult. Age-at-death estimation of BT2 is based on the state of fusion of later-fusing secondary centers of ossification, following [Owings Webb and Suchey \(1985\)](#), and on the morphology of the auricular surface of the ilium, following [Schmitt \(2005\)](#). The partial union of the epiphysis to the right medial clavicle and the morphology of the auricular surface of the ilium both identify BT2 as a young adult (20–29 years old).

3.2. The skull (cranium, mandible, and teeth)

In both individuals, the skull is fragmentary. The morphology of the neurocranium and the face of BT1 and BT2 is clearly modern, and none of the autapomorphic traits of Neanderthals (e.g., the suprainiac fossa, [Balzeau and Rougier, 2010](#)) is present for BT1 and BT2 partial skulls. It is however important to mention some features such as the presence of well-developed cranial structures (e.g., the external occipital protuberance) in both individuals, the partial mylohyoid bridging at the right side of the mandible of BT2, and the supernumerary ossicles of the cranial vault of BT1. The cranial capacity of BT2 can be estimated to $1502 \pm 64 \text{ cm}^3$ and to $1684 \pm 76 \text{ cm}^3$ (respectively from the third and eighth formulas of the Table 3 in [Olivier et al. \(1978\)](#)), in the upper part of the range of variation seen for the first part of the Upper Paleolithic [$1467 \pm 165 \text{ cm}^3$, $n = 29$ ([Trinkaus et al., 2014](#))].

Macroscopically, there is little to report on the tooth morphology. BT2 does not show evidence of heavy anterior tooth wear relative to the posterior teeth, contrary to some other Upper Paleolithic individuals ([Clement et al., 2012](#)). A comprehensive study of the teeth, including their internal structure, is planned in a near future.

3.3. Body mass, stature and body proportions

For both individuals, the dimensions used to calculate body mass, stature and body proportions have been estimated (see [SI 4](#)). Thus, it should be kept in mind that those figures are only indicative, and were used to place these individuals in the context of the other Upper Paleolithic

Table 1

Stature (in cm), body mass (in kg), and brachial and crural indices of BT individuals, and the comparative samples. Stature was always estimated from femoral maximum length using Trotter and Gleser (1952) equation for African-Americans. For body mass estimations, see Trinkaus and Ruff (2012) and SI 4. For crural and brachial indices, see Holliday (1999).

Tableau 1

Stature (en cm), masse corporelle (en kg), et indices brachiaux et cruraux pour les individus BT et les échantillons de comparaison. La stature est toujours estimée d'après la longueur maximale du fémur en utilisant les équations pour les Afro-Américains dans Trotter et Gleser (1952). Pour les estimations de la masse corporelle, voir Trinkaus et Ruff (2012) et Appendix BSI 4. Pour le calcul des indices brachiaux et cruraux, voir Holliday (1999).

	Stature	Body mass	Brachial index	Crural index
BT1	173.0	78.1	76.7	83.8
BT2	173.4	73.1	76.1	83.5
MUP Males	172.9 ± 5.0 (11)	75.9 ± 5.5 (12)	77.1 ± 1.4 (6)	84.5 ± 2.0 (8)
MUP Females	163.2 ± 4.7 (6)	64.3 ± 7.1 (6)	78.7 ± 2.4 (4)	84.3 ± 1.6 (3)
LUP Males	162.4 ± 4.6 (17)	69.4 ± 4.9 (17)	78.8 ± 2.4 (9)	85.6 ± 1.6 (11)
LUP Females	153.9 ± 4.3 (7)	60.0 ± 9.0 (8)	75.7 ± 1.5 (3)	84.7 ± 1.8 (3)

MUP: Middle Upper Paleolithic; LUP: Late Upper Paleolithic. The MUP sample does not include the BT individuals. The data for the comparative sample is presented as “mean ± standard deviation (number of individuals)”.

individuals. The body mass was estimated following the guidelines in Trinkaus and Ruff (2012), based on estimations of the supero-inferior diameter of the femoral head (see SI 4). BT1 and BT2 body masses are estimated to be 78.1 and 73.1 kg, respectively. Stature was estimated using Trotter and Gleser (1952) equation for African-Americans (based on femoral maximum length), as suggested by Formicola (2003) for European middle Upper Paleolithic specimens. The stature is of 173.0 ± 3.9 cm for BT1 and 173.4 ± 3.9 cm for BT2. All of these values fall in the range of variation seen for the MUP male sample (Table 1). Brachial and crural indices of BT1 and BT2 are slightly lower than the average values for the MUP and LUP samples (Table 1) but are still high when compared to recent Europeans (see Holliday, 1997).

3.4. Upper Limb functional adaptations: robusticity, asymmetry and pathology

Upper limbs measurements of the two BT individuals (see tables in SI 4) consistently fall in the upper portion of the variation seen for the Upper Paleolithic samples, and are even outliers for certain variables (e.g., distal radius circumference, see Fig. 1). In terms of “Traditional” robusticity computed from external measurements, the upper limb bones of BT individuals are relatively robust (Tables 2–4). When considering the mechanical robusticity via CSG properties, the humeri of the BT individuals (both sides) are consistently more robust than any middle Upper Paleolithic male in our comparative sample (Table 2, Fig. 2). As a result, BT individuals seem to fit better with the late Upper Paleolithic male sample. However, it is difficult to interpret this result from a functional adaptation point of view, given that differences in manipulatory behavior between the two periods are not well defined (see also below the discussion about upper limb asymmetry). In addition, it should be taken into account that the estimations of BT1 humeral length (see Table 11 in SI4) and of the femoral head diameter (both individuals, see Table 31 in SI4), from which body mass was calculated, suggest that the results should be interpreted with caution. CSG results for the forearm are more fragmentary, and the comparative sample size is smaller: only for BT2 was it possible to obtain CSG properties of the ulna, and only mid-proximally; the individual

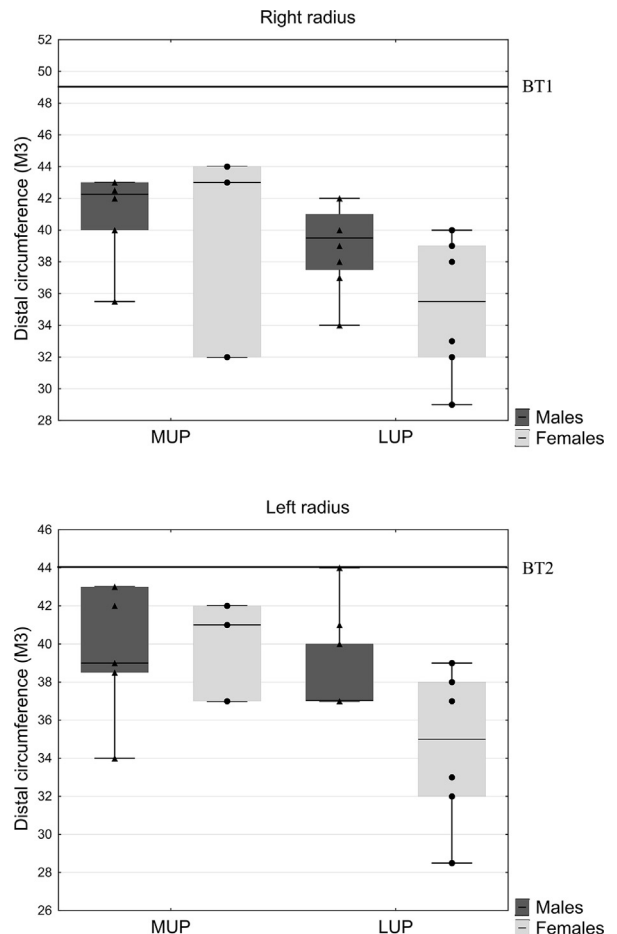


Fig. 1. Radius distal circumference. Values for BT individuals compared to the sample statistics of the Middle Upper (MUP) and Late Upper (LUP) Paleolithic specimens. Boxplots indicate the median (horizontal bar), the upper and lower quartiles (boxes), and the upper and lower non-outlier extremes (vertical bar).

Fig. 1. Circonférence du radius. Valeurs pour les individus BT comparées aux valeurs des échantillons du Paléolithique supérieur moyen (MUP) et récent (LUP). Les boîtes à moustaches indiquent la médiane (barre horizontale), le premier et le troisième quartiles (boîte) et les valeurs extrêmes sans les valeurs aberrantes (barre verticale).

Table 2

Humeral “Traditional” and biomechanical robusticity of BT individuals, and the comparative samples. See Table 1 for abbreviations and comments.

Tableau 2

Robustesse « classique » et robustesse « biomécanique » de l’humérus pour les individus BT et pour les échantillons de comparaison. Voir la légende du Tableau 1 pour les abréviations et commentaires.

	“Traditional” robusticity ^a		Biomechanical robusticity Mid-shaft Z _p (standardized) ^b		Biomechanical robusticity Mid-distal Z _p (standardized)	
	Right	Left	Right	Left	Right	Left
BT1	18.9	17.1			61.2	40.8
BT2	19.3	18.2	66.5	49.7	61.7	43.9
MUP Males	18.9 ± 1.1 (5)	17.6 ± 0.7 (6)	51.9 ± 6.8 (6)	38.5 ± 4.6 (8)	50.0 ± 7.6 (7)	34.5 ± 4.0 (8)
MUP Females	18.9 ± 0.1 (3)	18.3 ± 1.3 (4)	50.1 ± 9.7 (4)	43.1 ± 6.5 (5)	42.6 ± 11.6 (2)	37.6 ± 5.6 (3)
LUP Males	20.2 ± 0.5 (11)	19.2 ± 1.9 (9)	60.6 ± 8.5 (15)	50.6 ± 12.7 (14)	52.0 ± 7.1 (13)	42.3 ± 10.5 (13)
LUP Females	19.4 ± 0.7 (4)	19.1 ± 1.2 (6)	57.1 ± 8.7 (5)	53.0 ± 4.2 (4)	49.2 ± 8.1 (4)	48.2 ± 7.5 (5)

^a M7/M1 × 100.

^b Section modulus Z_p (mm³) standardized by dividing for body mass (kg) and bone length (mm).

Table 3

Ulnar “Traditional” and biomechanical robusticity of BT individuals, and the comparative samples. See Table 1 for abbreviations and comments.

Tableau 3

Robustesse « classique » et robustesse « biomécanique » de l’ulna pour les individus BT et pour les échantillons de comparaison. Voir la légende du Tableau 1 pour les abréviations et commentaires.

	“Traditional” robusticity ^a		Biomechanical robusticity Mid-proximal Z _p (standardized) ^b	
	Left	Right	Right	Left
BT2	13.9		37.9	30.9
MUP Males	11.1 ± 1.2 (3)		21.9 ± 5.4 (4)	19.8 ± 4.1 (4)
MUP Females	13.2 (1)		16.3 (1)	16.2 (1)
LUP Males			27.3 ± 3.0 (6)	20.3 ± 14.9 (6)
LUP Females	12.1 (1)			32.7 (1)

^a M3/M2(1) × 100.

^b Section modulus Z_p (mm³) standardized by dividing for body mass (kg) and bone length (mm).

is one of the most robust in the whole Upper Paleolithic sample (Table 3). BT1 has the right radius preserved, while the left is preserved in BT2. Both individuals tend to show high values of robusticity (Table 4, Fig. 1 and 2 in SI 2).

Upper limb values for external measurements and CSG properties are mostly greater for the right side (see SI 4). As a result, BT individuals share high levels of bilateral asymmetry with Upper Paleolithic (both middle and late) males (Table 5 and Fig. 3). Previous studies suggested that the level of CSG humeral asymmetry observed in Upper Paleolithic individuals, which is comparable with modern throwing athletes such as tennis players (Ireland et al., 2013; Shaw and Stock, 2009a; Trinkaus et al., 1994;

Warden et al., 2009), may be due to a hunting technique based on projectile weapons (e.g., Sládek et al., 2016; Sparacello et al., 2017). This activity is not only strenuous during hunting but requires continuous training during development for both strength and aim (Cattelain, 1997; Rhodes and Knüsel, 2005; Whittaker and Kamp, 2006). The high and intermittent loading rates correspond to the pattern that best stimulate osteogenic response (Burr et al., 1996, 2002; Robling et al., 2002). Experimental data on athletes also suggests that the forearm may be influenced by throwing behavior, but to a lesser extent and with greater variation in the results (Shaw and Stock, 2009a). The only element of the forearm for which bilateral CSG data were

Table 4

Radial “Traditional” and biomechanical robusticity of BT individuals, and the comparative samples. See Table 1 for abbreviations and comments.

Tableau 4

Robustesse « classique » et robustesse « biomécanique » du radius pour les individus BT et pour les échantillons de comparaison. Voir la légende du Tableau 1 pour les abréviations et commentaires.

	“Traditional” robusticity ^a		Biomechanical robusticity Mid-shaft Z _p (standardized) ^b		Biomechanical robusticity Mid-proximal Z _p (standardized) ^b	
	Right	Left	Right	Left	Right	Left
BT1	16.8		24.7		24.9	
BT2		16.4		20.1		19.8
MUP Males	14.7 ± 1.4 (5)	14.9 ± 0.7 (5)	16.4 ± 4.3 (6)	13.9 ± 2.7 (7)	13.4 ± 1.9 (4)	12.6 ± 2.3 (4)
MUP Females	13.5–16.48 (2)	15.9 ± 0.2 (3)	24.5 ± 8.0 (5)	20.0 ± 7.5 (4)	11.8 (1)	9.3 (1)
LUP Males	16.6 ± 0.9 (8)	16.1 ± 0.6 (7)	20.5 ± 3.6 (11)	18.0 ± 2.9 (12)	16.9 ± 1.3 (4)	20.5 ± 9.3 (2)
LUP Females	16.3 ± 0.8 (4)	15.1 ± 1.0 (4)	21.0 ± 1.6 (5)	19.9 ± 1.1 (3)	21.6 (1)	

^a M3/M1 × 100.

^b Section modulus Z_p (mm³) standardized by dividing for body mass (kg) and bone length (mm).

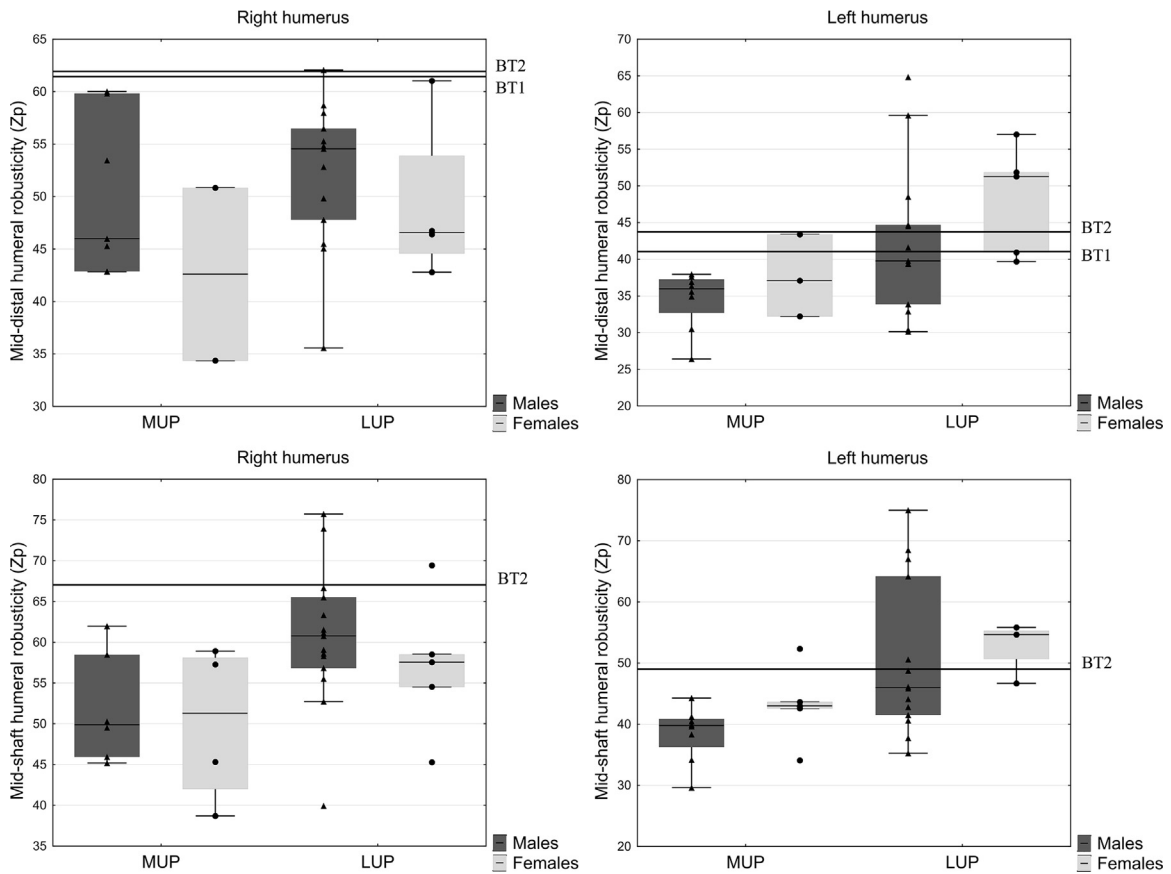


Fig. 2. Humeral robusticity [section modulus Z_p (mm^3) standardized by dividing for body mass (kg) and bone length (mm)]. For acronyms and explanations, see also Fig. 1.

Fig. 2. Robustesse de l'humérus [module de section polaire Z_p (mm^3) standardisé en le divisant par la masse corporelle (kg) et la longueur de l'os (mm)]. Pour les acronymes et explications, voir la légende de la Fig. 1.

available is the mid-proximal ulna of BT 2, which is the most lateralized in the middle Upper Paleolithic sample (Fig. 3 in SI 2).

This lateralized limb use is also indicated by a lesion at the right elbow of BT 2. The right common flexor origin on the medial epicondyle of BT2 was previously considered as a healthy enthesis (Villotte et al., 2010). However, a recent gentle cleaning of this area revealed an alteration of the attachment of the medial collateral ligament on the right side (Fig. 4a). The area exhibits an abnormal depression with a smooth cortical surface associated with a small

isolated bone protrusion. The left medial epicondyle does not display any change. Medial epicondyle enthesopathy (also called “thrower’s elbow”) is a rare condition seen mainly in sports employing the overhead throwing motion. This condition is also extremely rare in recent humans before 50 years of age (Villotte and Knüsel, 2014; Villotte et al., 2010).

This unilateral epicondylar lesion, and the high level of asymmetry observed in both the humerus and the forearm, suggest that stressful unimanual activities shaped the upper limb properties of BT individuals. These activities

Table 5

Humeral asymmetry of BT individuals, and the comparative samples. *J*: Polar moment of area, mm^4 . See Table 1 for abbreviations and comments.

Tableau 5

Asymétrie humérale pour les échantillons BT et pour les échantillons de comparaison. *J* : moment d’inertie polaire, mm^4 . Voir la légende du Tableau 1 pour les abréviations et commentaires.

	Max. length (M1)	Mid. max. diam. (M5)	Mid. min. diam (M6)	Mid. circum. (M7a)	Dist. min. circum. (M7)	Mid-distal <i>J</i>	Mid-shaft <i>J</i>
BT1					10.8	74.1	
BT2				4.3	9.4	66.9	56.0
MUP Males	0.8 ± 0.7 (3)	11.5 ± 4.6 (6)	8.7 ± 6.8 (6)	10.3 ± 5.9 (6)	11.4 ± 4.5 (6)	61.7 ± 28.7 (6)	52.5 ± 29.3 (6)
MUP Females	0–1.8 (2)	2.8 ± 0.4 (4)	3.4 ± 4.4 (4)	3.4 ± 1.2 (3)	2.6 ± 2.2 (4)	12.9 ± 12.7 (3)	20.3 ± 15.6 (5)
LUP Males	1.9 ± 1.4 (9)	14.6 ± 7.1 (10)	13.1 ± 5.9 (11)	11.8 ± 6.5 (7)	11.1 ± 4.3 (14)	58.6 ± 28.0 (14)	58.3 ± 29.5 (14)
LUP Females	2.1 ± 0.9 (4)	5.6 ± 3.7 (7)	6.7 ± 5.4 (7)	0.8 (1)	6.2 ± 2.9 (7)	12.5 ± 2.8 (4)	18.2 ± 15.6 (7)

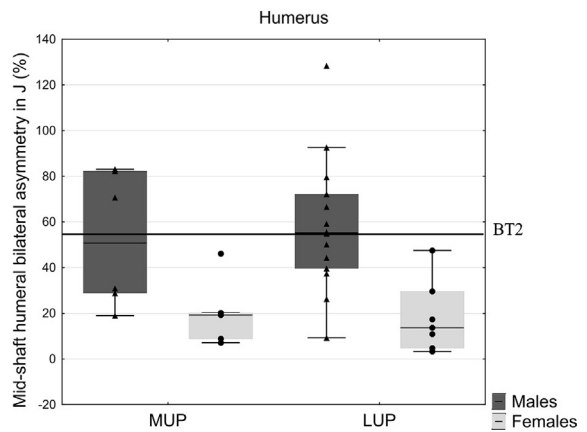
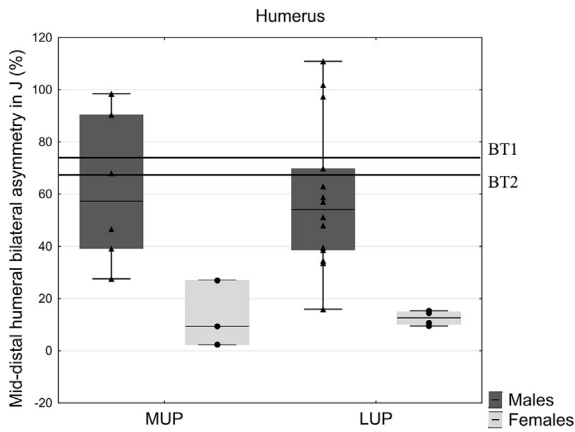


Fig. 3. Humeral bilateral asymmetry in diaphyseal rigidity [$100 \times (\max J - \min J) / \min J$]. *J*: polar moment of area, mm^4 . For abbreviations and explanations, see also Fig. 1.
Fig. 3. Asymétrie de la rigidité diaphysaire de l’humérus [$100 \times (\max J - \min J) / \min J$]. *J*: moment d’inertie polaire, mm^4 . Pour les acronymes et explications, voir la légende de la Fig. 1.

can be tentatively linked with the throwing motion, as suggested in several studies (see above). However, other activities may have contributed to the differential hypertrophy of the humeri through the Late Pleistocene, since repetitive domestic activities such as scraping, flint knapping, woodworking, and others, involve asymmetric recruiting of upper limb muscles (Shaw et al., 2012).

3.5. Lower limbs: locomotion, and mobility

BT individuals show large values of linear dimensions for the lower limbs (see SI 4), falling in the upper part of

the variation of the Upper Paleolithic male sample, and are even outliers for some variables (as illustrated for instance in Fig. 5). The femur and the tibia of the BT individuals appear robust (both in terms of external measurements and CSG properties) with respect to the Upper Paleolithic comparative samples (Tables 6 and 7, Fig. 6). Conversely, CSG fibular data, which was available only for BT 2, indicates a relatively less robust element, both in absolute terms and when compared with the tibia (Fig. 4 in SI 2); however, the comparative sample is small and shows high variance.

BT1 and BT2 femora exhibit very prominent gluteal buttresses leading to a low mERIC index (Table 6). Conversely, mid-shaft shape in both individuals is very elongated antero-posteriorly, as illustrated by both their pilastic index and CSG shape ratio (Table 6; Fig. 6), which are among the highest observed in the Upper Paleolithic sample. In contrast, in both BT individuals the midshaft tibia is eurycnemic (Table 7) and displays a low CSG shape index when



Fig. 4. a: medial epicondyle enthesopathy at the right humerus of BT2. The area of attachment of the medial collateral ligament exhibits an abnormal depression with a smooth cortical surface (white arrow) associated with a small isolated bone protrusion (black arrow); b: circular depression undercutting the left olecranon fossa of BT1; c: right fifth metatarsal of BT1: Bone lacuna distal to the articular surface for the fourth metatarsal.
Fig. 4. a : enthésopathie de l’épicondyle médial, humérus droit de BT2. La zone d’attachement du ligament collatéral médial présente une dépression anormale avec un fond régulier (flèche blanche) associée à une petite saillie osseuse isolée (flèche noire) ; b : dépression circulaire surcreusant la fosse olécranienne gauche de BT1 ; c : cinquième métatarsien droit de BT1 : lacune osseuse située en distal de la surface articulaire pour le quatrième métatarsien.

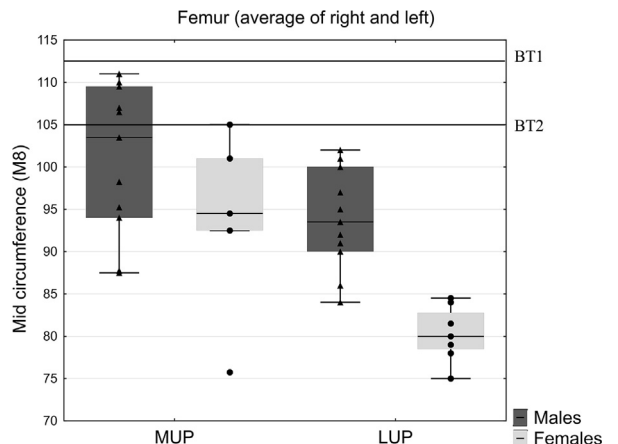


Fig. 5. Femoral midshaft circumference. For acronyms and explanations, see also Fig. 1.
Fig. 5. Circonférence fémorale à mi-diaphyse. Pour les acronymes et les explications, voir la légende de la Fig. 1.

Table 6

Femoral “traditional” and biomechanical robusticity, and “traditional” and CSG indices of BT individuals, and the comparative samples. See Table 1 for abbreviations and comments.

Tableau 6

Robustesse « classique » et robustesse « biomécanique » du fémur, et indices fémoraux pour les individus BT et pour les échantillons de comparaison. Voir la légende du Tableau 1 pour les abréviations et les commentaires.

	“Traditional” robusticity ^a	Biomechanical robusticity Mid-shaft Z_p (standardized) ^b	Meric index ^c	Pilastric index ^d	Shape index I_x/I_y ^e
BT1	23.1	127.8	80.3	134.1	2.0
BT2	21.7	133.3	84.6	131.5	2.0
MUP Males	20.1 ± 1.4 (9)	105.7 ± 25.0 (11)	75.9 ± 5.6 (11)	121.8 ± 8.4 (12)	1.55 ± 0.22 (11)
MUP Females	19.6 ± 1.5 (4)	105.2 ± 16.0 (6)	79.0 ± 8.2 (6)	124.8 ± 8.1 (5)	1.54 ± 0.41 (6)
LUP Males	21.3 ± 1.1 (12)	105.8 ± 11.0 (18)	79.1 ± 6.0 (15)	114.2 ± 7.8 (15)	1.38 ± 0.27 (18)
LUP Females	19.3 ± 0.8 (5)	96.7 ± 13.4 (7)	77.10 ± 5.3 (9)	113.4 ± 8.4 (9)	1.26 ± 0.27 (11)

^a $M8 \times 100/M1$.

^b Section modulus Z_p (mm^3) standardized by dividing for body mass (kg) and bone length (mm).

^c $M10 \times 100/M9$.

^d $M6 \times 100/M7$.

^e Ratio of the antero-posterior bending moment I_x on the medio-lateral bending moment I_y of the cross section.

compared with the rest of the Upper Paleolithic sample (Table 7, Fig. 6).

Lower limbs morphology is influenced by mobility patterns, load carrying, and the terrain on which those activities are performed (review in Carlson and Marchi, 2014). In CSG research, the rationale is that high terrestrial mobility will increase the frequency, stressfulness, and amount of antero-posteriorly directed loading, and therefore bending, of bones in the lower limb, which will lead to increased strength and high “shape indices” (ratios of antero-posterior and medio-lateral bending moments) at midshaft diaphysis. Accordingly, highly mobile hunter-gatherers, including Upper Paleolithic humans, generally show higher shape ratios (femoral I_x/I_y and tibial I_{\max}/I_{\min}) than sedentary agriculturalists (Carlson and Marchi, 2014). However, the scenario is complicated by the fact that body proportions and bone length might influence femoral shape (Ruff, 1995; Ruff et al., 2006b; Sparacello et al., n.d.). Also, different types of loading, for example running in a straight line versus frequent swerving, can have an impact on the functional adaptations of the tibio-fibular complex (Marchi and Shaw, 2011; Shaw and Stock, 2009b). Overall, the results obtained for BT individuals suggest high mobility levels, with high femoral shape indices and robust tibiae

(Holt, 2003; Shaw and Stock, 2009b). However, the very low CSG shape index of the tibia, at least for an Upper Paleolithic individual, observed in both BT1 and BT2 suggests a high degree of medio-lateral stress in the tibio-fibular complex (Shaw and Stock, 2009b). Interestingly, this does not result in a particularly robust fibula, as expected based on previous research (Hagihara and Nara, 2016; Marchi and Shaw, 2011; Sparacello et al., 2014). However, in a multivariate setting, BT2 conforms to the field hockey profile (Sparacello et al., n.d.), i.e. an individual performing high mobility with frequent swerving. This could be interpreted as indicating long-distance traversing of an uneven terrain, like the extremely mountainous inland of Liguria (Sparacello et al., 2014).

Further support to the scenario of high mobility is Fig. 7, which plots midshaft tibial rigidity (or polar moment of area, J) against midshaft humeral rigidity (cf. Shaw and Stock, 2013) for the Upper Paleolithic individuals, including BT 2. Samples with increased mobility appear to show a steeper linear fit, as suggested in Shaw and Stock (2013). In a pairwise comparison, the slope of the UP sample ($b=3.573$; standard error of $b=0.351$) is significantly steeper ($P<0.01$ or smaller) than all the comparative samples, except for the Late Stone

Table 7

Tibial “traditional” and biomechanical robusticity, and “traditional” and CSG indices of BT individuals, and the comparative samples. See Table 1 for abbreviations and comments.

Tableau 7

Robustesse « classique » et robustesse « biomécanique » du tibia, et indices tibiaux pour les individus BT et pour les échantillons de comparaison. Voir la légende du Tableau 1 pour les abréviations et commentaires.

	“Traditional” robusticity ^a	Biomechanical robusticity Mid-shaft Z_p (standardized) ^b	Platycnemic index ^c	Shape index I_{\max}/I_{\min} ^d
BT1	22.5	129.3	75.5	2.3
BT2	21.3	121.7	76.2	1.9
MUP Males	20.9 ± 1.6 (8)	111.8 ± 33.0 (11)	63.9 ± 7.3 (4)	2.98 ± 0.60 (11)
MUP Females	20.0 ± 2.1 (3)	106.0 ± 33.2 (6)	74.1 ± 5.0 (4)	2.18 ± 0.33 (6)
LUP Males	21.8 ± 1.1 (11)	109.4 ± 15.8 (16)	61.9 ± 4.7 (9)	2.85 ± 0.64 (16)
LUP Females	20.9 ± 0.4 (4)	101.2 ± 8.4 (5)	71.7–73.7 (2)	2.14 ± 0.27 (6)

^a $M10b \times 100/M1$.

^b Section modulus Z_p (mm^3) standardized by dividing for body mass (kg) and bone length (mm).

^c $M9 \times 100/M8$.

^d Ratio of the maximum bending moment I_{\max} on the minimum I_{\min} bending moment of the cross section.

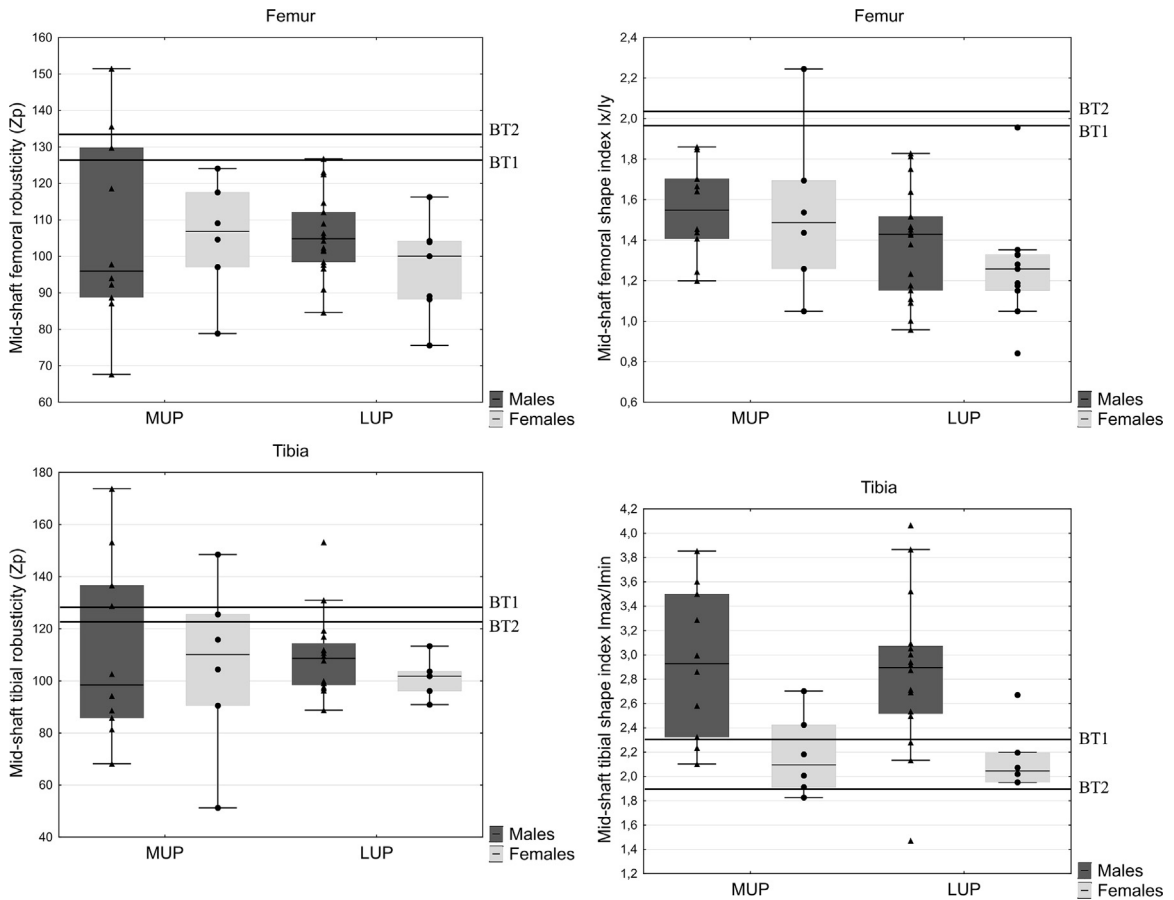


Fig. 6. Femoral and tibial robusticity [section modulus Z_p (mm^3) standardized by dividing for body mass (kg) and bone length (mm)], and femoral and tibial shape indices (for the femur: ratio of the antero-posterior bending moment I_x on the medio-lateral bending moment I_y of the section; for the tibia: ratio of the maximum bending moment I_{max} on the minimum I_{min} bending moment of the cross section). For abbreviations and explanations, see also Fig. 1. **Fig. 6.** Robustesse fémorale et tibiale [module de section polaire Z_p (mm^3) standardisé en le divisant par la masse corporelle (kg) et la longueur de l'os (mm)], et indices de forme pour le fémur (ratio du moment d'inertie antéro-postérieur I_x sur le moment d'inertie médio-latéral I_y) et le tibia (ratio du moment d'inertie maximum I_{max} sur le moment d'inertie minimum I_{min}). Pour les acronymes et explications, voir la légende de la Fig. 1.

Age southern Africans (Shaw and Stock, 2013). When a Bonferroni correction for multiple comparisons is applied (for the five samples being compared), the slope for the UP individuals is still steeper when compared to all the comparative samples ($P < 0.01$ or smaller), except for runners and Late Stone Age southern Africans. BT 2 falls close to the linear fit of the data, indicating that his values were typical of a group with presumably high mobility levels.

3.6. Minor abnormalities and pathologies

The anterior process of the left calcaneus of BT1 is abnormally elongated. The protuberance is oriented towards where the navicular bone would have been during life, although this bone has not survived. This individual also displays abnormal bossing of the dorsal part of the base of the right second metacarpal. A carpal boss, formed by an abnormal dorsal bossing of the left trapezoid and the base of the left second metacarpal was also found in BT2. These osseous modifications are likely related to congenital

tarsal and carpometacarpal coalitions. This suggests that these two adult males may have been genetically related (Villotte et al., 2011b).

Other minor abnormalities were also noticed for these individuals. The left olecranon fossa of BT1 (not preserved on the right side) is characterized by a circular depression (with a diameter of 7.5 mm and a depth of about 4 mm) in its upper part, undercutting the fossa (Fig. 4b). This change is likely due to a space-occupying lesion (i.e. a lesion that has impinged on the bone), but we were not able to identify a possible cause. However, it is worth remarking that this change appears completely different from an incomplete humeral aperture. BT1 also exhibits, on both fifth metatarsals, a bone lacuna distal to the articular surface for the fourth metatarsal, the floors of these lacunae resembling remodeled spongy bone (Fig. 4c). The diaphysis of BT2 fifth metacarpal is slightly oblique, maybe in relation with a healed fracture. BT2 exhibits some possible traces of a healed periosteal reaction on the right femur, whereas BT1 displays similar changes on the right tibia.

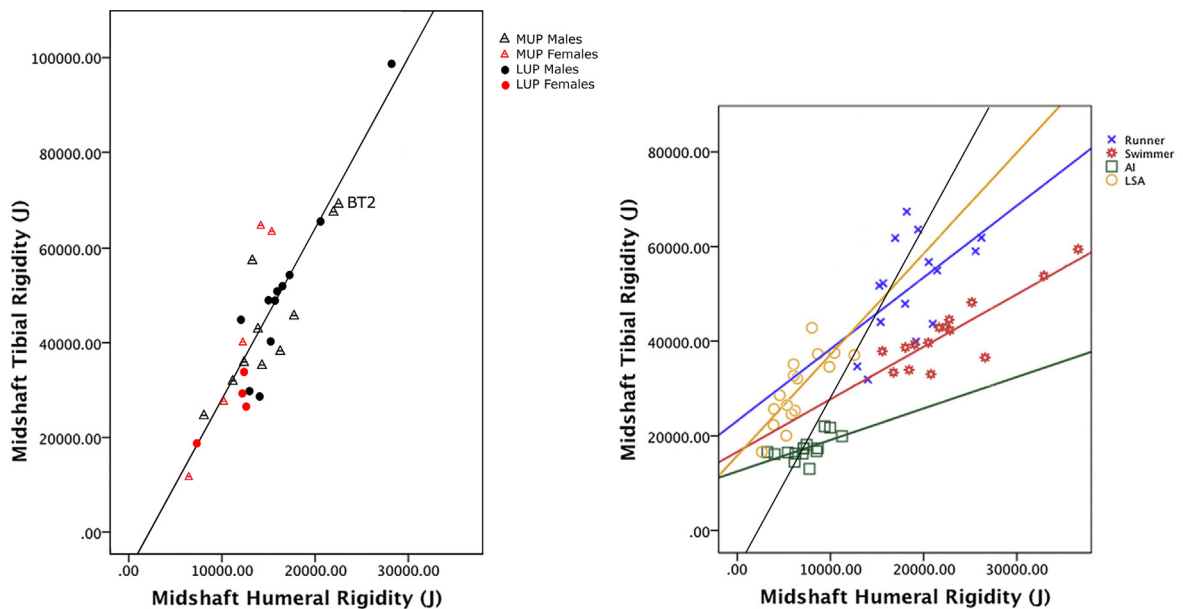


Fig. 7. Scatterplot of tibial midshaft rigidity (J) on humeral midshaft rigidity (J), with Least Squares fitting line of the data. J : polar moment of area, mm^4 . On the left, the results obtained for the Upper Paleolithic pooled sample. Individuals are labeled by sex and period (MUP: Middle Upper Paleolithic; LUP: Late Upper Paleolithic). Regression function: $[(J_{\text{tibia}} = -7869.3641 + 3.573 \times J_{\text{humerus}}); R^2 = 0.787, P < 0.00001]$. On the right, a reproduction of Fig. 2 from Shaw and Stock (2013) showing athletes (swimmers and runners), Adaman Islander males (AI), and Late Stone Age south Africans (LSA). The fitting line in black is the one obtained for the MUP and LUP individuals included in this study, and is shown in this graph to visually evaluate its slope when compared to the other samples.

Fig. 7. Diagramme de dispersion des moments d'inertie polaire (J en mm^4) pour le tibia par rapport à l'humérus, avec une droite de régression calculée par la méthode des moindres carrés. À gauche, les résultats obtenus pour l'échantillon du Paléolithique supérieur. Les sujets sont identifiés par sexe et par période [Paléolithique supérieur moyen (MUP) et récent (LUP)]. Équation de régression : $[(J_{\text{tibia}} = -7869,3641 + 3,573 \times J_{\text{humérus}}) ; R^2 = 0,787, p < 0,00001]$. À droite, une reproduction de la Fig. 2 dans Shaw et Stock (2013) montrant les données pour des athlètes (nageurs et coureurs), des Andamanais (AI) et des sujets d'Afrique du Sud du Late Stone Age (LSA). La droite de régression en noir est celle obtenue pour les sujets MUP et LUP inclus dans cette étude, présente ici pour visualiser sa pente comparée à celles des autres échantillons.

4. Conclusions

This article provides a comprehensive description of the well-preserved skeletons of two Upper Paleolithic individuals. BT1 and BT2 were two adult tall males, who died aged respectively between 20 and 50 years, and between 20 and 30 years. Their body proportions fall within the range of variation known for the middle Upper Paleolithic, and their skeletal remains are characterized by considerable osteometric values, which fall consistently in the upper part of, or even above, the Upper Paleolithic male sample variation. These two individuals were likely genetically related to each other, with a high degree of upper limb lateralization, and very robust lower limbs. They were probably involved in strenuous and/or repetitive unimanual tasks, and likely travelled repeatedly long distances in the extremely mountainous inland of Liguria. Our results thus reinforce hypotheses on Late Pleistocene population behavioral patterns, namely the existence of a division of labor between unimanual (mostly male) and bi-manual tasks (mostly female), and high levels of mobility. Those behavioral patterns appear unchanging throughout the Upper Paleolithic, even if major population turnover(s) took place in Europe during the Late Glacial.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2016.09.004>.

References

- Balzeau, A., Rougier, H., 2010. Is the suprainiac fossa a Neandertal autapomorphy? A complementary external and internal investigation. *J. Hum. Evol.* 58, 1–22.
- Bräuer, G., 1988. Osteometrie. In: Knussmann, R. (Ed.), *Anthropologie: handbuch der vergleichenden Biologie des Menschen*. G. Fischer, Stuttgart, pp. 160–232.
- Brewster, C., Meiklejohn, C., von Cramon-Taubadel, N., Pinhasi, R., 2014. Craniometric analysis of European Upper Palaeolithic and Mesolithic samples supports discontinuity at the Last Glacial Maximum. *Nat. Commun.* 5.
- Brůžek, J., 2002. A method for visual determination of sex, using the human hip bone. *Am. J. Phys. Anthropol.* 117, 157–168.
- Burr, D.B., Milgrom, C., Fyhrig, D., Forwood, M., Nyska, M., Finestone, A., Hoshaw, S., Saieg, E., Simkin, A., 1996. In vivo measurement of human tibial strains during vigorous activity. *Bone* 18, 405–410.
- Burr, D.B., Robling, A.G., Turner, C.H., 2002. Effects of biomechanical stress on bones in animals. *Bone* 30, 781–786.
- Carlson, K.J., Marchi, D., 2014. *Reconstructing Mobility*. Springer.
- Cattelain, P., 1997. Hunting during the Upper Paleolithic: Bow, Spearthrower or Both? In: Knecht, H. (Ed.), *Projectile Technology*. Springer, New York, pp. 213–240.
- Churchill, S.E., 1994. Human upper body evolution in the Eurasian later Pleistocene. Ph.D. thesis, anthropology. University of New Mexico, Albuquerque (395 p.).
- Churchill, S.E., Rhodes, J.A., 2009. The evolution of the human capacity for “killing at a distance”: the human fossil evidence for the evolution of projectile weaponry. In: Hublin, J.-J., Richards, M.P. (Eds.), *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence*. Springer, Dordrecht, pp. 201–210.
- Churchill, S.E., Formicola, V., Holliday, T.W., Holt, B.M., Schumann, B.A., 2000. The Upper Palaeolithic population of Europe in an evolutionary perspective. *Hunters of the Golden Age*, pp. 31–57.
- Clement, A.F., Hillson, S.W., Aiello, L.C., 2012. Tooth wear, Neanderthal facial morphology and the anterior dental loading hypothesis. *J. Hum. Evol.* 62, 367–376.
- Finnegan, M., 1978. Non-metric variation of the infracranial skeleton. *J. Anat.* 125, 23–37.
- Formicola, V., 2003. More is not always better: Trotter and Gleser's equations and stature estimates of Upper Paleolithic European samples. *J. Hum. Evol.* 45, 239–244.
- Formicola, V., Holt, B.M., 2015. Tall guys and fat ladies: Grimaldi's Upper Paleolithic burials and figurines in an historical perspective. *J. Anthrop. Sci.* 93, 71–88.
- Fu, Q., Posth, C., Hajdinjak, M., Petr, M., Mallick, S., Fernandes, D., Furtwängler, A., Haak, W., Meyer, M., Mittnik, A., Nickel, B., Peltzer, A., Rohland, N., Slon, V., Talamo, S., Lazaridis, I., Lipson, M., Mathieson, I., Schiffels, S., Skoglund, P., Dereviianko, A.P., Dроздов, N., Slavinsky, V., Tsybancov, A., Cremonesi, R.G., Mallegni, F., Gély, B., Vacca, E., Morales, M.R.G., Straus, L.G., Neugebauer-Maresch, C., Teschler-Nicola, M., Constantin, S., Moldovan, O.T., Benazzi, S., Peresani, M., Coppola, D., Lari, M., Ricci, S., Ronchitelli, A., Valentin, F., Thevenet, C., Wehrberger, K., Grigorescu, D., Rougier, H., Crevecoeur, I., Flas, D., Semal, P., Mannino, M.A., Cupillard, C., Bocherens, H., Conard, N.J., Harvati, K., Moiseyev, V., Drucker, D.G., Svoboda, J., Richards, M.P., Caramelli, D., Pinhasi, R., Kelso, J., Paterson, N., Krause, J., Pääbo, S., Reich, D., 2016. The genetic history of Ice Age Europe. *Nature* 534, 200–205.
- Hagihara, Y., Nara, T., 2016. Morphological features of the fibula in Jomon hunter-gatherers from the shell mounds of the Pacific coastal area. *Am. J. Phys. Anthropol.*, <http://dx.doi.org/10.1002/ajpa.23000> (Epub ahead of print).
- Hauser, G., De Stefano, G.F., 1989. *Epigenetic Variants of the Human Skull*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Henry-Gambier, D., 2001. La sépulture des enfants de Grimaldi (Grotte des Enfants site des Baoussé-Roussé, Italie). *Anthropologie et paléontologie funéraire des populations de la fin du Paléolithique supérieur*. éditions du CTHS, Paris.
- Henry-Gambier, D., 2008. Comportement des populations d'Europe au Gravetti, Pratiques funéraires et interprétations. *Paleo* 20, 399–438.
- Holliday, T.W., 1997. Body proportions in Late Pleistocene Europe and modern human origins. *J. Hum. Evol.* 32, 423–447.
- Holliday, T.W., 1999. Brachial and crural indices of European Late Upper Paleolithic and Mesolithic humans. *J. Hum. Evol.* 36, 549–566.
- Holt, B., 1999. Biomechanical evidence of decreased mobility in Upper Paleolithic and Mesolithic Europe. Ph. D. dissertation. University of Missouri-Columbia.
- Holt, B.M., 2003. Mobility in Upper Paleolithic and Mesolithic Europe: evidence from the lower limb. *Am. J. Phys. Anthropol.* 122, 200–215.
- Holt, B.M., Formicola, V., 2008. Hunters of the Ice Age: The biology of Upper Paleolithic people. *Am. J. Phys. Anthropol.* 137, 70–99.
- Ireland, A., Maden-Wilkinson, T., McPhee, J., Cooke, K., Narici, M., Degens, H., Rittweger, J., 2013. Upper limb muscle-bone asymmetries and bone adaptation in elite youth tennis players. *Med. Sci. Sports Exerc.* 45, 1749–1758.
- Knüsel, C.J., 2000. Bone adaptation and its relationship to physical activity in the past. In: Cox, M., Mays, S.A. (Eds.), *Human osteology in archeology and forensic science*. Greenwich Medical Media, London, pp. 381–401.
- Marchi, D., Shaw, C.N., 2011. Variation in fibular robusticity reflects variation in mobility patterns. *J. Hum. Evol.* 61, 609–616.
- Murail, P., Bruzek, J., Houët, F., Cunha, E., 2005. DSP: a tool for probabilistic sex diagnosis using worldwide variability in hip-bone measurements. *Bull. Mem. Soc. Anthropol. Paris n.s.* 17, 167–176.
- Mussi, M., 1986. Italian Palaeolithic and Mesolithic Burials. *Hum. Evol.* 1, 545–546.
- Mussi, M., 2001. *Earliest Italy: an overview of the Italian Paleolithic and Mesolithic*. Kluwer Academic Publishers, New York.
- Olivier, G., Aaron, C., Fully, G., Tissier, G., 1978. New estimations of stature and cranial capacity in modern man. *J. Hum. Evol.* 7, 513–518.
- Owings Webb, P.A., Suchey, J.M., 1985. Epiphyseal union of the anterior iliac crest and medial clavicle in a modern multiracial sample of American males and females. *Am. J. Phys. Anthropol.* 68, 457–466.
- Posth, C., Renaud, G., Mittnik, A., Drucker, Dorothee G., Rougier, H., Cupillard, C., Valentin, F., Thevenet, C., Furtwängler, A., Wißing, C., Francken, M., Malina, M., Bolus, M., Lari, M., Gigli, E., Capecchi, G., Crevecoeur, I., Beauval, C., Flas, D., Germonpré, M., van der Plicht, J., Cottiaux, R., Gély, B., Ronchitelli, A., Wehrberger, K., Grigorescu, D., Svoboda, J., Semal, P., Caramelli, D., Bocherens, H., Harvati, K., Conard, Nicholas J., Haak, W., Powell, A., Krause, J., 2016. Pleistocene Mitochondrial Genomes Suggest a Single Major Dispersal of Non-Africans and a Late Glacial Population Turnover in Europe. *Curr. Biol.* 26, 827–833.
- Rivière, E., 1887. *Antiquité de l'homme dans les Alpes-Maritimes*. J.-B. Bailière, Paris.
- Rhodes, J.A., Knüsel, C.J., 2005. Activity-related skeletal change in Medieval humeri: cross-sectional and architectural alterations. *Am. J. Phys. Anthropol.* 128, 536–546.
- Robling, A.G., Hinant, F.M., Burr, D.B., Turner, C.H., 2002. Improved bone structure and strength after long-term mechanical loading is greatest if loading is separated into short bouts. *J. Bone Miner. Res.* 17, 1545–1554.
- Ruff, C.B., 1995. Biomechanics of the hip and birth in early *Homo*. *Am. J. Phys. Anthropol.* 98, 527–574.
- Ruff, C.B., 2000. Biomechanical analyses of archaeological human skeletons. In: Katzenberg, M.A., Saunders, S.R. (Eds.), *Biological Anthropology of the Human Skeleton*. Wiley-Liss, New York, pp. 71–102.
- Ruff, C.B., 2002. Long bone articular and diaphyseal structure in old world monkeys and apes. I: locomotor effects. *Am. J. Phys. Anthropol.* 119, 305–342.
- Ruff, C.B., Holt, B.M., Trinkaus, E., 2006a. Who's afraid of the big bad Wolff? Wolff's law and bone functional adaptation. *Am. J. Phys. Anthropol.* 129, 484–498.
- Ruff, C.B., Holt, B.M., Sládek, V., Berner, M., Murphy, W., zur Nedden, D., Seidler, H., Recheis, W., 2006b. Body size, body proportions, and mobility in the Tyrolean 'Iceman'. *J. Hum. Evol.* 51, 91–101.
- Schmitt, A., 2005. Une nouvelle méthode pour estimer l'âge au décès des adultes à partir de la surface sacro-pelvienne iliaque. *Bull. Mem. Soc. Anthropol. Paris n.s.* 17, 89–101.
- Scott, G., Turner, C., 2000. *The anthropology of modern teeth: Dental morphology and its variation in recent human populations*. Cambridge University Press, Cambridge.

- Shaw, C.N., Stock, J.T., 2009a. Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern athletes. *Am. J. Phys. Anthropol.* 140, 160–172.
- Shaw, C., Stock, J., 2009b. Intensity, repetitiveness, and directionality of habitual adolescent mobility patterns influence the tibial diaphysis morphology of athletes. *Am. J. Phys. Anthropol.* 140, 149–159.
- Shaw, C.N., Stock, J.T., 2013. Extreme mobility in the Late Pleistocene? Comparing limb biomechanics among fossil *Homo*, varsity athletes and Holocene foragers. *J. Hum. Evol.* 64, 242–249.
- Shaw, C.N., Hormann, C.L., Petraglia, M.D., Stock, J.T., Gottschall, J.S., 2012. Neandertal humeri may reflect adaptation to scraping tasks, not spear thrusting. *PLoS One* 7 (7), e40349.
- Sládek, V., Trinkaus, E., Hillson, S.W., Holliday, T.W., 2000. The people of the Pavlovian. Skeletal catalogue and osteometrics of the Gravettian fossil hominids from Dolní Věstonice and Pavlov. Academy of Sciences of the Czech Republic, Brno.
- Sládek, V., Ruff, C.B., Berner, M., Holt, B., Niskanen, M., Schuplerová, E., Hora, M., 2016. The impact of subsistence changes on humeral bilateral asymmetry in Terminal Pleistocene and Holocene Europe. *J. Hum. Evol.* 92, 37–49.
- Smith, B.H., 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J. Phys. Anthropol.* 63, 39–56.
- Sparacello, V.S., Marchi, D., Shaw, C.S., 2014. The importance of considering fibular robusticity when inferring the mobility patterns of past populations. In: Carlson, K., Marchi, D. (Eds.), *Reconstructing mobility: environmental, behavioral, and morphological determinants*. Springer, New York, pp. 91–111.
- Sparacello, V.S., Villotte, S., Shaw, C.N., Fontana, F., Mottes, E., Starnini, E., Marchi, D., n.d. Changing mobility patterns at the Pleistocene-Holocene transition: the biomechanics of the lower limb of Italian Gravettian and Mesolithic individuals, in: Cristiani, E., Borgia, V. (Eds.), *Palaeolithic Italy*. Sidestone Press, Cambridge.
- Sparacello, V.S., Villotte, S., Shackelford, L.L., Trinkaus, E., 2017. Patterns of Humeral Asymmetry among Late Pleistocene Humans. *C. R. Palevol* (this issue).
- Trinkaus, E., 2015. The appendicular skeletal remains of Oberkassel 1 and 2. In: Giemsch, L., Schmitz, R.W. (Eds.), *The Late Glacial Burial from Oberkassel Revisited*. Verlag Phillip von Zabern, Darmstadt, pp. 75–132.
- Trinkaus, E., Buzhilova, A.P., Mednikova, M.B., Dobrovolskaya, M.V., 2014. *The People of Sunghir. Burials, Bodies, and Behavior in the earlier Upper Paleolithic*. Oxford University Press, New York.
- Trinkaus, E., Churchill, S.E., Ruff, C.B., 1994. Postcranial robusticity in *Homo*. II: Humeral bilateral asymmetry and bone plasticity. *Am. J. Phys. Anthropol.* 93, 1–34.
- Trinkaus, E., Ruff, C.B., 2012. Femoral and Tibial Diaphyseal Cross-Sectional Geometry in Pleistocene *Homo*. *PaleoAnthropology*, 13–62.
- Trotter, M., Gleser, G., 1952. Estimation of stature from long limb bones of American Whites and Negroes. *Am. J. Phys. Anthropol.* 10, 463–514.
- Verneau, R., 1906. *Les grottes de Grimaldi (Baoussé-Roussé)*, Anthropologie II-1. Imprimerie de Monaco, Monaco.
- Villotte, S., 2011. Les comportements au Gravettien : apport des « marqueurs osseux d'activité ». In: Goutas, N., Guillermin, P., Klaric, L., Pesesse, D. (Eds.), *À la recherche des identités gravettiennes: actualités, questionnements et perspectives*, Actes de la table ronde sur le Gravettien en France et dans les pays limitrophes. *Mem. Soc. Prehist. Fr.*, 52, pp. 209–216.
- Villotte, S., Churchill, S.E., Dutour, O., Henry-Gambier, D., 2010. Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: evidence from upper limb enthesopathies. *J. Hum. Evol.* 59, 35–43.
- Villotte, S., Henry-Gambier, D., 2010. The rediscovery of two Upper Palaeolithic skeletons from Baouso da Torre cave (Liguria-Italy). *Am. J. Phys. Anthropol.* 141, 3–6.
- Villotte, S., Knüsel, C.J., 2014. “I sing of arms and of a man...”: medial epicondylitis and the sexual division of labour in prehistoric Europe. *J. Archaeol. Sci.* 43, 168–174.
- Villotte, S., Brůžek, J., Henry-Gambier, D., 2011a. Caractéristiques biologiques des sujets adultes gravettiens: révision de l'âge au décès et du sexe. In: Goutas, N., Guillermin, P., Klaric, L., Pesesse, D. (Eds.), *À la recherche des identités gravettiennes: actualités, questionnements et perspectives*, Actes de la table ronde sur le Gravettien en France et dans les pays limitrophes. *Mem. Soc. Prehist. Fr.*, 52, pp. 209–216.
- Villotte, S., Knüsel, C.J., Mitchell, P.D., Henry-Gambier, D., 2011b. Probable carpometacarpal and tarsal coalition from Baouso da Torre Cave (Italy): Implications for burial selection during the Gravettian. *J. Hum. Evol.* 61, 117–120.
- Warden, S.J., Bogenschutz, E.D., Smith, H.D., Gutierrez, A.R., 2009. Throwing induces substantial torsional adaptation within the midshaft humerus of male baseball players. *Bone* 45, 931–941.
- Whittaker, J.C., Kamp, K.A., 2006. Primitive weapons and modern sport: atlatl capabilities, learning, gender, and age. *Plains Anthropol.* 198, 213–221.