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The Late Upper Paleolithic skeleton Villabruna 1 (Italy): a source of data on biology and behavior of a 14.000 year-old hunter

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Summary - *The Late Upper Paleolithic burial Villabruna 1 (Val Cismon, Belluno, Italy), directly dated to about 14,000 years ago (calibrated chronology), includes a well preserved skeleton accompanied by grave goods and covered with painted stones. The skeleton belongs to an adult male, about twenty-five years old, characterized by a relatively tall stature for the time period, short trunk and more linear body proportions than its contemporaries, similar to those of recent North-African populations. Multivariate statistical analysis of craniofacial characteristics place Villabruna 1 close to Le Bichon 1, a geographically and chronologically nearby specimen, suggesting genetic affinity among the last hunter and gatherers from the alpine region. Observations on dental wear and microwear indicate that the anterior dentition was involved in non-alimentary activities such as the mastication of fibrous materials including large abrasive contaminants. Whereas the information on dietary habits drawn from dental wear is not conclusive, stable isotopes analysis points to a terrestrially based diet rich in animal proteins. Biomechanical study of major long bones indicates heightened overall robusticity and marked humeral asymmetry. These results suggest intense unimanual activity, possibly linked to repeated throwing movements in hunting, and the combined effect of mobile lifestyle and mountainous terrain, as far as the femur is concerned. Paleopathological analysis did not reveal signs of any major event which might help identify a possible cause of death. However, macroscopic and radiographic examination of the skull reveals traces of porotic hyperostosis, indicative of a healed anemic condition. Finally, localized tibial periostitis, probably of traumatic origin, and lumbar hyperlordosis associated with deformations of vertebral bodies and L5 spondylolysis provide evidence of additional, minor, pathological changes.*

Keywords - *Skeletal biology, Late Upper Paleolithic, Italy, Villabruna 1.*

Introduction

In the late '80s, the removal of a detrital cone in Val Cismon (Sovramonte, Belluno, Italy) led to the discovery of several rock shelters located at 500 m asl showing traces of prehistoric human activity (Fig. 1).

These rock shelters, named "Ripari Villabruna" after their discoverer, belong to a complex logistic system of sites ranging from valley

Fig. 1 - Map of Italy. The marker indicates the location of the Ripari Villabruna (Val Cismon, Belluno). The colour version is available online at the JASs web site.

bottom to alpine prairies (Broglio & Villabruna, 1991). Archeological deposit analysis suggests various short-term anthropogenic events, starting during the Late Epigravettian. Radiocarbon dating of the basal layer (R-2023: 12,040±150 b.p.; calibrated: 14,350÷13,450 B.P.; OxCAl 3.0, 2σ) (Broglio & Improta, 1995) indicates that human occupation of Ripari Villabruna began as early as 14,000 years ago (in calibrated chronology), extending throughout the Würmian Tardiglacial and subsequently up to the mid-Holocene. Anthracological data and correlations with contemporary sites suggest that the surrounding environment consisted of alpine prairies, with scarce arboreal vegetation including *Pinus sylvestris/montana*. Faunal remains found in the Epigravettian levels mostly belong to *Capra ibex*, *Rupicapra rupicapra* and *Cervus elaphus*. Traces of butchery marks on the bones indicate human activity as the main reason for the accumulation of animal remains (Aimar *et al.*, 1992).

During systematic excavations that took place in 1988, Broglio and co-workers (a team from the University of Ferrara and from the "Gruppo Amici del Museo di Belluno") discovered a burial including a well preserved skeleton (Fig. 2), situated at the base of the archeological deposit (Broglio, 1995, 2000). The skeleton was cast in situ by G. Giacobini and is currently preserved at the Museo Civico di Belluno. The direct AMS date of the skeletal remains (KIA-27004: 12,140±70 b.p.; calibrated: 14,160÷13,820 B.P., OxCal 3.0, 2σ), indicates that the burial event occurred during the earliest phases of human occupation of the rock shelter. The skeleton was laid extended and supine in a narrow and shallow (30-40 cm) pit, the head reclined to the left and the upper limbs extended at the side. Six grave goods, most probably originally contained in a bag were recovered from the left side of the skeleton. They include what has been proposed as the equipment for a Paleolithic hunter: a flint knife, a flint nucleus, a stone used as a hammer, a flint blade, a bone point and a pellet made of ochre and propolis (Cattani, 1993). Atop the burial were found several calcareous stones, some of which exhibit well-defined drawings painted in red ochre. According to the discoverers, the stones were placed to mark the burial location (Broglio, 1992, 1998). Six vertical bands painted in red ochre, which were discovered on the walls of the rock shelter jutting above the burial, may have served an analogous purpose.

The excellent preservation of the skeleton Villabruna 1 allows investigation of various aspects of the skeletal biology (body size, cranio-facial morphology, dental wear, functional anatomy, as well as nutritional and pathological aspects) of an Upper Paleolithic hunter living in the alpine region approximately 14,000 years ago. By comparing data collected on Villabruna 1 with those drawn from fossil and recent samples, this paper aims to improve our comprehension of biocultural adaptations, life conditions and subsistence strategies of European Late Upper Paleolithic populations.

The material

The skeleton is in an overall excellent state of preservation, although the distal portions of both lower limbs are incomplete due to damage that occurred during the working activities that led to the discovery of the site. Both the skull and the mandible are complete, while LI^1 has been lost post-mortem, and LP_4 and RM^2 are no longer available. All vertebral elements, sacrum, *os coxae*, clavicles, humeri, ulnae, right radius and femur and left patella are complete or only slightly damaged. The left radius and femur, tibiae and fibulae are severely damaged and largely incomplete. Sternum, ribs and scapulae are incomplete. Almost all the bones of both hands are preserved, while foot bones are represented by the right talus, two metatarsals and two phalanges only. The main cranial and postcranial measurements are reported in the appendix.

Sex and Age

Sex determination and age at death estimation, carried out on the basis of several highly diagnostic features (Ferembach *et al.*, 1979; Krogman & Işcan, 1986), identify the individual as a young adult male.

In particular, results of metric and morphologic analyses of the pelvis (cotylo-sciatic index, ischiopubic index, acetab ulum-pubic index, pelvic index, sub-pubic angle, ischiopubic ramus characteristics) concur in indicating male sex. Age-at-death estimates, obtained using various parameters – cranial sutures synostosis, pubic symphysis morphology, ilium auricular surface morphology, epiphysial fusion and cancellous bone resorption in the humeral head–, are all in agreement with an age assessment in the mid third decade, i.e. of about 25 years, consistent with the clavicle's medial epiphysis fusion status.

Body Size and Proportions

Stature and Body Mass Estimation

Villabruna's stature was calculated using femoral length and regression equations suggested for European Late Upper Paleolithic (19-10 ky bp) specimens (Formicola & Franceschi, 1996; Formicola, 2003). Results from the various formulas are quite similar: 167.6 cm (Pearson, 1899), 167.2 cm (Trotter & Gleser, 1952, equations for African Americans) and 169.1 cm (Formicola & Franceschi, 1996). These results are in agreement with a stature estimate of 168.2 cm obtained using the anatomical method of Fully (1956). It is noted

Fig. 2 – The Late Upper Paleolithic burial Villabruna 1. Photograph by and courtesy of A. Broglio. The colour version is available online at the JASs web site.

that, in order to apply the anatomical method, it was necessary to reconstruct the dimensions of incomplete (tibia) and missing (calcaneus) bones. Missing measurements were estimated using Müller's (1935) formulae for tibia length and by comparisons with contemporary male specimens from Arene Candide (Savona, Italy).

According to Formicola and Giannecchini (1999), the average stature of the European LUP males is about 165.6 cm (SD = 3.5). Consequently, the estimate obtained for Villabruna 1 falls within the upper part of the range of its contemporaries.

Body mass was evaluated using the "morphometric" method developed by Ruff and co-workers (2005), which models the human body as a cylinder. In this model, cylinder's height is represented by the stature (ST) and its width is approximated by the bi-iliac breadth (BIB). The resulting estimate of 66.2 kg falls below the 69-72kg range obtained with the "mechanical" methods based on the femoral head diameter (FHAP) (Ruff *et al.*, 1991; McHenry, 1992; Grine *et al.,* 1995). According to Auerbach and Ruff (2004) estimates obtained through the former method are more reliable since the technique has been calibrated on large recent samples and accounts for body proportion differences among human populations.

Body Proportions

Body proportions have long been known to vary clinally in relation to climatic conditions, especially mean annual temperature. The rationale for such allometric variation is improved efficiency in thermal exchanges, according to Bergmann's (1847) and Allen's (1877) ecogeographic rules. Determination of body proportions can therefore foster useful information on climatic adaptation and geographic origin of human populations (Ruff 1991, 1994; Holliday & Falsetti 1995; Holliday, 1997).

Body proportions analysis was performed on several skeletal parameters: length of the main long bones (humerus, radius, femur, and tibia), anterior-posterior diameter of the femoral head, skeletal trunk height and bi-iliac breadth. All required measurements were taken according to Holliday (1997), except tibial length, which was estimated (see above) due to the lack of the distal part. The study was carried out by means of bivariate and multivariate statistical comparisons of Villabruna 1's skeletal data with those relative to European Early and Late Upper Paleolithic (herein indicated as EUP and LUP respectively), Mesolithic, and recent populations. Modern comparative samples include long-limbed, tropically-adapted groups (Sub-Saharan Africans), relatively short-limbed populations from temperate regions (Europeans), and groups whose characteristics are intermediate between these two morphotypes (North Africans).

Bivariate Analysis

Bivariate analysis was based on: 1) intralimb proportions; 2) limb length relative to trunk height; 3) ponderal index, and 4) relative body breadth. Summary statistics are shown in Table 1 (for abbreviations and definitions refer to table legend).

Intralimb indices of Villabruna 1 (RL/HL; TL/FL) provide values similar to those of the North African sample and intermediate between those exhibited by Sub-Saharan and European populations. Moreover, absolute skeletal trunk height, evaluated as sum of vertebral bodies height from T1 to L5 (STH = 484.5 mm), is short when compared to both the LUP sample (X = 504.6, SD = 15.98, n = 10) and recent Europeans (X = 503.3, n = 67) (Holliday, 1995, 1997). These observations are confirmed by the ratios between limb bones and skeletal trunk height, which place Villabruna 1 near to the tropically-adapted EUP morphotype, among fossil series, and close to North Africans, among recent samples. Therefore, limb bones/trunk proportions suggest that Villabruna 1 retains warm-climate adaptations characterizing EUP populations more than his contemporaries (Holliday, 1997).

These findings, however, are not in agreement with the results provided by the ponderal index, whose skeletal proxy is the ratio FHAP/FL. This parameter is correlated with overall climatic

Tab. 1 – Summary statistics for body proportions of Villabruna 1 and comparative samples. RL, HL and TL indicate the maximal length of radius, humerus and tibia respectively; FL stands for bicondylar femoral length; STH is the skeletal trunk height, FHAP the anterior-posterior femoral head diameter, and BIB the bi-iliac breadth. Indices marked with * have been calculated on male samples only (From Holliday, 1997; n.d.).

		RL/HL	TL/FL	HL/STH	RL/STH	FL/STH	TL/STH	FHAP/FL*	BIB/FL*
Villabruna 1		**77.5**	**84.3**	**66.0**	**51.2**	**94.5**	**79.7**	**10.5**	**58.3**
Mesolithic	M.	77.5	85.5	61.7	47.9	87.4	74.0	10.7	61.9
	S.D.	1.9	2.6	3.7	2.7	3.9	4.0	0.5	3.6
	n	10	10	7	7	7	7	6	5
LUP	M.	78.6	85.1	61.2	48.3	86.6	73.6	10.8	62.1
	S.D.	3.0	1.9	2.8	2.4	3.4	3.5	0.7	5.6
	n	17	22	15	12	15	13	15	11
EUP	M.	77.9	85.0	69.2	55.3	96.8	84.9	10.0	55.4
	S.D.	2.3	2.6	4.3	2.8	5.1	4.4	0.3	3.3
	n	16	13	7	6	6	5	9	4
Recent Europeans	M.	75.1	82.9	63.6	47.9	88.6	73.6	10.6	61.2
	S.D.	2.5	2.4	3.4	2.8	2.4	4.3	0.5	3.4
	n	240	243	124	123	123	124	134	126
Recent North Africans	M.	78.6	85.0	66.0	51.9	94.2	79.8	9.9	57.3
	S.D.	2.4	2.3	3.8	3.4	5.5	4.9	0.6	4.4
	n	136	133	62	62	63	60	72	60
Recent Sub Saharans	M.	79.6	86.1	70.2	55.8	99.3	85.5	9.5	52.1
	S.D.	2.5	2.2	4.0	3.7	6.7	5.9	0.6	3.0
	n	67	66	43	43	43	43	43	42

conditions and exhibits a typical clinal distribution with latitude. In this respect, Villabruna 1 is more similar to recent Europeans, LUP and Mesolithic populations, and differs from African samples. Further information on specific climatic adaptations can be drawn from the relationship between bi-iliac breadth and stature (BIB/FL), the latter having its most reliable skeletal proxy in femoral length. The result obtained highlights once more the similarity with the North African sample, thus implying a physique more linear than that of both LUP and Mesolithic specimens.

In conclusion, the results of bivariate analyses suggest that Villabruna 1 had a relatively slender physique, intermediate in its nature between the tropically-adapted constitution characteristic of EUP and the temperate-adapted structure of contemporary LUP people. When compared with modern samples, the specimen shows highest similarities with North Africans populations. As previously mentioned, the ponderal index is the only parameter in disagreement with this general pattern. In order to evaluate the importance of the latter characteristic in a generally differently oriented morphocomplex, a multivariate analysis of Villabruna 1's body proportions was carried out.

Multivariate Analysis

Multivariate analysis has been performed as per Darroch & Mosimann's (1985) procedure using the software SPSS 9.05 for Windows. This technique allows evaluating overall differences in both size and shape and has been successfully applied to the study of human body proportions (Holliday, 1995, 1997). Principal components analysis (PCA) was carried out on the variance/covariance matrix of linear measurements in order to evaluate morphological and dimensional traits (log size & shape) and pure morphological traits (log shape). Villabruna 1 was compared to LUP and EUP male samples (data from Holliday, 1995).

Tab. 2 – First two principal components of size & shape and shape variables for body proportions.

Eigenvector Coefficients	Size & Shape		Shape	
	PC1	PC2	PC1	PC2
FHAP	0.300	-0.250	-0.166	-0.239
FL	0.449	0.003	0.205	0.111
HL	0.484	0.231	0.384	0.062
TL	0.460	0.138	0.296	0.112
RL	0,439	0.289	0.352	-0.079
BIB	0.205	-0.580	-0.478	-0.655
STH	0.164	-0.667	-0.585	0.692
Eigenvalues	0.0293	0.0045	0.0070	0.0025
%Total Variance	75.18	11.43	56.86	20.24

Tab. 3 – Measurements and specimens considered in the analysis of cranio-facial morphology.

Measurements		Specimen	Period	Source of Data
G-Op	(M1)	Barma Grande 5	EUP	Formicola, unpublished data
Eu-Eu	(M8)	Cro Magnon	EUP	Vallois & Billy 1965
Ft-Ft	(M9)	Arene Candide 1, 4, 5	LUP	Paoli *et al.* 1980
Ba-Br	(M17)	Chancelade	LUP	Vallois 1941-1946
Ba-Pr	(M40)	Le Bichon	LUP	Simon & Formicola, n.d.
Zy-Zy	(M45)	Vado all'Arancio	LUP	Pardini & Lombardi Pardini 1981
N-Pr	(M48)	Rochereil	MES	Ferembach 1974
Mf-Ec	(M51)	Mondeval de Sora	MES	Alciati, unpublished data
Orb. ht	(M52)	Petit Marais	MES	Valentin 1995
Al-Al	(M54)	Hoëdic 9; Téviec 2, 4, 8, 11, 13,16	MES	Vallois & Felice 1977
N-Ns	(M55)	Unseburg	MES	Bach & Bruchhaus 1988
Go-Go	(M66)	Gramat	MES	Lacam *et al.* 1944

The first component (PC1) of log size & shape PCA accounts for 75% of total variance and, since all the eigenvector coefficients are positive, it is essentially considered a size component, probably linked to climatic factors (Tab. 2). The second component (PC2) represents 11.43% of total variance and contrasts limb bones length with bi-iliac breadth, femoral head size and skeletal trunk height. The scatter plot for log size & shape principal components (Fig. 3) places Villabruna 1 in the upper range of LUP variability, not far from the lower limit of EUP distribution. Log shape variables are obtained from log size & shape standardized for their geometric mean and are therefore employed to evaluate pure shape differences among individuals. PC1 accounts for 56.86% of total variance and, contrasts long bones length to bi-iliac breadth, femoral head size and skeletal trunk height.

PC2 explains 20.24% of variance and contrasts femoral head size and trunk height. Plotting the first two Log Shape components it is evident that PC1 separates tropically-adapted from cold-adapted individuals, while PC2 tends to segregate specimens on the basis of their size (Fig. 3). In particular, PC2 separates individuals

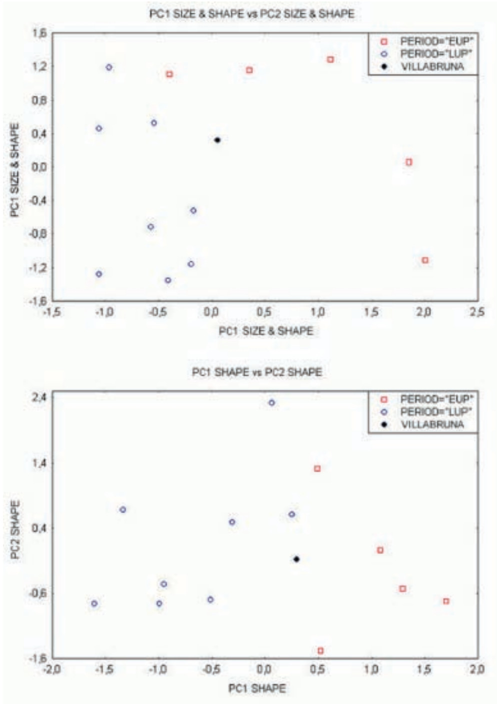

Fig. 3 – Body Proportions – Scatter plots of Log size & shape and Log Shape principal components (PC2 on PC1). The colour version is available online at the JASs web site.

characterized by big femoral heads and narrow pelvises from those exhibiting small FHAP and high BIB values (Tab. 2). The scatter plot for Log Shape variables confirms previous results: once again Villabruna 1 presents an intermediate pattern between LUP and EUP (Fig. 3).

In conclusion, the results of both bivariate and multivariate analyses demonstrate that Villabruna 1 had body proportions intermediate between those of EUP and LUP and generally very similar to the pattern presently exhibited by recent North African populations. Thus, this specimen fits well in the general microevolutionary trend which took place during the Upper Paleolithic and led to the progressive acquisition of body proportions characterizing recent European populations. Nevertheless, Villabruna 1, more then the majority of his contemporaries, retains climatic adaptation typical of the ancestral African population.

Cranio-Facial Morphology

Size and shape of the skull and face represent a valuable source of information on genetic affinity among individuals and populations (Howells, 1973, 1989, 1995; Relethford, 1994; Roseman & Weaver, 2004). Villabruna 1's cranio-facial morphology (Fig. 4) was analyzed in the geographic and chronological context provided by Upper Paleolithics and Mesolithics from surrounding regions using a multivariate statistical approach (PCA). Villabruna's measurements were directly taken on the material, while data for comparative specimens were obtained from the literature (Tab. 3). Only EUP, LUP and Mesolithic male individuals for whom all measurements were available were included in the analysis. Multivariate analysis was performed after Darroch & Mosimann's (1985) technique on both morpho-dimensional (Log size & shape variables) and morphological (Log shape variables) data, using SPSS 9.05 for Windows.

Log size & shape PC1 is mainly dimensional and accounts for 35.15% of total variance, whereas PC2 accounts for 23.88% of total variance and is both morphological and dimensional in nature (Tab. 4).

The scatter plot provided in Figure 4a demonstrates that specimens roughly segregate according to the period they belong as well as their geographical area. As far as size and shape characteristics are considered, Villabruna 1 shows highest similarities with the contemporaneous LUP Le Bichon 1, found in the Swiss Alps (Neuchâtel). This result is confirmed by the analysis of shape variables (Tab. 4). In this case, PC1 accounts for 35.99% of total variance, while PC2 accounts for 15.05% (Fig. 5b). These striking similarities between Villabruna 1 and Le Bichon 1 suggest genetic affinity among the late hunter and gatherers from the alpine region.

Dental Wear and Microwear

Analyzing Villabruna 1 dentition, Alciati and co-workers (1993) note that advanced wear affects

Fig. 4 – Villabruna 1- Frontal and lateral views of the skull. The colour version is available online at the JASs web site.

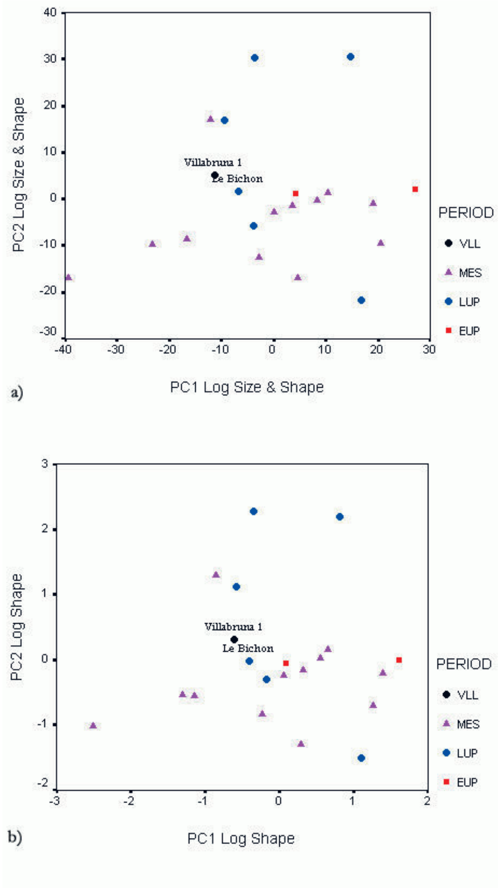

Fig. 5 – Cranio-facial morphology – Scatter plot of PC2 on PC1, Log size & shape (a) and Log shape data (b). The colour version is available online at the JASs web site.

anterior teeth (incisors and canines) only, whereas the posterior dentition is only slightly worn. In particular, the crowns of maxillary central incisors, lateral incisors and canines were no longer in occlusion with their mandibular counterparts at the time of death, and are worn down to about a third, half and two thirds of original height respectively. Crown height reduction is more pronounced in the right hemiarcade and is accompanied by labial rounding of the incisors. This wear pattern suggests that this part of the dentition was employed in a variety of activities performed with right hand support (Macchiarelli & Salvadei, 1985; Larsen, 1985). Unlike the anterior dentition, the occlusal surfaces of the premolars and molars preserve most enamel surrounding discrete patches of dentine. In addition, molar wear is uniform, i.e. there is no cupping of the masticatory surface, in agreement with the typical pattern observed in hunter-gatherers (Smith, 1984).

Microscopic analysis was carried out in order to collect information on materials and activity patterns responsible for Villabruna's anterior dentition wear. The study was performed on epoxidic resin (Araldite LY554 + hardener HY954) casts of upper and lower incisors and canines obtained with a high definition siliconic paste (PROVIL LCD). Optic microscope at variable magnification (7.5X – 62.5X) allowed examining tooth surfaces in their entirety as well as single microwear features. To better record and describe microwear patterns, the occlusal surface was divided into two medio-lateral sectors, buccal (B) and lingual (L). Each sector was evaluated for the presence and type of microfeatures (for microfeatures definition see Minozzi, 1994-1995). Prevalent microfeatures are sub-parallel (incisors) and crossed streaks (canines), which cover one to two thirds of total occlusal surface. The streaks observed on the incisors' surface are characterized by greater dimensions than those detected on other teeth (e.g., canines), for which size never reaches 30 µm. Interestingly, an abundance of sub-parallel vertical streaks was observed also on the buccal surface of incisors. Overall, the microscopic analysis reveals the presence of microfeatures, such as microflakes, chipping, crushing and microfractures that reflect levels of biomechanical stress. The abundance of microfeatures, along with the occurrence of broad grooves, suggests the mastication of hard materials and large-sized contaminating particles. It is difficult to ascertain whether the etiology of these microconfigurations is primarily attributable to alimentary or working activities. Comparison of the observed microscopic wear pattern with that found in other skeletal samples from different time periods (Repetto, 1987-88, 1994; Minozzi, 1994-95) suggests similarity between Villabruna 1 and populations from the Tierra del Fuego whose dentition was subjected to high biomechanical stresses, resulting from both tough food and non-alimentary activities (Minozzi, 1994-95).

In sum, despite not conclusive, macro- and microscopic examination of the occlusal surface of the Villabruna 1 teeth suggests intense para/extra-alimentary activities performed with right hand support. While it is not possible to determine specific activity patterns, these findings suggest that Villabruna 1 used his dentition to hold or pull either food or working materials containing relatively large-sized contaminants.

Tab. 4 – First two principal components of log size & shape and log shape variables for cranio-facial morphology.

Eigenvector Coefficients	Log Size & Shape		Log Shape	
	PC1	PC2	PC1	PC2
Maximum Cranial Length (M1)	0.174	-0.015	-0.059	-0.110
Maximum Cranial Breadth (M8)	0.163	-0.151	-0.160	-0.138
Minimum Frontal Breadth (M9)	0.146	-0.024	-0.019	-0.309
Basion-Bregma Length (M17)	0.131	0.132	0.084	-0.047
Basion-Prosthion (M40)	0.119	0.267	0.191	-0.291
Bizygomatic Diameter (M45)	0.130	-0.215	-0.180	0.093
Nasion-Prosthion (M48)	0.134	0.219	0.173	0.174
Orbital Breadth (M51)	0.132	-0.283	-0.245	-0.077
Orbital Height (M52)	0.102	-0.138	-0.097	0.235
Nasal Breadth (M54)	0.061	-0.255	0.164	-0.147
Nasal Height (M55)	0.155	0.193	0.186	0.271
Bigonial Wirth (M66)	0.140	-0.147	-0.134	0.213
Eigenvalues	4.546	2.327	3.506	1.947
%Total Variance	37.88	19.39	29.21	16.22

Upper and Lower Limb Cross-Sectional Geometry

A biomechanical approach to skeletal biology has recently joined traditional morphological analyses of robusticity and activity levels and pattern reconstruction. The application of the "hollow beam model" to human long bones allows making inferences about the magnitude and direction of habitual stresses applied to the bones (Lovejoy *et al.,* 1976; Ruffs & Hayes, 1983). Cross-sectional data on both humeri (respectively taken at 35%, 50% and 65% of articular length) and right femur (at 50% and 80% of mechanic length) were collected and standardized by body dimensions according to the technique described in Churchill (1994) and Holt (1999, 2003). Geometric properties for Villabruna and comparative samples are reported in Tables 5, 6 and 7. Information on the comparative material employed in the analysis – EUP and LUP male samples – can be found in Churchill (1994) and Holt (1999).

Upper limb

Cross-sectional properties of Villabruna 1 humeri exhibit polar moments of area (J) above the average in the distal part of the bone, pointing to a resistance to torsional forces higher than that of the comparative samples. The values obtained for J at mid-diaphysis, however, are slightly below average. At this level, the greatest difference from EUP and LUP resides in bending strength. While the two Paleolithic samples exhibit the greatest resistance on the medial-lateral axis ($I_x < I_y$), both humeri of Villabruna 1 are more robust on the anterior-posterior axis, with the maximum resistance on an anteriorlateral-posteriormedial plane. This leads to the conclusion that Villabruna's

Tab. 5 – Principal geometric properties of humeral diaphysis for Villabruna 1 and comparative samples (mean and S.D.).

HUMERUS	35%						50%						65%					
Geometric Properties	EUP		LUP		Villabruna 1		EUP		LUP		Villabruna 1		EUP		LUP		Villabruna 1	
Side	R (n = 3)	L (n = 4)	R (n = 7)	L (n = 6)	R	L	R (n = 2)	L (n = 5)	R (n = 6)	L (n = 4)	R	L	R (n = 2)	L (n = 5)	R (n = 6)	L (n = 4)	R	L
TA	306.2	246.2	319.8	275.0	336.5	271.9	356.7	295.5	381.8	315.4	368.0	290.2	356.7	295.5	381.8	315.4	368.0	290.2
	7.6	32	54.1	50.4			14.4	30.3	69.1	46.2			14.4	30.3	69.1	46.2		
CA	226.2	181.2	252.8	201.9	296.6	232.9	215.3	193.3	231.7	201.9	272.6	239.7	215.3	193.3	231.7	201.9	272.6	239.7
	22.6	27.7	41.4	30.9			42.6	33.5	37.5	19.9			42.6	33.5	37.5	19.9		
MA	80.0	65.0	67.0	73.1	39.9	39.0	141.4	113.0	150.1	113.5	95.4	50.5	141.4	113.0	150.1	113.5	95.4	50.5
	15.3	7.7	27.9	31.1			28.2	24.4	46.3	47.6			28.2	24.4	46.3	47.6		
Ix	846.4	515.6	879.0	617.8	938.8	589.2	869.8	683	1000.1	728.3	1042.3	725.8	8.0	683.0	1000.1	728.3	1042.3	725.8
	92.8	135.7	318.8	188.9			59.1	217.5	330.7	166.2			69.8 59.1	217.5	330.7	166.2		
Iy	589.2	409.5	759.2	547.0	853.9	581.5	851	667.3	1071.5	675.0	999.9	593.3	851.0	667.3	1071.5	675.0	999.9	593.3
	57.6	102.3	271.8	209.5			214.5	221.6	451.3	144.3			214.5	221.6	451.3	144.3		
J	1435.5	925	1638.2	1164.8	1792.7	1170.7	1720.8	1350.3	2071.6	1403.4	2042.2	1319.1	1720.8	1350.3	2071.6	1403.4	2042.2	1319.1
	150.4	235.5	582.0	391.8			273.6	430.6	771.5	303.7			273.6	430.6	771.5	303.7		
%CA	73.8	73.4	79.3	74.7	88.2	85.7	60.2	65.5	61.1	64.8	74.1	82.6	60.2	65.5	61.1	64.8	74.1	82.6
	5.6	2.9	7.1	7.6			9.5	10.4	6.8	9.4			9.5	10.4	6.8	9.4		
Ix/Iy	1.4	1.3	1.2	1.1	1.1	1.0	1.1	1.0	1.0	1.1	1.0	1.2	1.1	1.0	1.0	1.1	1.0	1.2
	0	0.1	0.1	0.2			0.2	0.1	0.1	0.1			0.2	0.1	0.1	0.1		

arms were involved in activities that produced stresses different from those typically observed in both EUP and LUP. Interestingly, the pattern observed in Villabruna 1 is very similar to that characterizing the contemporary specimen Le Bichon 1 (Churchill & Holt, n.d.). The geographic proximity of these two individuals suggests the possibility of similar activity patterns among LUP of the alpine region. Percent cortical area (%CA), a parameter indicative of resistance to axial loads, is a further characteristic differentiating both humeri of the specimen under study from EUP and LUP %CA values (Tab. 5) at the three levels of both humeri fall beyond mean plus one standard deviation of the fossil comparative samples (Churchill, 1994).

Tab. 6 – Percentage asymmetry ([100 x maximum value – minimum value]/ minimum value) relative to cortical area and polar moment of area at 35% and 65% of humeral diaphysis for Villabruna 1 and two fossil comparative samples (median, quartile, range). EUP and LUP data are from Churchill & Formicola, 1997.

	CA			J		
	EUP	**LUP**	**Villabruna 1**	**EUP**	**LUP**	**Villabruna 1**
35%	26.2 11.6-29.6 11.4-40.8 n = 6	20.6 19.5-33.9 0.8-56.8 n = 12	27.38	50.1 39.9-68.0 17.8-96.4 n = 6	47.4 21.4-74.3 2.4-132.2 n = 12	53.13
65%	9.9 8.5-138.0 6.4-40.0 n = 5	20.5 18.3-33.7 1.1-46.3 n = 9	13.75	40.0 26.7-53.2 0.5-85.4 n = 5	44.8 39.6-58.2 18.7-108.3 n = 9	54.82

Tab. 7 – Principal geometric properties of right femoral diaphysis for Villabruna 1 and comparative samples (mean and S.D.).

FEMUR	50%			80%		
Geometric Properties	**EUP (n=10)**	**LUP (n=13)**	**Villabruna**	**EUP (n=10)**	**LUP (n=12)**	**Villabruna**
TA	985.90 99.24	956.34 106.65	1003.98	1088.33 93.97	1063.81 163.16	1022.17
CA	728.87 132.24	774.27 116.54	889.29	792.67 129.72	807.38 123.11	877.47
MA	257.51 82.33	182.31 52.74	114.69	295.81 60.27	256.42 129.64	144.71
Ix	1361.50 429.50	1279.71 295.73	1545.19	1112.30 321.37	1143.36 347.51	981.67
Iy	873.45 190.93	956.42 242.05	1064.00	1578.85 295.85	1565.90 474.50	1616.43
J	2234.94 610.67	2234.7 495.34	2609.20	2691.15 556.85	2709.26 749.31	2598.11
%CA	73.68 8.75	80.70 6.060	88.58	72.50 6.750	76.45 9.76	85.84
Ix/Iy	1.54 0.21	1.37 0.25	1.45	0.71 0.16	0.75 0.17	0.61

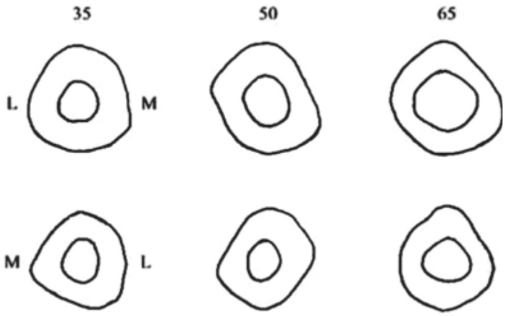

Fig. 6 – Cross-sections of Villabruna 1's right (top) and left (bottom) humeral diaphyses at 35%, 50% and 65% of articular length.

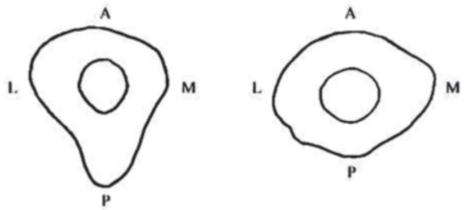

Fig. 7 – Cross-sections of Villabruna 1 right femoral diaphysis at 50% (left) and 80% (right) of mechanical length.

Finally, geometric properties of the Villabruna 1 humeri exhibit pronounced bilateral asymmetry. This feature, appreciable even macroscopically (Fig. 6), is properly expressed by asymmetry indices and emerges from comparisons with EUP and LUP (Tab. 6). Asymmetry in CA shows a distal-proximal decrease, with a value for Villabruna 1 higher than LUP's average at 35% of diaphyseal length to a value lower than the LUP average at 65%. Mean % asymmetry in J for Villabruna 1 is greater than average for EUP and LUP at both % diaphyseal lengths, yet falling within the range of both comparative groups.

The pattern observed in Villabruna 1 can be interpreted as the combined effect of diaphyseal dimensional increase at the deltoid tuberosity and the application of more intense torsional stresses on the humeral distal portion. Polar moment (J) asymmetry exhibits no significant difference between the two diaphyseal levels taken in consideration and is only slightly higher then the comparative samples' mean values. The asymmetry found in Villabruna 1's upper limb is not unusual in LUP male specimens (Churchill & Formicola, 1997) and results from the co-presence of a right humerus characterized by geometric properties and dimension slightly above the mean and a left one less robust than average. Such asymmetry points toward unimanual activities or bimanual tasks differently involving the upper limbs. In particular this condition, along with the archeological evidence for the period, suggests the use of throwing weapons (Churchill *et al.*, 1996).

Lower limb

Femoral geometric properties at 50% of articular length, even though often falling within both LUP and EUP's variability, are generally higher than comparative sample mean values (Tab. 7). Absolute (CA) and relative (%CA) values of cortical area indicate marked diaphyseal robusticity and resistance to axial loads such as traction and compression. Femoral overall robusticity is emphasized by geometric properties such as second moments of area (I_x,I_y, I_{max}, I_{min} and J), that reveal a resistance to bending and torsional stresses on anatomical axes higher than that of contemporary specimens. Diaphyseal morphology (Fig. 7) is intermediate between that of EUP and LUP and is characterized by a high I_x/I_y ratio. In particular, Villabruna 1's femur shaft is less anterior-posteriorly elongated than EUP's, but shows a more pronounced pilaster than the LUP specimens. Anterior-posterior diaphyseal elongation is the result of deambulatory stresses exerted along this plane, and is usually connected with high mobility and the nature of the terrain. The analysis of femoral diaphyses at 80% confirms previous findings on overall robusticity of the bone. Villabruna 1 is set apart from EUP and LUP samples by a marked anterior-posterior flattening and medio-lateral expansion (low I_x/I_y ratio). This morphology of the proximal end of the diaphysis is attributable to an intense activity of the gluteus maximus.

In sum, all femoral geometric properties imply that the lower limbs of Villabruna 1 were subjected to mechanical stresses higher than those affecting the femora of his contemporaries. It is likely that such stresses were mostly due to two concurring factors: high mobility and mountainous environment. Very interesting in this regard is the comparison between Villabruna 1 and the LUP specimens from Arene Candide (Savona, Italy), a site located in the hilly region of Liguria (Fig. 8). Villabruna 1 and Arene Candide specimens have very similar values for all the geometric properties considered and are more robust than other LUP specimens from non mountainous environment. These data are in agreement with the results of recent analyses on Neolithic skeletal remains from mountainous regions (Marchi *et al.*, 2006; Ruff *et al.,* 2006) indicating the importance of the terrain in lower limb robusticity.

Paleodietary Analyses

Stable isotope analysis was performed on bone collagen extracted from a fragment of Villabruna 1 fibula. After collagen extraction, carbon and nitrogen stable isotope ratios were measured at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, following procedures outlined in Richards & Hedges (1999) with the addition of an ultrafiltration step (Brown *et al.,* 1988). The results of Villabruna's collagen isotopic analysis, as well as those obtained from three animal bones associated with the burial, are provided in Table 8. Two of the samples had well preserved collagen, while the other two had C:N ratios just outside the accepted range of 2.9 to 3.6 (De Niro, 1985). Carbon and nitrogen isotope values of mammal bone collagen provide information about the sources of dietary protein over the last years of life, especially the amount of marine *vs.* terrestrial protein and the amounts of plant *vs.* animal protein (Katzenberg, 2000; Sealy, 2001).

As shown in Table 8, isotopic values of Villabruna 1 are consistent with a completely terrestrial diet. It is difficult to determine the amount of animal protein in the diet without more data on isotope values of associated animal remains. However, preliminary observation based on the $\delta^{15}N$ value of 1.6 ‰ for deer bone, it appears that the Villabruna 1's bone has a quite high $\delta^{15}N$ value, indicative of a diet mainly consisting of animal protein. The deer value is actually quite low, much lower than Holocene European deer $\delta^{15}N$ values. However, low $\delta^{15}N$ values at approximately 12,000 BP have been observed for Northern Europe deer (Richards & Hedges, 2003) probably linked to the colder climate associated with this period. Indeed these

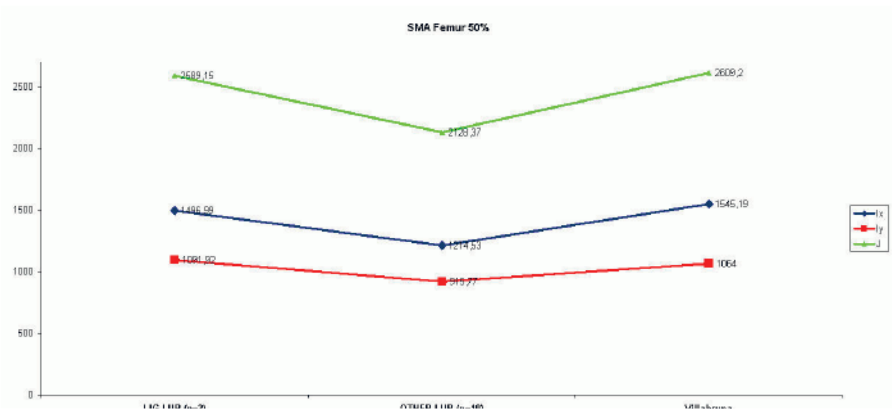

Fig. 8 – Comparison between geometric properties of Villabruna 1 right femoral diaphysis at 50% and LUP samples from Liguria (LIG-LUP) and non mountainous regions of Europe (Other LUP). The colour version is available online at the JASs web site.

Tab. 8 – Collagen isotopic results for four bone samples from Ripari Villabruna.

Sample	Species	d13C (‰)	d15N (‰)	C:N
S-EVA-415	Human	-19.7	8.0	3.6
S-EVA-416	Deer	-19.8	1.6	3.6
S-EVA-417	Carnivore	-21.1	1.5	3.7
S-EVA-418	Unknown	-20.3	1.2	3.7

isotopic values are very similar to those published by Richards and co-workers (2000) for the contemporary site of Gough's Cave in England, where humans also had relatively high $\delta^{15}N$ values compared to the fauna, although all of the mammals had lower $\delta^{15}N$ values than observed in the Holocene.

Paleopathological Aspects

Paleopathological analysis of the skeleton did not reveal traces of any major event which might help identify a possible cause of death. In fact, there is evidence of neither perimortal traumas nor skeletal alterations indicative of severe pathological conditions. The skeleton is well-developed, robust and does not show signs of growth disturbances such as Harris lines or marked enamel hypoplasia (Alciati *et al.,* 1993).

However, the examination of the skeleton has highlighted diffuse porosity affecting parietals and occipital squama as well as slight perforations of orbital roofs (Fig. 9). This condition can be most probably related to anemic conditions suffered long before the time of death, as suggested by the advanced healing of the lesions (Vercellotti, 2005). General skeletal robusticity, dietary analyses, and scanty evidence of such pathology among hunter and gatherers (Larsen, 1997), suggest parasitic infestations or acute disease rather than dietary or hereditary etiologies as possible causes for this condition (Aufderheide & Martín, 1998; Meiklejohn & Zvelebil, 1991).

In addition, Villabruna 1 shows ossification anomalies, such as bilateral persistence of acromial bone and spondylolisis of the fifth lumbar vertebra (Fig. 10). Even though bipartite acromion may be related to occupational stresses (İşcan & Kennedy, 1989; Scheuer & Black, 2000), its bilateral occurrence in a specimen characterized by high upper limb asymmetry, suggests a genetic rather than acquired condition. Spondylolisis on L5 probably resulted from genetic predisposition in association with heavy loading of the lower vertebral column. The hypothesis of intense biomechanical stresses on the rachis is confirmed by an articular accessory facet for the left sacral wing on L5 and by regular depressions exhibited by the inferior surface of the lumbar vertebral bodies, likely resulting from intervertebral disk swelling (Fig. 10). The sagittal rachigram of Villabruna 1, elaborated after Mafart (1983), highlights marked lumbar hyperlordosis, probably due to the combined effect of two factors: complete separation of L5 neural arch and consequent change of load distribution, and application of intense axial loads on the column. Transportation of heavy objects and mobility on uneven terrains might explain the extent of the vertebral changes. Intense physical activity might have been responsible also for the periostitis observed in the left tibial diaphysis (Fig. 11), likely the result of a traumatic event, or stress fractures (microfractures). Finally, additional paleopathological changes of minor importance exhibited by Villabruna 1 include an occlusal caries on the mandibular third molar and a small sized button osteoma on the posterior part of the right parietal bone.

Conclusions

About 14,000 years ago (in calibrated chronology) a young adult male individual, about 25 years old, was buried under a rock shelter occasionally used by Late Upper Paleolithic hunter-gatherers from the alpine region. The body was laid in a supine position in a shallow pit and the burial was marked with painted stones.

Analysis of the skeleton indicates that Villabruna 1 was tall for the time period and characterized by body proportions more linear than his contemporaries'. Bivariate and multivariate statistical analysis shows that Villabruna 1 had body proportions intermediate between those of EUP and LUP and generally very similar to the pattern commonly displayed by recent North African populations. These data suggest that while Villabruna 1 retains more ancestral condition indicative of African origin than its contemporaries, this specimen fits well in the microevolutionary process that affected European Upper Paleolithic populations leading to the progressive acquisition of body proportions typical of temperate regions.

Multivariate statistical analyses of craniofacial characteristics place Villabruna 1 in the morpho-complex of the time period and, interestingly, close to a geographically and chronologically nearby specimen (Le Bichon). This suggests genetic affinity among paleo-mesolithic populations from the alpine region. However, mitochondrial DNA analyses carried out on prehistoric human remains from this region highlighted in Villabruna 1 a sequence not observed in contemporary European populations (Di Benedetto *et al.,* 2000), raising the possibility of genetic discontinuity between the last hunter-gatherers from the Alps and subsequent populations.

Observations on dental wear and microwear show that the anterior dentition was likely involved in non-alimentary activities and in the mastication of fibrous and tough materials including large abrasive contaminants. Whereas the information on dietary habits drawn from dental wear is not conclusive, stable isotopes analysis points to a terrestrial based diet rich in animal proteins.

Biomechanical analysis of upper and lower limb bones stresses the overall bone robusticity and strength of Villabruna 1, likely effect of a

Fig. 9 – Superior view of Villabruna 1 cranium and close up view of the right parietal bone. Note the fine pinpointed, and diffuse porosity characteristic of PH.

Fig. 10 – Ossification anomalies in Villabuna 1. Top: bilateral presence of acromial bone. Bottom: spondylolysis of L5 and modifications of the lumbar vertebrae inferior surface.

Fig. 11 – Periostitis in the left tibia. The colour version is available online at the JASs web site.

demanding lifestyle. Marked humeral asymmetry suggests repeated throwing movements in hunting, while the magnitude of femoral diaphysis remodeling likely results from the combined effect of mobile lifestyle and mountainous territory. Localized tibial periostitis, probably of traumatic origin, and lumbar hyperlordosis associated with deformations of vertebral bodies and L5 spondylolysis, also seems to point to a demanding lifestyle.

Macroscopic and radiographic analysis of the skull reveals traces of porotic hyperostosis, result of healed anemic conditions. This finding does not contradict the overall good health and nutritional conditions suggested by stature, robusticity of the skeleton, paleodietary analyses and by the lack of significant developmental disturbances on bones and teeth.

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References

Aimar A., Alciati G., Broglio A., Castelletti L., Cattani L., D'Amico C., Giacobini G., Maspero A. & Peresani M. 1992. Les Abris Villabruna dans la Vallée du Cismon. *Preist. Alpina*, 28/1: 227-254.

Alciati G., Coppa A., Macchiarelli R. & Pertile F. 1993. La dentizione del cacciatore epigravettiano del riparo Villabruna A (valle del Cismon, Belluno). *Quaderni d'Anatomia Pratica*, 49:73-100.

Allen J.A. 1877. The influence of physical conditions in the genesis of species. *Rad. Rev.*, 1:108:140.

Auerbach B.M. & Ruff C.B. 2004. Human body mass estimation: a comparison of "morphometric" and "mechanical" methods. *Am. J. Phys. Anthropol.*, 125:331-342.

Aufderheide A. C.& Rodriguez–Martín C. 1998. *Cambridge enciclopedia of human paleopathology*. Cambridge University Press, Cambridge.

Bach A. & Bruchhaus H. 1988. Das mesolitische Skelett von Unseburg, Kr. Stafrest. *Jschr. mitteldt. Vorgesch.,* 71:21-36.

Bergmann C. 1847. Űber die Verhaltnisse der Warmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien,* 3:595-708.

Broglio A. & Improta S. 1995. Nuovi dati di cronologia assoluta del Paleolitico superiore e del Mesolitico del Veneto, del Trentino e del Friuli. *Atti Ist. Ven. SS. LL. AA.*, 103:1-45.

Broglio A. & Villabruna A. 1991. Vita e morte di un cacciatore di 12000 anni fa. Risultati preliminari degli scavi nei ripari Villabruna (Valle del Cismon. Val Rosna, Sovramonte, Belluno). *Odeo Olimpico*, 1-19.

Broglio A. 1992. Le pietre dipinte dell' Epigravettiano recente del Riparo Villabruna A in Val Cismon.Val Rosna (Dolomiti Venete). *Atti XXVIII Riun. Scient. Ist. Ital. Preist. Protost.*, 223-238.

Broglio A. 1995. Les sepultures épigravettiennes de la Vénétie (Abri Tagliente et Abri Villabruna). *ERAUL*, 68:845-867.

Broglio A. 1998. Considerazioni sulla produzione artistica dell'Epigravettiano recente del Veneto e del Trentino. Due nuove pietre dipinte del Riparo Villabruna A. *Riv. Sci. Preist.,* 49:103-121.

Broglio A. 2000. The Epigravettian funeral structure of the Villabruna shelter A: a tendency to mythicize the dead? *ERAUL*, 102:121-129.

Brown, T.A., Nelson D.E., Vogel J.S. & Southon J.R. 1988. Improved collagen extraction by modified Longin method. *Radiocarbon,* 30:171-177.

Cattani L. 1993. Contenuto pollinico di materiali resinosi come elemento di corredo funebre. *Antrop. Contemp.,* 16:55-60.

Churchill S.E. & Formicola V. 1997. A case of marked bilateral asymmetry in the upper limbs of an Upper Paleolithic male from Barma Grande (Liguria), Italy. *Int. J. Osteoarch*., 7:18-38.

Churchill S.E. & Holt B.M. n.d. *Cross-sectional geometry of Le Bichon 1*. Unpublished manuscript.

Churchill S.E. 1994. *Human upper body evolution in the Eurasian Later Pleistocene*. Ph.D. dissertation, University of New Mexico, Albuquerque.

Churchill S.E., Weaver A.H. & Niewoehner W.A. 1996. Late Pleistocene human technological and subsistence behavior: Functional interpretation of upper limb morphology. *Quat. Nova*, 6:18-51.

Darroch J.N.& Mosimann J.E. 1985. Canonical and principal components of shape. *Biometrika*, 72:241-252.

De Niro M.H. 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to paleodietary reconstruction. *Nature*, 317:806-809.

Di Benedetto G, Nasidze I.S., Stenico M., Nigro L., Krings M., Lanzinger M., Vigilant L., Stoneking M., Paabo S. & Barbujani G. 2000. Mitochondrial DNA sequences in prehistoric human remains from the Alps. *Eur. J. Hum. Genet*., 8:669-77.

Ferembach D. 1974. Le squelette humain azilien de Rochereil (Dordogne). *Bull. Mém. Soc. Anthrop. Paris,* 2:271-291.

Ferembach D., Schwidetzky I. & Stloukal M. 1979. Recommandations pour déterminer l'âge et le sexe sur le squelette. *Bull. Mém. Soc. Anthrop. Paris,* 6:7-45.

Formicola V. & Franceschi M. 1996. Regression equations for estimating stature from long bones of Early Holocene European samples. *Am. J. Phys. Anthropol.,* 100:83-88.

Formicola V. & Giannecchini M. 1999. Evolutionary trends of stature in Upper Paleolithic and Mesolithic Europe. *J. Hum. Evol.,* 36:319-333.

Formicola V. 2003. More is not always better: Trotter and Gleser's equations and stature estimates of Upper Paleolithic European samples. *J. Hum. Evol.,* 45:239-243.

Fully G. 1956. Une nouvelle méthode de détermination de la taille. *Ann. Méd. Légale,* 36: 266-273.

Grine F.E., Jungers W.L., Tobias P.V. & Pearson O.M. 1995. Fossil *Homo* femur from Berg Aukas, northern Namibia. *Am. J. Phys. Anthropol*., 26:67-78.

Holliday T.W. & Falsetti A.B. 1995. Lower limb length of European early modern humans in relation to mobility and climate. *J. Hum. Evol.,* 29:141-153.

Holliday T.W. 1995. *Body size and proportions in the Late Pleisocene Western Old World and the origins and modern humans*. Ph.D. dissertation. University of New Mexico, Albuquerque.

Holliday T.W. 1997. Body proportions in Late Pleistocene Europe and modern human origins. *J. Hum. Evol.,* 32: 423-448.

Holliday T.W. n.d.. Body proportion of Le Bichon 1. Unpublished manuscript.

Holt B.M. 1999. *Biomechanical evidence of decreased mobility in Upper Paleolithic and Mesolithic Europe.* Ph.D. dissertation. University of Missouri, Columbia, Missouri, USA..

Holt B.M. 2003. Mobility in Upper Palaeolithic and Mesolithic Europe: Evidence from the lower limb. *Am. J. Phys. Antrhopol*., 122:200-215.

Howells W.W. 1973. *Cranial variation in man: a study by multivariate analysis of patterns of difference among recent human populations*. Harvard University, Cambridge.

Howells W.W. 1989. *Skull shapes and the map: craniometric analyses in the dispersion of modern Homo*. Harvard University, Cambridge.

Howells W.W. 1995. *Who's who in skulls: ethnic identification of crania from measurements.* Harvard University, Cambridge.

İşcan M.Y. & Kennedy K.A.R. 1989. *Reconstruction of life from the skeleton*. Wiley-Liss Publisher, New York.

Katzenberg M.A. 2000. Stable isotope analysis: a tool for studying past diet, demography and life history. In M.A Katzenberg, S.R. Saunders (eds.): *The biological anthropology of the human* *skeleton*, pp. 305-327. John Wiley and Sons, New York.

Krogman W.M. & İşcan M.Y. 1986. *The human skeleton in forensic medicine.*C. Thomas, Springfield, Illinois.

Lacam R., Niederlander A. & Vallois H.V. 1944. Le gisement mésolithique du Couzoul de Gramat. *Arch. Inst. Paléont. Hum.*, 21.

Larsen C.S. 1985. Dental modifications and tool use in Western Great Basin. *Am. J. Phys. Anthropol.,* 67:393-402.

Larsen C.S. 1997. *Bioarcheology: Interpreting behavior from the human skeleton*. Cambridge University Press, Cambridge.

Lovejoy C.O., Burstein A.H. & Heiple K.G. 1976. The biomechenical analysis of bone strength: A method and its application to platycnemia.. *Am. J. Phys. Anthropol.,* 44:489-506.

Macchiarelli R. & Salvadei L. 1985. Dental wear and extra-masticatory anterior function in the Iron-age Alfedena community (Abruzzi, Italy). *Antrop. Contemp.,* 3:203-210.

Mafart B-Y. 1983. *Paléoecologie de l'homme fossile 5: Pathologie osseuse au Moyen Age en Provence*. Editions du CNRS.

Marchi D., Sparacello V., Holt B.M. & Formicola V., 2006. Biomechanical Approach to the Reconstruction of Activity Patterns in Neolithic Western Liguria, Italy. *Am. J. Phys. Anthropol.,*131:447–455.

McHenry H.M. 1992. Body size and proportions in early Hominids. *Am. J. Phys. Anthropol.*, 87:407-431.

Meiklejohn C. & Zvelebil M. 1991. Health status of European populations at the agricultural transition and the implications for the adoption of farming. *BAR International Series,* 567: 129-145.

Minozzi S. 1994-1995. *Il contributo della microusura dentaria nella ricerca antropologica: metodologie, tecniche e differenti applicazioni*. Tesi di Dottorato di Ricerca in Scienze Antropologiche. Università di Pisa.

Müller G. 1935. Zur Bestimmung der Länge beschädigter Extremitatenknochen. *Anthrop. Anz.,* 12:70–72.

Paoli G., Parenti R. & Sergi S. 1980. Gli scheletri mesolitici della caverna delle Arene Candide (Liguria). *Mem. Ist. It. Paleont. Um.*, 3:33-154.

Pardini E. & Lombardi Pardini E.C. 1981. I paleolitici di Vado all'Arancio (Grosseto). *Arch. Antrop. Etnol.*, 111:75-119.

Pearson K. 1899. Mathematical contributions to the theory of evolution. On the reconstruction of the stature of prehistoric races. *Philos. Trans. R. Soc. London*, 192:169-244.

Relethford J.H. 1994. Craniometric variation among modern human populations. *Am. J. Phys. Anthropol.,* 95:53-62.

Repetto E. 1987-88. *Ricostruzione del comportamento alimentare e della biomeccanica masticatoria dei primati non umani e nell'uomo: il contributo della microusura dentaria*. Tesi di Dottorato di Ricerca in Scienze Antropologiche. Università di Pisa.

Repetto E. 1994. Il contributo della microusura dentaria negli studi di paleonutrizione: il sito della media età del Bronzo di Toppo Daguzzo (Basilicata). *Bull. Palet. It.*, 85:349-365.

Richards M.P. & Hedges R.E.M. 1999. Stable isotope evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe. *J. Archaeol. Sci.,* 26:717-722.

Richards M.P., Jacobi R., Currant A., Stringer C., &. Hedges R.E.M. 2000. Gough's Cave and Sun Hole Cave human stable isotope values indicate a high animal protein diet in the British Upper Palaeolithic. *J. Archaeol. Sci.,* 27:1-3.

Richards, M.P. & Hedges R.E.M. 2003. Bone collagen δ13Cand δ15N values of fauna from Northwest Europe reflect palaeoclimatic variation over the last 40,000 years. *Palaeogeol. Palaeoclim. Palaeoecol.,* 193:261-267

Roseman C.C. & Weaver T.D. 2004. Multivariate apportionment of global human craniometric diversity. *Am. J. Phys. Anthropol.,* 125:257-263.

Ruff C.B. 1991. Climate and body shape in hominid evolution. *J. Hum. Evol.,* 21:81-105.

Ruff C.B. 1994. Morphological adaptation to climate in modern and fossil hominids. *Yearb. Phys. Anthropol.,* 37:65-107.

Ruff C.B. & Hayes W.C. 1983. Cross-sectional geometry of Pecos Pueblo femora and tibiae. A biomechanical investigation: I. Method and general patterns of variation. *Am. J. Phys. Anthropol.,* 60:359-381.

Ruff C.B., Holt B.M., Sládek V., Berner M., Murphy Jr. W.R., zur Nedden D., Seidler H. & Recheis W. 2006. Body size, body proportions, and mobility in the Tyrolean "Iceman". *J. Hum. Evol.,* 51: 91-101.

Ruff C.B., Niskanen M., Junno JA. & Jamison P. 2005. Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher latitude humans. *J. Hum. Evol.,* 48:381-392.

Scheuer L. & Black S. 2000. *Developmental juvenile osteology*. Academic Press, San Diego.

Sealy J. 2001. Body tissue chemistry and palaeodiet. In D.R Brothwell, A.M. Pollard (eds.): H*andbook of Archaeological Sciences*, pp. 269-279. John Wiley and Sons, Chichester.

Simon C. & Formicola V. n.d. L'homme du Bichon. Unpublished manuscript.

Smith B.H. 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J. Phys. Anthropol.*, 63:39-56.

Trotter M. & Gleser G.C. 1952. Estimation of stature from long bones of American Whites and Negroes. *Am. J. Phys. Antrhopol.*, 10:463-514.

Valentin F. 1995. Le squelette mésolithique du Petit Marais de la Chaussée-Tirancourt (Somme, France). *C. R. Acad. Sci. Paris*. 321, IIa:1063-1067.

Vallois H.V. 1941-1946. Nouvelle recherches sur le squelette de Chancelade. *L'Anthropologie,* 50:162-202.

Vallois H.V. & Billy G. 1965. Nouvelle recherches sur les hommes fossiles de l'Abri de Cro-Magnon. *L'Anthropologie,* 69:249-272.

Vallois H.V. & Felice S. 1977. Les mésolithiques de France. *Arch. Instit. Paléont. Hum.*, 37.

Vercellotti G. 2005. *Lo scheletro paleolitico Villabruna 1. Una fonte di dati su biologia e comportamento di un cacciatore paleolitico di 14.000 anni fa*. Tesi di Laurea in Scienze Biologiche. Università di Pisa.

Associate Editor, Rita Vargiu

Appendix 1 - Anthropometric Measurements (in mm).

Skull	
Maximum cranial length (M1)	181.0
Cranial base length (M5)	94.0
Maximum cranial breadth (M8)	137.5
Minimum frontal breadth (M9)	97.0
Basion-bregma height (M17)	133.5
Porion-bregma (M20)	108.0
Basion-prosthion length (M40)	91.0
Bizygomatic diameter (45)	141.0
Upper facial height (48)	66.0
Orbital breadth (M51a)	42.0 R; 43.0 L
Orbital height (M52)	28.5 R: 28.5 L
Nasal breadth (M54)	26.3
Nasal height (M55)	48.0
Maxillo-alveolar length (M60)	65.5
Maxillo-alveolar breadth (M61)	43.0
Bigonial width (M66)	107.5
Anterior mandibular width (M67)	45.0
Mandibular length (M68)	82.0
Maximum ramus height (M70)	62.0
Minimum ramus breadth (M71a)	36.0 R; 35.0 L
Facial profile angle (M72)	80°
Mandibular angle (M79)	123°

Post-cranium	R	L
Clavicle: Maximum length (M1)	145.0	143.0
Clavicle: Circumference at midshaft (M6)	38.0	35.0
Humerus: Maximum length (M1)	320.0	319.0
Humerus: Physiologic length (M2)	313.0	312
Humerus: Epicondylar breadth (M4)	56.0	57.0
Humerus: Maximum diameter at midshaft (M5)	23.0	20.0
Humerus: Minimum diameter at midshaft (M6)	17.5	16.0
Humerus: Minimum circumference (M7)	65.0	58.0
Humerus: Circumference at midshaft (M7a)	67.0	59.0
Ulna: Maximum length (M1)	(268.0)	265.0
Ulna: Minimum circumference (M3)	35.0	33.0
Ulna: Anterior-posterior diameter (M11)	15.0	14.0
Ulna: Medio-lateral diameter (M12)	14.0	13.5

Post-cranium (continued)	R		L
Ulna: Circumference at midshaft	46.0		44.0
Radius: Maximum length (M1)	248.0		---
Radius: Minimum circumference (M3)	39.0		---
Radius: Medio-lateral diameter (M4)	15.0		---
Radius: Anterior-posterior diameter (M5)	11.5		---
Radius: Circumference at midshaft	41.0		---
Femur: Maximum length (M1)	459.0		---
Femur: Bicondylar length (M2)	458.0		---
Femur: Anterior posterior midshaft diam. (M6)	34.5.0		(32.0)
Femur: Medio-lateral midshaft diameter (M7)	29.0		27.0
Femur: Midshaft circumference (M8)	99.0		95.0
Femur: Anterior posterior subtroch. diam. (M10)	26.5		25.0
Femur: Medio-lateral subtroch. diam. (M9)	33.5		33.0
Femur: Anterior posterior head diameter (M19)	48.0		48.0
Femur: Epicondylar breadth (M21)	80.0		78.0
Tibia: Total length (M1)	(386.0)		---
Tibia: Maximum prox. epiphys. breadth (M3)	78.0		77.0
Tibia: Anterior posterior midshaft diameter (M8)	36.0		---
Tibia: Medio-lateral midshaft diameter (M9)	25.0		---
Os coxae: Maximum height (M1)	225.5		224.0
Os coxae: Iliac breadth (M12)	159.0		157.0
Os coxae: Maximum acetabular diameter (M22)	59.5		57.0
Os coxae: Pubis length (Novotny, 1983)	67.0		66.0
Os coxae: Ischium length (Novotny, 1983)	113.0		114.0
Os coxae: Ischium height (Sauter & Privat, 1952)	43.0		41.0
Os coxae: Cotylo-sciatic breadth (M14-1)	40.0		38.0
Pelvis: Maximum diameter (M2)		267.0	
Pelvis: Anterio-posterior diameter (Turner, 1886)		114.0	
Pelvis: Transversal diameter(Turner, 1886)		115.0	
Sacrum: Anterior length (M2)		(100.0)	
Sacrum: Anterior superior breadth (M5)		103.0	