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Multi-proxy analysis suggests Late Pleistocene affinities of human skeletal remains attributed to Balzi Rossi

Margherita Micheletti Cremasco[1], Giuseppe D'Amore[2], Vitale Stefano Sparacello[3,4], Margherita Mussi[5], Manon Galland[6], Antonio Profico[7], Melchiorre Masali[1], Sylvia Di Marco[2], Roberto Miccichè[8], Martin Friess[6] & Luca Sineo[8]

1) *Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy*

2) *I.S.A. - Istituto di Studi Archeo-Antropologici, Via delle Cascine 46, 50018 Scandicci (Firenze), Italy*

3) *Dipartimento di Scienze della Vita e dell'Ambiente, Università degli Studi di Cagliari, Cittadella Universitaria, 09042 Monserrato, Cagliari, Italy*

4) *PACEA, UMR 5199, CNRS, Univ. Bordeaux, 33615 Pessac, France*

5) *Dipartimento di Scienze dell'Antichità, Università di Roma Sapienza, Piazzale Aldo Moro 5, 00185 Roma, Italy*

6) *Muséum National d'Histoire Naturelle, Département Homme et Environnement, UMR7206 du CNRS, Université Paris Diderot, 17 Place du Trocadéro, 75016 Paris, France*

7) *Palaeohub, Department of Archaeology, University of York, UK*

8) *STEBICEF, Dipartimento di Scienze e Tecnologie Biologiche, Chimiche e Farmaceutiche, Università di Palermo, Via Archirafi 18, 90123 Palermo, Italy*

e-mail: luca.sineo@unipa.it

Summary - *In two publications from 1967 and 1971, M. Masali described human skeletal remains presumed to have been found in the Balzi Rossi caves (Ventimiglia, Italy), based on a signed note dated to 1908. Since then, the remains – dubbed "Conio's Finds" and preserved at the University of Torino – had not been further studied. We performed a multidisciplinary investigation aimed at clarifying the geographical and chronological attribution of these specimens. Collagen extraction for AMS dating was unsuccessful, but we obtained two direct dates on the best-preserved crania via $^{231}Pa/^{235}U$ direct gamma-ray spectrometry (10,500±2,000 years BP and 12,500±2,500 years BP). We analyzed the metrics and morphology of the crania and femora by comparing them with samples belonging to the Upper Paleolithic, Mesolithic, and Neolithic periods, and evidenced that the "Conio's Finds" are morphologically more compatible with a Late Pleistocene rather than Holocene attribution. We analyzed the literature regarding the history of excavations at Balzi Rossi, and we propose that – if any credence should be given to the note accompanying the material – the remains may have been found in front of Grotta dei Fanciulli or Grotta del Caviglione, in the redeposited soil dug up during the installation of lime kilns carried out between the late 18th and the early 19th centuries. These hypotheses may be tested in the future by comparing the speleothem deposited on one of the crania and the remaining deposit at the site.*

Keywords - *Craniofacial morphometrics, Cross-sectional geometry, U-Pa series dating, Gravettian, Epigravettian, Grimaldi Caves, Late Pleistocene, Western Europe.*

Introduction

In its relatively long history, paleoanthropological research has seen several episodes of lost or destroyed specimens, due to misplacement, appropriation, war events, and other mishaps (e.g. MacCurdy 1924; Dart 1959; Janus and Brashler 1975; Jia and Huang 1990;

Teschler-Nicola 2006; Svoboda 2008; De Groote et al. 2014; Buck and Stringer 2015; Trinkaus 2017). Occasionally, crucial human remains resurface, and are made again available to the scientific community, thanks to the effort of researchers "digging" into archives, museum deposits, and private collections (e.g. Svoboda 2008; Villotte and Henry-Gambier 2010; De Groote et al. 2014; Moggi-Cecchi 2014; Trinkaus et al. 2014, 2019; Sparacello et al. 2019a,b, 2021). These events have not spared the renowned prehistoric sites in western Liguria (Italy), particularly the caves of Grimaldi (Balzi Rossi; Ventimiglia) and of the Finalese area (e.g. Arene Candide), which were explored since the first decades of the 19th century by naturalists, geologists, amateurs and looters. Scientific methods were first introduced by the team of the prince Albert I of Monaco from 1895 to 1902, and more modern excavations began in Liguria in the 1930s and 1940s (Maggi 1997; De Pascale 2007, 2008; Mussi et al. 2008; Rossi et al. 2014; Formicola and Holt 2015). Before modern laws protecting the archaeological and paleo-ethnological record, the skeletal remains and artifacts resulting from these excavations were often part of private collections, that were sometimes sold and transferred abroad, contributing to the current dispersion and incompleteness of the remains (e.g. Almagro 1955, 1957; Parenti and Messeri 1962; Moggi Cecchi 2014; Mussi et al. 2008; Panelli and Rossi 2015, 2017). In these early decades, poor curation of the specimens and of their documentation (when available in the first place), the destructive events of two world wars, looting, and even scuffles around invaluable burials, have resulted in a number of documented destructions and losses (e.g. Bachechi 2008; Mussi et al. 2008; Panelli and Rossi 2015, 2017), and a large amount of archaeological and anthropological material whose chronology, and provenience in some cases, are uncertain (e.g. Sparacello et al. 2019b).

The skeletal remains presented here belong to this last category and consist of a small assemblage of cranial and postcranial elements currently kept at the Department of Life Sciences and Systems Biology, University of Torino (Italy). They were found, accompanied by a note signed Stefano Conio, an otherwise unknown amateur archaeologist, in the deposits of the Institute and Museum of Anthropology and Ethnography of the same university, by Melchiorre Masali, who published a first description in 1967 (Masali 1967). The note, in Italian, accompanying these "Conio's finds", is reproduced in Supplementary Material 1 Figure S1, and is translated below:

"Several years ago, being a student in San Remo, I visited the caves and the Museum of Baussi Rosse near Menton. On this occasion, strolling around outside the caves and the Museum, I collected some stuff that I could not classify, being profane in the subject. Today, that these bones of prehistoric men and animals (along with various stones) come back into my hands, I offer them to this Museum of Antiquities, certain that they will be accepted with pleasure. Looking forward to a response: Stefano Conio, student"

This brief note was followed by a full address (Corso Vittorio Emanuele 68, Torino), and the date, October 9th, 1908. Unfortunately, the "stones" were not included with the skeletal material, which could have helped the chronological determination. Commenting on the plausibility of the letter's content, Masali (1967) noted that they were most probably unearthed during an unauthorized excavation. Although every detail in the note could have been fabricated, including the signature and the date, the provenience of the remains was deemed plausible given the reddish-brown color of the stalagmitic crust partially enclosing one of the crania (see below; Masali 1967), which was considered compatible with the red color of the terrain and stones of Balzi Rossi ("Red Rocks" in the local dialect). Additionally, similarly to the other famous burials unearthed from Grimaldi caves since the mid-1800s (e.g. Barma Grande, Grotte des Enfants, Barma del Caviglione, Baousso da Torre; Rivière 1873, 1887; Verneau 1899, 1906, 1908; De Villeneuve et al. 1906-19; Mussi 1986; Henry-Gambier 2001; Villotte and Henry-Gambier 2010; Formicola and Holt 2015; De Lumley 2016) the material was heavily stained with red ochre, and a typological analysis of the cranial morphology, following the methods of the time, suggested affinities with the "Cromagnonoid type" (Masali 1967, 1971).

The skeletal material was not investigated further in the following decades, probably due to its uncertain origin and chronology. Except for the brief period (1997-1999) during which one of the crania (labeled BR 1, see below) was put on display at the Museum of Anthropology and Ethnography of the Department of Life Sciences and Systems Biology, University of Torino, the "Conio's finds" are largely unknown to the public and to the scientific community. The purpose of this study is to gain new information on the provenience, chronology, and biological affinity of this skeletal assemblage, using a range of modern techniques. Any extant evidence clarifying the provenience and chronology comes from the finds themselves, from the accompanying note, and from the history of archeological discoveries up to year 1908. The chronology was investigated via direct dating, while morphometric and biomechanical analysis will aid to the assessment of morpho-functional affinities of the remains with prehistoric skeletal series spanning from the Upper Paleolithic to the Neolithic. We will discuss the plausibility of an attribution of the material to one of the Balzi Rossi sites based on the available documentation. To get as close as possible to the original context of the skeletal remains, we make use of the detailed repertoire of archaeological investigations by A. Issel, *Liguria preistorica*, of 768 pages plus tables. Luckily, it was published in 1908, i.e. exactly when Conio donated his finds to the then Regio Museo di Antichità (later ending in the collections of the Institute and Museum of Anthropology and Ethnography of the University of Torino). This allows to grasp if there is any alternative to the Balzi Rossi as the real find spot. Further clues are provided by both Rivière (1887) and De Villeneuve (1906). The relevant hypothesis will be discussed below after the full description of the specimens of the "Conio's finds".

With this study, we aim at restituting to the scientific community this long-forgotten collection of human remains, which can be potentially important for our understanding of past biological variability, and we provide testable hypotheses that may be explored by further analyses.

Materials

The specimens consist of remains of four crania, two of which are almost complete, and postcranial elements: two contralateral femora, fragments of sacra and ossa coxae, and two small rib fragments. The elements and their possible association are listed in Appendix 1, and detailed photographs are presented in Supplementary Material 1. The minimum number of individuals is four, based on the count of crania; three of them were adults, and one was a juvenile.

The first adult is represented by the cranium labeled BR 1, which is almost complete, missing only a portion of the left temporal squama, albeit its observation is partially obscured by the encrustation/speleothem (Fig. 1). Based on cranial traits (cf. Supplementary Material 2), BR 1 has been classified as a female individual, confirming the sex determination proposed by Masali (Masali 1967). The dentition was complete at the time of death; visual observation and CT scan analysis (see below) show that five teeth were lost *post-mortem* (right canine and left incisors, canine and second premolar). The thickness of the encrustation does not allow for a detailed assessment of wear, which nevertheless appears evident especially in the anterior dentition and first molar (Fig. 1 and Supplementary Material 1,2).

The encrustation layer, covering part of the neurocranium with a thin ca. 1 mm layer, becomes a thick speleothem (stalagmite) in most of the splanchnocranium and basicranium, reaching ca. 30-40 mm in the right aspect of the facial cranium. The shape and orientation of the speleothem allow for inferring the orientation in which the cranium laid for at least part of its depositional history, i.e. resting on the surface between the left parietal eminence and the sagittal suture (Fig. 1; Masali 1967). The portion of the skull free of concretion shows some reddish-brown ochraceous staining.

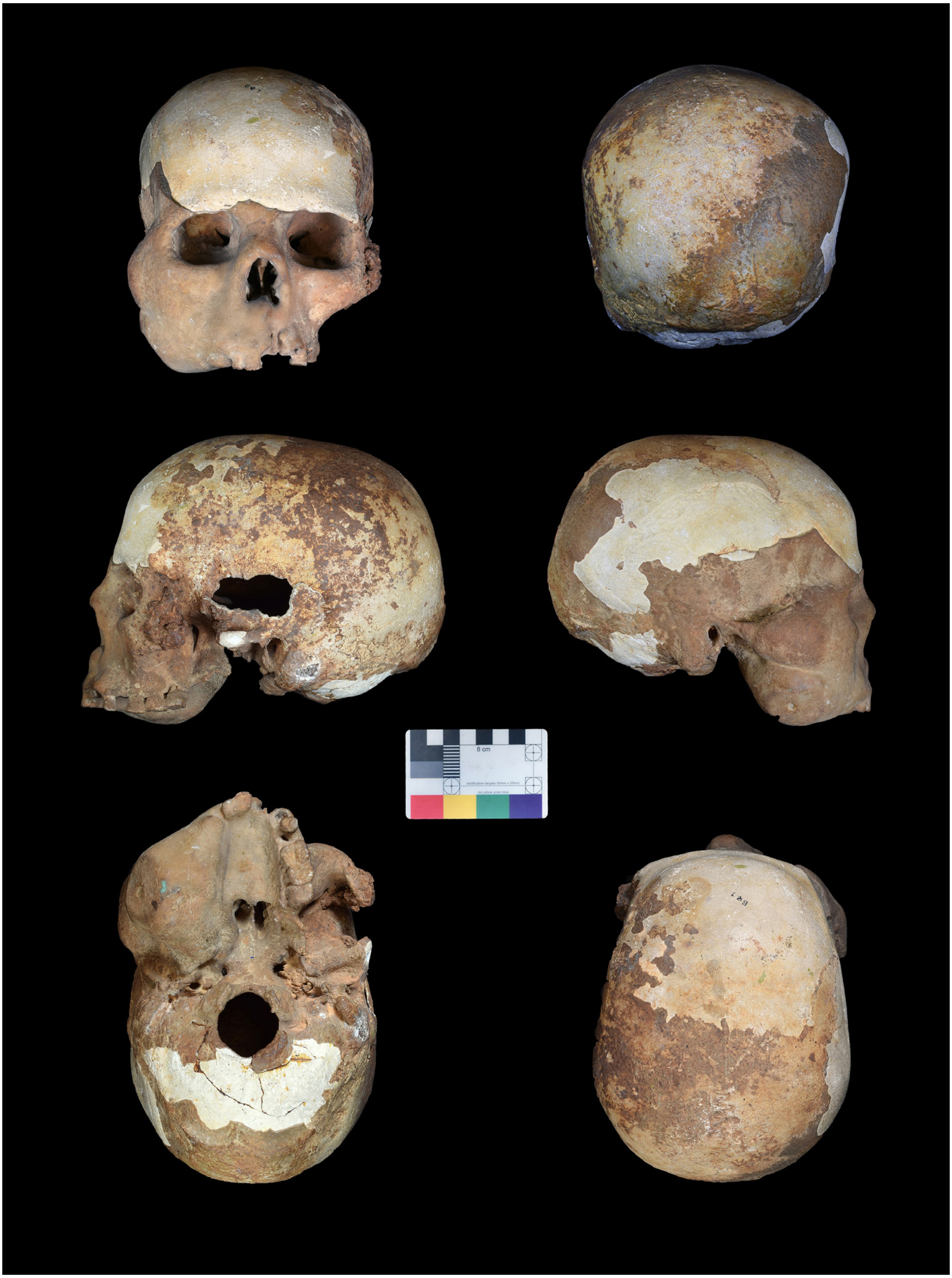


***Fig. 1** – The cranium labeled BR 1 (Individual 1).*

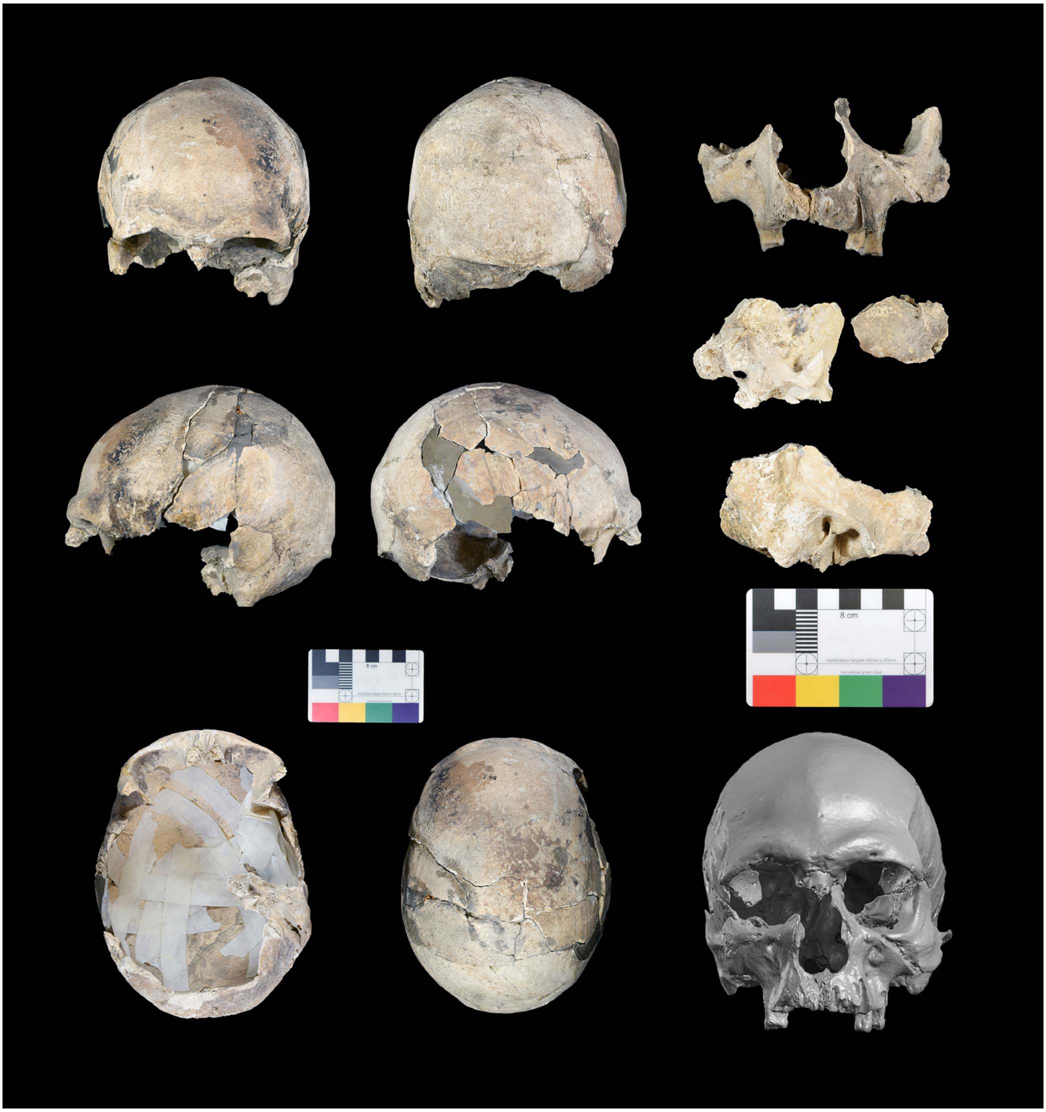


Fig. 2 – The cranium labeled BR 2 (Individual 2), with a virtual reconstruction of the piecing together of the fragments.

The second adult consists of a male (see Supplementary Material 2) cranium labeled BR 2, partially reconstructed with glue and plaster, which is currently separated into several fragments due to recent degradation (cf. Fig. 2 with Masali, 1967). Most of the right zygomatic, sphenoid and basicranium are missing, and most cranial bones are incomplete. Only three teeth are preserved: the left first premolar, and both first molar, showing moderate wear (4 for the premolar, 6 for the molars, in Smith's scale; Smith 1984). The second molars and the right canine were lost *intra vitam*, while it is difficult to determine the reason for the absence of the

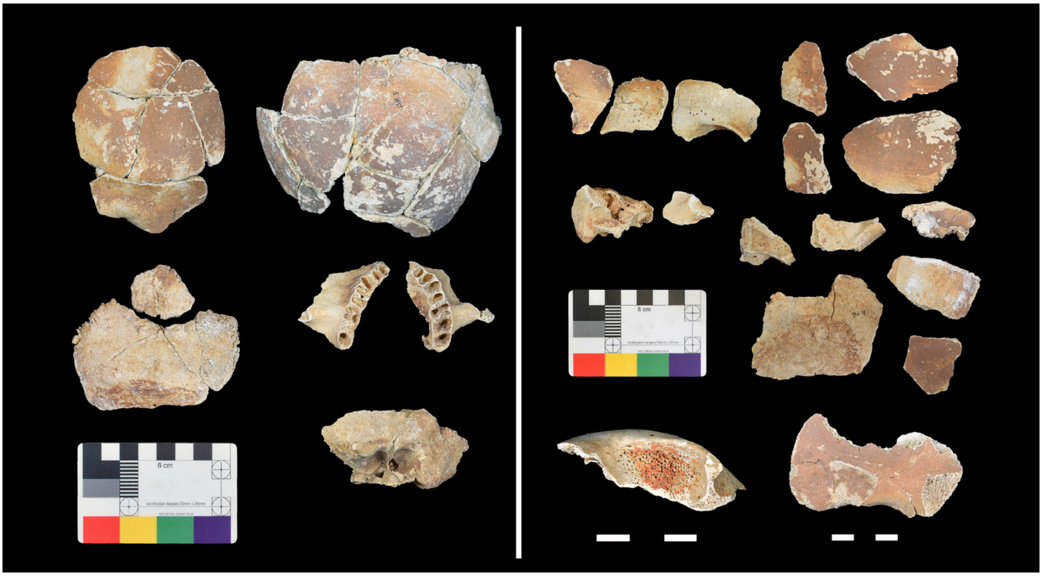


***Fig. 3** – Left: the cranium labeled BR 5 (Individual 3), heavily stained with ochre. Right: the cranium labeled BR 12; at the bottom left, detail of cribra orbitalia; at the bottom right, the iliac fragment labeled BR 16. Both elements have been attributed to the juvenile Individual 4.*

third molars, due to taphonomic damage. The remaining teeth were lost *post mortem* (Fig. 2, and Supplementary Material 1). This cranium shows only some traces of reddish-brown pigment in the left portion of the frontal (Fig. 2).

Conversely, the fragmentary remains of the third adult cranium, labeled BR 5, are heavily stained with this reddish-brown pigment, both in the ectocranial and (partially) endocranial surfaces. Preserved elements consist of a fragmented calvarium and partial maxillary bones (Fig. 3 left and Supplementary Material 1). The lack of remodeling in the maxillary alveola indicates that all upper teeth were present at the time of death, and were lost *post mortem*, leaving in place only some fragments of roots.

The fourth individual is represented by a very fragmentary cranium, labeled BR 12, of a juvenile individual belonging to the "late childhood" or "*Infans* II" age class (Scheuer and Black 2004), based on the size and thickness of the vault. The presence of active *cribra orbitalia* is also more compatible with a young age (Walker et al. 2009a). This cranium shows the same pattern and type of reddish-brown staining as the third cranium in the ectocranial and endocranial surfaces (Fig. 3 right, and Supplementary Material 1).

Postcranial elements belong to a minimum of three individuals. Four fragments of innominate and sacrum articulate to form an incomplete pelvis attributed to an adult male, while two fragmentary innominate bones and one fragment of sacrum belong to a young adult female (Appendix 1, Fig. 4 and Supplementary Material 1; Masali 1967). The two contralateral femora are almost complete, and their femoral heads appear more compatible in size with the acetabula of the male pelvis (Masali 1967; Fig. 5). The third individual is represented by a fragment of left iliac bone belonging to a juvenile, c. 6-8 years old based on size, and therefore compatible in age with the aforementioned subadult cranial remains, and with one of the two fragments of ribs, the second belonging to an adult (Appendix 1, Supplementary Material 1). All the postcranial remains, particularly the pelvic elements, are heavily stained with the same reddish-brown pigment that covers the crania of individuals 1, 3, and 4 (Fig. 4).

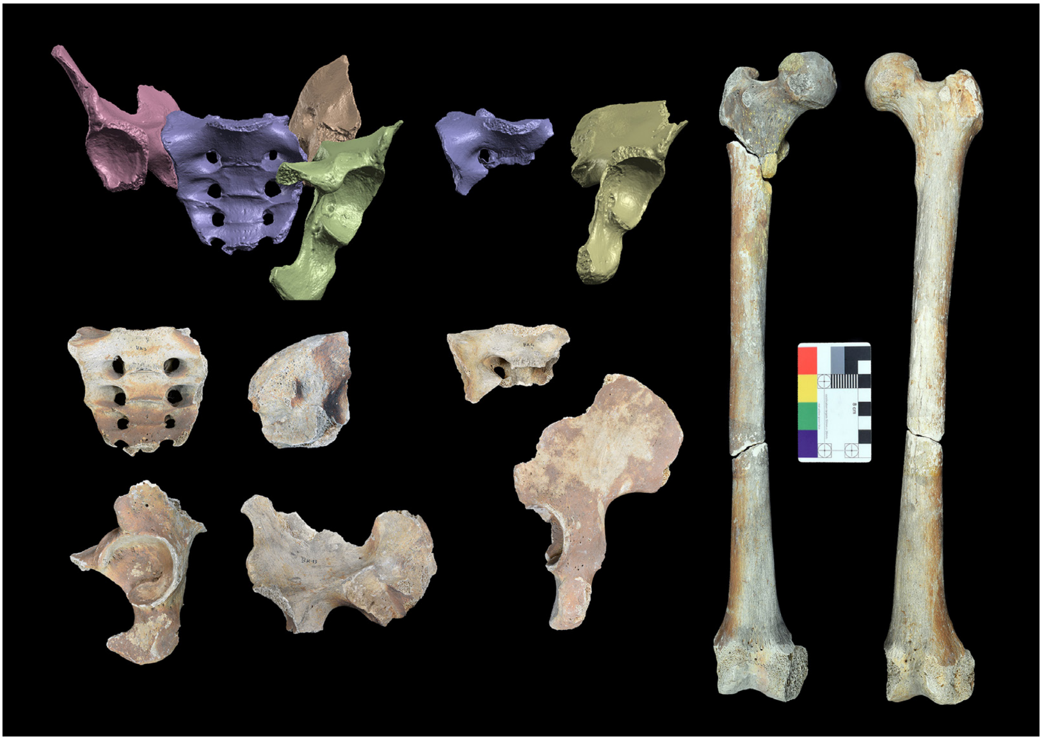


Fig. 4 – The pelvic elements attributed to a male (left: labeled BR 3, BR 9, BR 13, BR 15) and to a female (center: BR 4 and BR 4/bis) individual. In the right, the femora labeled BR 6 and BR 7.

Methods

Direct dating

Three fragments of bone, from individuals BR 2, 3, and 4 (Appendix 1), were treated for collagen extraction at the LAMPEA laboratory (UMR 7269, Aix-en-Provence), according to the laboratory standard protocols. Sampling was aimed at radiocarbon age determination via AMS. Samples were abraded with aluminum oxide by a sandblaster in order to remove the superficial layer of bone. The clean sample was then demineralized in HCl (0.05M) at 4°C for several days and rinsed with distilled water after demineralization was completed. Samples were then cleaned in NaOH for 20h to remove potential remaining contaminant, rinsed and solubilized in HCl (0.01M) at 70°C for 24h. Solubilized collagen was filtered with EzeeFilter® device.

Additionally, the crania of individuals 1 and 2 (BR 1 and BR 2) were directly dated via a non-destructive method, $^{231}Pa/^{235}U$ gamma-ray spectrometry, carried out at the Department of Chemistry of the IENI-CNR, University of Pavia (Dr. Vera Caramella Crespi). The U/Pa method is based on the existing disequilibrium between radionuclides of the natural family of Uranium 235, evaluated by direct gamma spectrometry. During its permanence in the ground, a buried bone rapidly absorbs uranium (U) from the percolating waters, and during fossilization, bones may incorporate uranium but not thorium (Th) or protactinium (Pa) (Ivanovich and Harmon 1992; Berzero et al. 1997; Simpson and Grün 1998). As a result, the fossil bones come to contain much more uranium than fresh ones (from 5 to 10 mg/kg compared to less than 0.1 mg/kg) and, over time, the $^{230}Th/^{238}U$ and $^{231}Pa/^{235}U$

ratios increase until equilibrium is reached. Measuring these relationships in the specimen allows for its direct dating. In this study, a non-destructive method (gamma spectrometry) was preferred, as done for other prehistoric specimens (Cavagna et al. 1995; Sineo et al. 2002; D'Amore et al. 2007). As a detection system, a super-pure Canberra germanium crystal (relative efficiency 31.9%, resolution 1.76 KeV compared to the 1332 KeV line of ^{60}Co) and a computerized spectral analysis system (Ortec Mod. 919) were used. The two crania were placed in the detection chamber for a period of approximately 4,000,000 seconds each (corresponding to about 46 days).

Cranial morphometrics

In order to evaluate the biological affinities of the BR 1 and BR 2 crania, a multivariate approach was used by applying two different analytical methods, 3D Geometric Morphometrics (GMM) and linear measurements. Comparative samples dating to the Upper Paleolithic, Mesolithic, and Neolithic were used in both analyses.

Morphometric analysis on linear measurements

A set of 15 craniofacial measurements, as defined by Martin and Saller (1957) and Bräuer (1988), were reported by one of the authors (Masali, 1967, 1971). These measurements were re-checked on the original crania and on the 3D models, virtually removing the encrustations using segmentation of CT scan data (BR 1), or virtually piecing together the neurocranium and facial cranium (BR 2).

The measurements were used to calculate some traditional craniofacial indices (also defined in Martin and Saller 1957 and Bräuer 1988) which were used for a basic morphometric description (provided in Supplementary Material 3). In addition, a multivariate comparative morphometric analysis of the BR 1 and BR 2 crania was conducted by using a sample of 998 crania, summarized in Appendix 2, dated to the Upper Paleolithic, Mesolithic and Neolithic of Europe and West Asia. Data were obtained from the literature (e.g., Yakimov 1960; Parenti and Messeri 1962; Riquet 1970, 1972; Denisova 1975; Bach 1978; Kővári 2008; Brewster et al. 2014; Cheronet et al. 2016); the complete list of sources is provided in Supplementary Material 3, Table S3-1. For this analysis, ten craniofacial measurements (M1, 8, 9, 17, 45, 48, 51, 52, 54, 55 according to the definitions and numerical code system of Martin and Saller 1957 and Bräuer 1988) were selected out of the previous fifteen, because these are the most frequently available in literature. The resulting dataset was also used to perform a multivariate morphometric test for sex assessment of the two BR crania (see below).

The comparative sample includes crania dated to the Late Pleistocene (*sensu* IUGS, Gibbard et al. 2010) / Upper Paleolithic (UP, N=72), to the Early and Middle Holocene / Mesolithic (Mes, N=363) and to the Neolithic (Neo, N=563) of Europe and West Asia, with presumed sex available for all the specimens (the complete list is provided in Supplementary Material 3, Tab. S3-1). Only specimens with ≤3 missing data (MD) were included; 645 MD out of 9980 (corresponding to 6.46 % of the whole dataset) were estimated by multiple regression separately by sex and chronology (UP, Mes, Neo). Other measurements not included in the multivariate analysis (M10, 20, 51a) have been used in the estimation of missing data. 579 specimens were complete (58.02%); 267 (26.75%) had one MD, 96 (9.62%) two MD and 56 (5.61%) three MD.

Raw measurements were preliminarily size-adjusted through the Q-standardization procedure and transformed into Mosimann shape variables (Darroch and Mosimann 1985; Jungers et al. 1995); in such a way, size variation has been excluded from the analysis and only shape variation has been used in morphological comparisons. Size-adjusted data were used in all the analyses, except for the multivariate morphometric analysis for sex estimation of BR 1 and BR 2, for which both raw and size-adjusted data were tested.

The following methods were used in order to assess the morphological similarity of BR skulls:

A first PCA on the complete 1000×10 size-adjusted data matrix, including BR 1, BR 2 and the 998 crania of the whole comparative sample (i.e. including the Neolithic sample, in order to provide a possible check for the absolute dating results of BR 1 and BR 2). Maximum likelihood method for extracting the factors was used (Cattell 1978), with projection of the first two factors (PC1 and PC2) and identification of individual scores for the two BR skulls, of average scores ("centroids") and fifty-percent normal distribution ellipses for UP+Mes (collectively hunter-gatherers, HG, N=435) and Neo (early farmers: EF, N=545) individuals divided by sex (namely, HG-M, N=276, HG-F, N=159, EF-M, N=327, EF-F, N=236), thus providing an assessment of their morphometric relationships. Factor loadings of measurements resulting for PC1 and PC2 were scrutinized in order to identify the most significant measurements in contributing to the morphological variation.

A second PCA on a selected 437×10 size-adjusted data matrix, including BR 1, BR 2 and 435 UP and Mes crania, in order to provide an assessment of the biological affinities of BR 1 and BR 2 in the context of other, possibly coeval, HG comparative samples. Maximum likelihood method for extracting the factors from the correlation matrix was again used, with projection of PC1 and PC2 and identification of individual scores for the two BR skulls and of centroids for 39 sub-samples (groups or OTUs), defined according to primarily chronological and secondarily geographical criteria. These 39 sub-samples are listed and synthetically described in Appendix 2, with further details provided in the Supplementary Material 3, Table S3-1. Factor loadings of measurements resulting for PC1 and PC2 were scrutinized in order to identify the most significant measurements in contributing to the morphological variation.

A discriminant function analysis (DFA) was also performed on both size-adjusted data matrices, in order to provide a possible mutual check for the results obtained with PCA, since PCA does not use any *a priori* distinction between groups whereas DFA does. A further DFA was also carried out on the selected 437×10 raw data matrix including HG individuals only, in order to obtain a morphometric sex estimation for BR 1 and BR 2. A jackknife cross-validation test was used in order to check that the results were externally as well as internally valid (Efron 1982). This is a common test used in DFA where cases are classified without using the misclassified individuals in computing the classification function (Pietrusewsky 2000). All these tests are described in the Supplementary Material 3.

3D GMM analysis

The 3D models of BR 1 and BR 2 crania were obtained from CT scans performed at the Mircoservice S.r.l (Torino, Italy) with a voxel size of 0.13 mm. The 3D models belonging to the comparative sample were collected by the authors or kindly provided by institutions (see Acknowledgements section), and were variously obtained from CT scans or surface scans. The surface scans have been acquired by using different devices: NextEngine HD (www.nextengine.com), Breuckmann Smartscan stereo (www.breuckmann.com), and Structured Light Scanner DAVID SLS-3 (David Vision Systems GmbH - David 3D Solutions 2007-2015, now acquired by Hewlett-Packard Development Company, L.P, 2016). Appendix 3 displays the comparative sample used in the GMM analysis, consisting of 130 crania belonging to recent human populations (N=77) and to Western Eurasian Upper Paleolithic (N=21), Mesolithic (N=15), and Neolithic (N=17) individuals. References for these data are in Supplementary Material 4.

On each cranium we acquired 39 anatomical landmarks. The landmark configuration captures the overall cranial morphology (location and anatomical descriptions of all landmarks are presented in Supplementary Material 4), and data were acquired by a single observer (MG) using the Landmark Editor software (Wiley 2005). Missing bilateral landmarks were estimated by mirroring-imaging and missing landmarks in the sagittal plane or bilateral landmarks missing on both sides were estimated by the Thin-Plate-Spline interpolation (Gunz et al. 2009) by deforming the closest specimens onto the deficient configurations (Schlager 2017). Repeatability was assessed through five non-consecutive repeat measurements on ten specimens. The intra-observer error (mean 0.8 mm) is below the threshold used in craniometrics (Bräuer 1988). The estimation of missing landmarks and all statistical analyses were performed using R (R Development Core Team 2016).

We performed a GPA (translation, rotation and scaling) on the 132 landmark configurations and the standardized coordinates were subjected to Principal Component Analysis (PCA). We calculated the associated shape variation at the extreme values (negative and positive) of the first two PC scores. The shape variations are visualized calculating the local morphological differences, meant as the local area contraction/expansion compared to the mean shape by using the Arothron R package (Profico et al. 2020). We compared the cranial morphology of BR 1 and BR 2 with the mean shapes pooled by sex of the Upper Paleolithic, Mesolithic and Neolithic sub-samples.

The entire shape information defined by the PC scores has been used as input to build an UPGMA cluster by defining as input the Procrustes distance matrix for all specimens

Postcranial osteometrics and biomechanics

Pleistocene and Holocene humans are characterized by different body size and proportions, with Middle Upper Paleolithic people retaining a tall and narrow body shape, followed by a dramatic reduction in stature with the Late Upper Paleolithic, and the prevalence of stockier proportions in the Neolithic (Churchill 1994; Holliday 1995, 1997, 2002; Formicola and Franceschi 1996; Pearson 1997; Formicola and Giannecchini 1999; Ruff et al. 2006a). In order to place the materials from Torino in this framework, the osteometric measurements of the pair of femora BR 6 and BR 7 (Appendix 1, henceforth referred to as BR_T) were compared with a sample of Italian Gravettian (Middle Upper Paleolithic, MUP; c. 30-18,000 BCE), Epigravettian (Late Upper Paleolithic, LUP; c. 18-10,000 BCE), Mesolithic (MESO, c. 10-6000 BCE), and Neolithic (NEOL, c. 6000-4000 BCE) individuals. Comparative metric data were collected from the literature and by one of the authors (VSS), and are provided, with the references, in Supplementary Material 5. When available, in both BR_T femora and comparative individuals, the average between sides was used.

Among the same groups, due to changes in subsistence patterns, postcranial traits are markedly different also in terms of structural diaphyseal adaptations, particularly activity-related (e.g. mobility) biomechanical properties as inferred from cross-sectional geometry (Holt 1999, 2003; Holt et al. 2000; Marchi et al. 2006, 2011; Holt and Formicola 2008; Sparacello et al. 2018b; Varalli et al. 2020). The cross-sectional geometric properties (CSG) of long bones were analyzed applying beam theory, under the widely accepted notion that bone tissue optimizes to its mechanical environment so as to maintain physiological strains within the normal limits ("Wolff's Law", better referred to as "bone functional adaptation"; Pearson and Lieberman 2004; Ruff et al. 2006b). Although bone robusticity is influenced by multiple factors (Pearson and Lieberman 2004), it is generally presumed that variation in CSG properties correlate with activity levels and types, once the effect of body size is factored out (Ruff et al. 2006b). This residual level of mechanical strength after standardization by body size is called "robusticity" in CSG research (Ruff et al. 2006b), and can be assessed by dividing the polar second moment of area (J; torsional and (twice) average bending rigidity of the beam) raised to the power of 0.73 (which approximates Zp, or section modulus) by bone mechanical length (as defined in Ruff 2002) and body mass (Ruff 2000). Body mass is estimated from the supero-inferior diameter of the femoral head following the guidelines in Trinkaus and Ruff (2012). Given their correlation with mobility levels, other relevant variables are the CSG shape index, which is calculated via ratio between I_x (second moment of area, or bending rigidity, in the anteroposterior plane) and I_y (second moment of area in the mediolateral plane) or ratio of I_{max} (maximum second moment of area) to I_{min}, (minimum second moment of area) (Holt 2003; Shaw and Stock 2009; Carlson and Marchi 2014; Macintosh and Stock 2018).

The cross sections at midshaft of the BR_T femora were reconstructed from 3D surface scans (collected using the DAVID SLS-3 structured light scanner), which were virtually positioned according to the reference planes following Ruff (2002). Due to slightly damaged femoral condyles, particularly the lateral distal condyle in the right femur, and the medial in the left femur, certain measurements, as well as the orientation of the femur for CSG analysis (Ruff 2002), were approximated. This was done through the virtual mirroring and superimposition of one femur on the contralateral. The oriented models were virtually cut using the function "slice" in Netfabb Standard 2018 for PC (copyright by Autodesk 2017). CSG properties were calculated using a version of the program SLICE (Nagurka and Hayes 1980) adapted as a macro routine inserted in Scion Image release Beta 4.03. The "Solid CSG" method was employed to estimate actual CSG properties from the periosteal contour via regression equations (provided in Sparacello and Pearson 2010; Marchi et al. 2011), as justified in previous research (Stock and Shaw 2007; Sparacello and Pearson 2010; Macintosh et al. 2013).

Comparative data for femoral CSG analysis, consisting of Italian MUP, LUP, MESO, and NEOL individuals was collected from the literature, and is provided, with the list of references, in Supplementary Material 5 - OSTEOCSG. When available, in both BR_T femora and comparative individuals, the average between sides was used.

Results

Direct dating

Two of the samples treated for collagen extraction did not yield any collagen (individual BR 2 and 4), while the amount extracted from individual BR 3 was below the minimum requirements for a reliable radiocarbon determination via AMS (less than 1 mg and less than 1% collagen yield; van Klinken 1999). Therefore, it was not possible to proceed with the AMS analysis.

The $^{231}Pa/^{235}U$ direct gamma-ray spectrometry measurement dated BR 1 and BR 2 skulls as follows:

- BR 1: 10,500 ± 2,000 years BP. Because of the low content of uranium, the error associated with the measurement of the various emission lines is quite high.
- BR 2: 12,500 ± 2,500 years BP. The bone of this specimen showed a still lower uranium content than the previous one.

The high error associated with the dates is due to both the low uranium content present in the samples, and to the impossibility of using the most abundant gamma emission lines due to the interference caused by the simultaneous presence of ^{232}Th. This error could be due to applicability problems of the U-series method in this context: the high content of ^{232}Th found in both specimens, together with the relatively low content of ^{238}U, does not offer sufficient guarantees to consider the specimens a "closed" system. The U/Pa method, however, ensures more reliable dating estimates than the U/Th method, even in the presence of non-radiogenic ^{230}Th (Sineo et al. 2002). Moreover, secondary phenomena of fixing, leaching and migration of uranium in the fossil bones occur mainly at the level of the bone surface. The reported ages are based on the assumption that uranium is rapidly absorbed (early uptake or EU assumption), which, for specimens with an age of less than 100,000 years, appears reasonably plausible (Schwarcz 2001).

Cranial morphometrics

Morphometric analysis based on linear measurements

Craniofacial measurements of BR 1 and BR 2 crania are reported in Appendix 4a. Measurements were partially published in Masali (1967, 1971), and re-checked and partially corrected for this study. Since the BR 1 cranium is partially covered by concretion, measurements number 9, 10, 45, 48, 54 and 55 (following Martin and Saller 1957; Bräuer 1988) were estimated by taking into account the thickness of the encrustation. Measurements were taken also on 3D models: for BR 1, a segmentation tool was used to virtually remove the thick encrustation, which allowed for a refining of the estimates listed above. For BR 2, the virtual reconstruction re-pieced together the fragments of the calotte and facial cranium that are currently separated due to recent degradation of the specimen (cf. Fig. 2). Measurements are largely overlapping except for internal palatal breadth (Supplementary Material 3).

The first PCA, performed on the larger (1000×10) size-adjusted data matrix, produced a scatterplot showing a certain separation along PC1 axis between the HG (UP+Mes) and EF (Neo) individuals (Fig. 5a). Overlap between ellipses was greater between sexes of the same group and between HG-F / EF-M, whereas HG-M and EF-F produced a minimal overlap. Both BR 1 and BR 2 fall in the HG side or morphospace. More precisely, BR 2 falls in the HG-M morphospace, very close to the HG-F morphospace, while BR 1 falls in the HG-F and EF morphospaces. Values for factor loadings are reported in Supplementary Material 3, Figure S1 and Table S2; they summarize the observation that bizygomatic breadth M45 and orbit height M52 play a major role in differentiating HG and EF groups along PC1, with the HG crania having wider faces and lower orbits and the EF crania having narrower faces and taller orbits. Additionally, the two measurements M45 and M52 also produced, along PC1, a differentiation between the sexes within each of the HG and EF groups, with males having wider faces and lower orbits and females having narrower faces and taller orbits. Regarding PC2, its axis described a differentiation between taller and lower faces and noses, without involving the height of orbits, with males having taller faces and noses than females within each of the HG and EF groups. With respect to this second axis, BR 1 resulted a little more on the "lower faces" side of the plot, whereas BR 2 resulted on a somewhat advanced position on the side of "taller faces".

The second PCA, performed on the selected (437×10) size-adjusted data matrix including only HG individuals, produced a scatterplot where the average scores (centroids) of the 39 sub-samples or groups and the individual scores of the BR 1 and BR 2 crania were calculated and projected onto the morphospace formed by PC1 and PC2 (Fig. 5b). In order to facilitate visualization of proximity or distance between groups of similar age or provenance, groups were identified as belonging to "macro-groups" defined according to their absolute or cultural chronology and gross geographical origin, as listed in the column "period and region" of Appendix 2, where abbreviations are also provided. A first separation along PC1 axis between the oldest groups, dated to the Pre-Last Glacial Maximum time period (Early Upper Paleolithic, EUP "macro-group"), and all the other, more recent (Late Upper Paleolithic and Mesolithic) groups, is clearly observable, with EUP groups all with negative scores for PC1. Then, a trend towards a partial distinction between, on the one side, the LUP macro-group (including groups of late Epigravettian, Magdalenian and related Late Glacial period cultures) of western and central Europe, and the Mesolithic macro-groups from Iberia and from West-Central Europe, mainly with negative PC1 and PC2 scores, and, on the other side, the early and late Mesolithic macro-groups from East and North Europe (including Scandinavia, Russia, Ukraine and the "Ceramist late HG" groups from the Forest-Steppe Zone in the Baltic and Pontic regions) and the early Mesolithic groups of South Europe (including Sicily and the Balkan region), mainly with positive PC1 and PC2 scores, seems sufficiently appreciable. The Natufian macro-group of West Asia occupied an intermediate position in between the above described "clusters". The overall pattern seems to suggest somewhat a both chronological and geographical differentiation, since the oldest groups belonging to the EUP, LUP and WAP macro-groups were rather separated from many of the most recent groups represented by the Ceramist late HG groups from the Baltic and Pontic Forest-Steppe Zone and, similarly, Western Europe macro-groups were overall distinguishable from Eastern Europe macro-groups, with the group 5 (East Europe and Levant Pre-Last Glacial Maximum) of macro-group EUP who was closer to the "Eastern side" of PC1 axis.

On this picture, BR 1 placed closer to LUP and WCM macro-groups (near groups 7: EG, 14: NWM, 17: CEM), thus demonstrating its greater morphological affinities with penecontemporary and geographically neighboring samples. BR 2, on the contrary, occupied a more isolated position of the morphospace, in proximity of North and East Europe HG groups, of which some have a very late date (36: Bolshoy Olenii Ostrov, 38: Vaesterbjers).

Analysis of factor loadings of measurements for PC1 and PC2, summarized as previously in Supplementary Material 3, Figure S2 and Table S3, revealed that the measurement which contributed most and by far to the separation along PC1 was M52, with taller orbits for positive scores on this axis; a lesser contribution was given also by M1 and M54, with longer neurocrania and wider noses for negative scores. As far as PC2, measurement M9 produced wider frontals for negative scores, M48 and M55 taller faces and noses for positive scores. Therefore, EUP groups tend to possess longer neurocrania, wider noses, lower orbits and, sometimes, wider frontals and lower faces and noses. Based on this pattern of variation, BR 1 would have moderately expressed the following morphometric features: long neurocranium, wide frontal and nose, low face, orbits and nose. On the contrary, BR 2 should be characterized as showing clearly expressed the opposite condition, that is, short neurocranium, narrow frontal and nose, tall face, orbits and nose.

DFA was also performed on both the two size-adjusted data matrices, in order to provide a possible mutual check for the results obtained with PCA. A further DFA was also carried out on the selected 437×10 raw data matrix including HG individuals only, in order to obtain a morphometric sex estimation for BR 1 and BR 2. The results are presented in the Supplementary Material 3, showing that both BR 1 and BR 2 are best classified in HG *a priori* groups, more precisely BR 1 in HG-F and BR 2 in HG-M. Furthermore, in the second DFA, BR 1 and BR 2 resulted much more spatially close to each other than found in the PCA, with BR 1 confirming its closer morphological affinities with coeval and geographically closer samples, whereas BR 2 resulted morphologically more distant and "atypical". Finally, in the sex estimation DFA test, resulting distance and posterior probability of membership for the BR 1 and BR 2 crania showed that BR 1 was better classified in the female *a priori* group in both raw and size-adjusted data tests, whereas BR 2 was practically equally classifiable as male or female in the raw data test, while it produced a slightly better probability of classification as male in the size-adjusted test. Results by jackknife cross-validation tests revealed higher percentages of correct classification; overall, jackknifed results for the BR crania seemed not to differ substantially from those obtained by standard procedure.

3D GMM analysis

The first two PC scores account for the 23.56% of the total variance (Fig. 6a). The groups (Upper Paleolithic, Mesolithic, Neolithic and recent humans) largely overlapped along the PC1 (13.82%) and PC2 (9.74%). Modern human populations tend to show positive values of the PC1 and they are distributed along all the range of the PC2. The Neolithic sample is positioned at negative values of the PC1 and along most of the range of the PC2. In the PCA plot, Mesolithic individuals are mainly positioned on positive values of the PC2 and along most of the variability along the PC1.

The observed pattern of shape variations is represented by the stylized models of crania of different shape in lateral views, arranged at the extremes of the PC1 and PC2 axes; shades of two colors indicate local pattern of area expansion (blue) and contraction (red) with respect to the mean shape. At the negative extreme of PC1 the cranium is elongated antero-posteriorly, the facial complex is vertical paired with the presence of alveolar prognathism. The zygomatic bone is vertically expanded suggesting a robust cranial architecture. On the contrary, at positive value of the PC1 the neurocranium is more globular and the facial complex is reduced in size resembling a "gracile" morphology. The shape

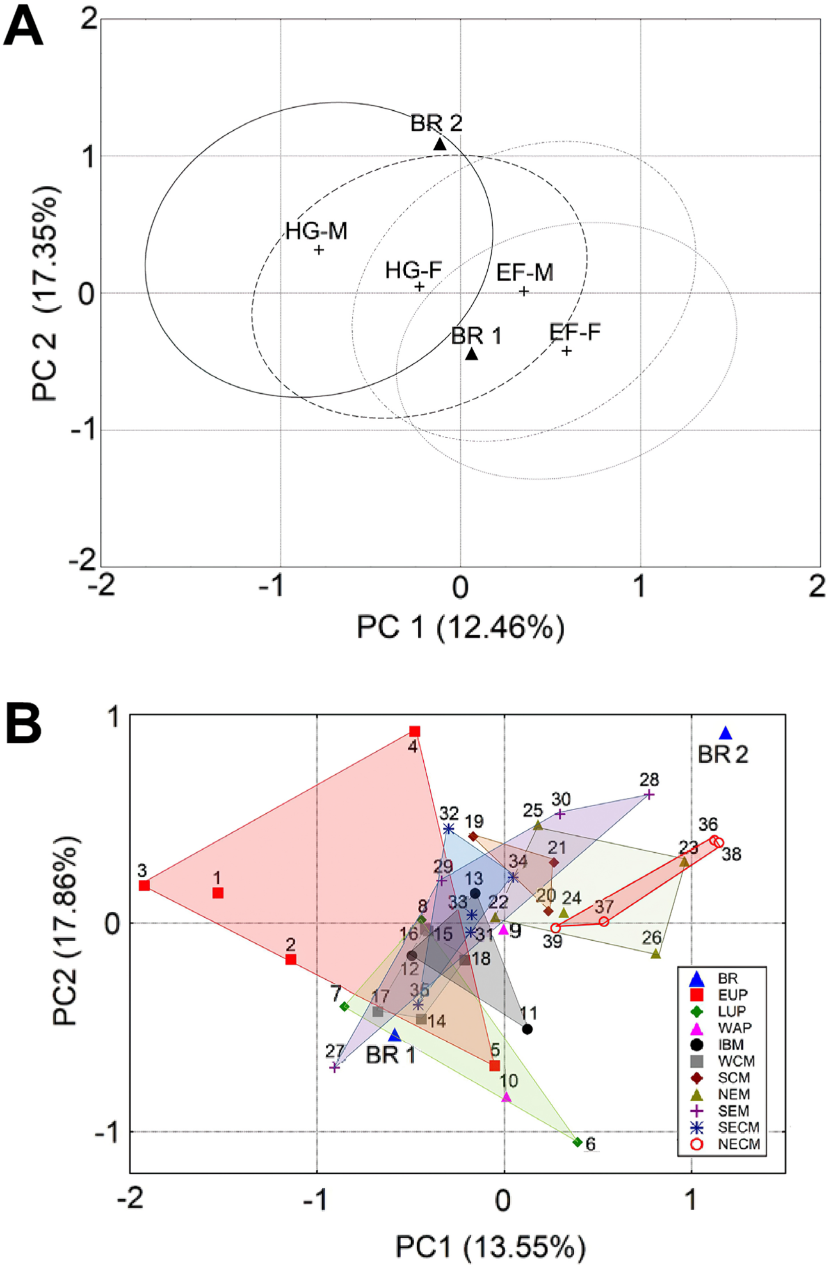
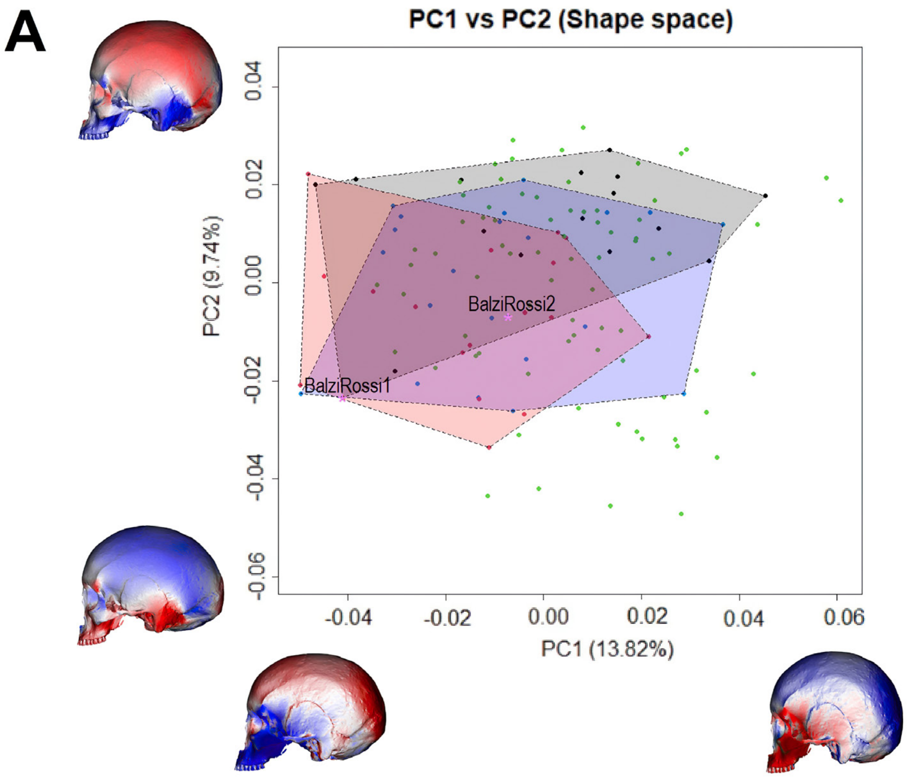


***Fig. 5** – A) Plot of the first two PC scores for the first PCA of morphometric analysis based on linear measurements. Average scores (centroids) and fifty-percent normal distribution ellipses (solid line: HG-M, dashed line: HG-F, dotted line: EF-M, dashed-dotted line: EF-F) of HG and EF groups divided by sex, and of individual scores of BR crania. B) Plot of the first two PC scores for the second PCA of morphometric analysis based on linear measurements. Scatterplot of average scores (centroids) of the 39 sub-samples or groups and of individual scores of the BR 1 and BR 2 crania. For abbreviation see text.*



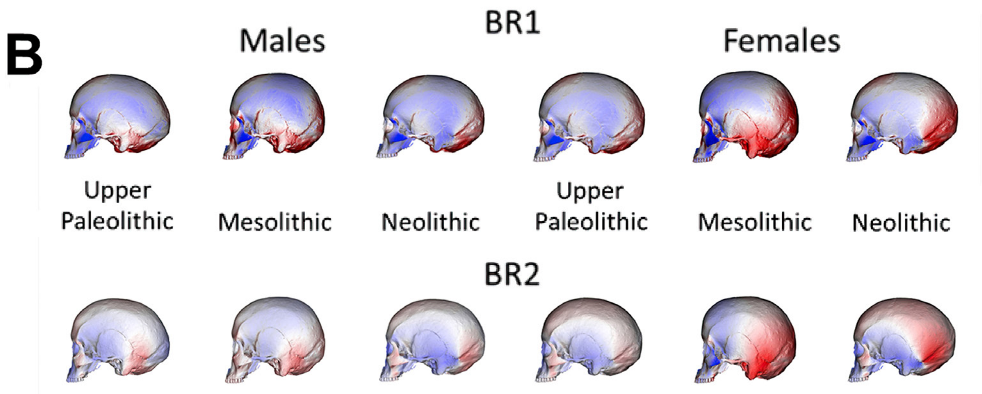


***Fig. 6** – A) Plot of the first two PC scores of 3D GMM analysis. The specimens belonging to Upper Paleolithic (blue), Mesolithic (black) and Neolithic (red) are delimited by convex hulls. Recent modern humans are in green. BR 1 and BR 2 are starred in violet. At the extreme of the PC1 and PC2 axes the shape variations are reported. B) A reference 3D model has been warped on the Upper Paleolithic (left), Mesolithic (middle) and Neolithic (right) mean shapes pooled by sex (male on the first 3 columns, female on the last three columns). For explanation see text.*

variations associated to the PC1 seems to mainly record morphological differences between modern humans and other human groups.

At the extreme of the PC1 the Neolithic group is located at negative values and the "recent" group at positive values. On the PC2 all the four groups are largely overlapped except for the Mesolithic group located mainly at the positive extreme. The shape variations associated to the PC2 recorded mainly variations linked to the neurocranial height and breadth and to the morphology of the facial complex. On positive values of the PC2 the mastoids are expanded and vertically oriented. On negative value of the PC2 the face is flat (i.e., absence of alveolar prognathism), the orbit appears bigger in size and the zygomatic bone is backward positioned; the frontal bone is characterized by the presence of a bulging and by a moderate post-orbital constriction. The opposite pattern is visible at positive values of the PC2, in fact the face protrudes anteriorly, the frontal bone is robust as highlighted by the presence of a well-defined supraorbital sulcus as well as a marked post-orbital constriction.

BR 1 is located at extreme negative value of the PC1 and at negative value of the PC2. BR 2 is placed at both neutral values of the first two PC scores (Fig. 6a).

The PC scores of a sub-group of specimens defined excluding recent human populations have been used to build a matrix of morphological distances between the specimens. The matrix of distances has been subjected to the UPGMA clustering method (Supplementary Material 4, Fig. S2). The UPGMA does not show a clear diachronic pattern or a trend resembling changes in morphology related to the emergence of cranial derived traits. BR 1 represents a basal group close to two Mesolithic and one Upper Palaeolithic individuals. BR 2 is located in a cluster mainly formed by Mesolithic and Neolithic specimens.

In addition, a direct comparison between BR 1 and BR 2 cranial morphology with the mean shapes of Upper Paleolithic, Mesolithic and Neolithic groups pooled by sex is reported in Figure 6b, in which a reference 3D model has been warped on the Upper Paleolithic (left), Mesolithic (middle) and Neolithic (right) mean shapes pooled by sex. The color map shows the local difference expressed as local area variations from BR 1 and BR 2 to the female and male mean shape. Blue and red indicate local pattern of area expansion and contraction, respectively. The local pattern of shape variation between the two crania from Balzi Rossi and the mean shapes of the human groups shows a higher morphological affinity between BR 1 and the female of the Upper Paleolithic group. BR 2 shows slight differences in shape when compared to both Upper Paleolithic and Mesolithic males.

Postcranial osteometrics and biomechanics

Osteometric measurements and CSG properties of the BR_T femora are provided in Appendix 4b, and high-resolution images of the boxplots and scatterplots described below are available in Supplementary Material 5. Femoral length, as expected based on previous studies on stature, is the variable that best characterizes groups based on chronology, and also shows high sexual dimorphism. Gravettian (MUP) individuals show on average the longest femora, and Neolithic the shortest, with the male mean being higher in all groups (Fig. 7a). The maximum femoral length of BR_T is above the range of variation of Neolithic individuals from Liguria, but is short when compared to most Gravettian males. It appears most compatible with Gravettian females, albeit the sample size is small, or with the tallest Epigravettian and Mesolithic males (Fig. 7a). Articular dimensions of BR_T are not as large as in Gravettian males, but are generally above the range of variation of Mesolithic and Neolithic females [M13, upper epiphyseal length, M18, vertical head diameter, M21, distal bicondylar width (estimated measurement); Supplementary Material 5, Fig. SI5-1]. When plotting the variables commonly used to estimate stature (M1) and body mass (M18), the resulting body proportions of BR_T do not overlap with the range of any group except for Gravettian females (Fig. 7b). However, sample size is small, and when using 95% CI ellipses instead of ranges there is much more overlap among groups.

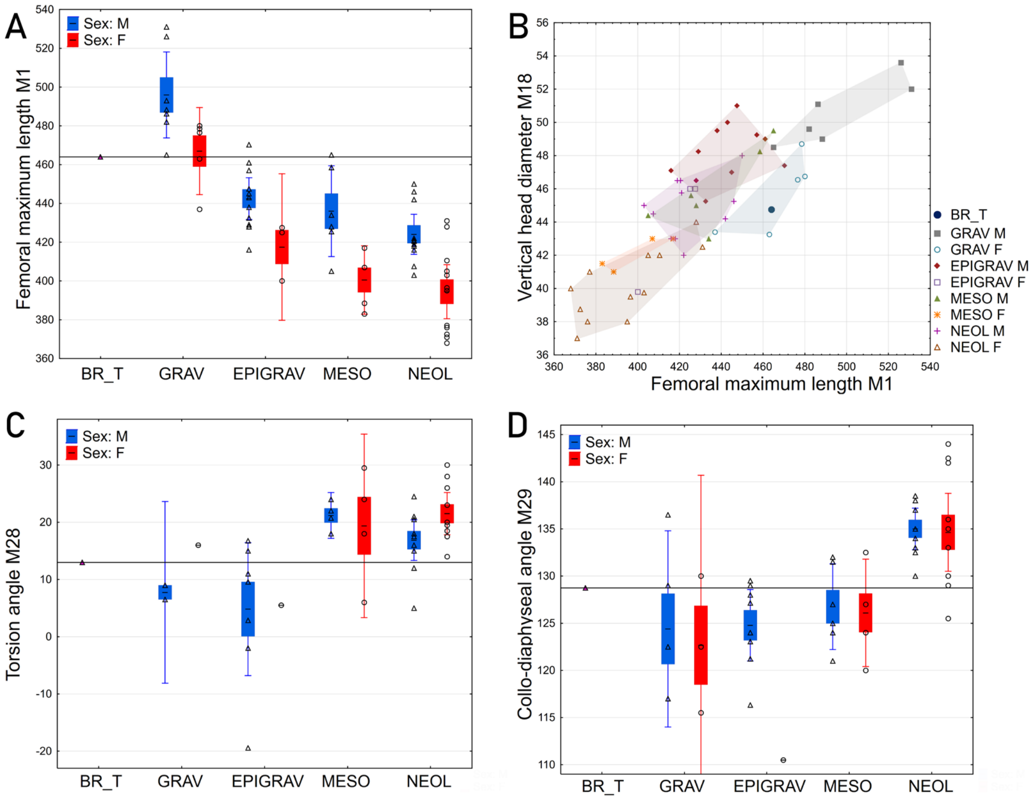


***Fig. 7** – A) Maximum length (Martin's M1) of the BR_T femora (BR 6 and BR 7); B) Scatterplot of two femoral measurements used as a proxy for body proportions: maximum length (Martin's M1) as a proxy for stature, and vertical head diameter (Martin's M18) as a proxy for body mass; C) Torsion angle (Martin's M28); D) Collo-diaphyseal angle (Martin's M29). BR_T femora are compared to Italian Gravettian, Epigravettian, Mesolithic, and Ligurian Neolithic individuals. The box/whisker indicates the mean, the standard error, and the 95% confidence interval.*

The Neolithic and Mesolithic samples show a higher femoral angle of torsion (M28; both sexes; Fig. 7c), while the Neolithic sample (both sexes) display on average a high collo-diaphyseal angle (M29; Fig. 7d), with several individuals characterized by *coxa valga* (M29 > 135). For both variables, the BR_T femora appear more compatible with Pleistocene rather than Holocene individuals.

When considering femoral CSG properties, Pleistocene and Holocene Italian groups are not markedly different in terms of overall femoral robusticity, i.e. when the overall torsional rigidity is standardized by body dimensions, showing only a slight decreasing diachronic trend, with the confidence intervals for size-standardized Zp largely overlapping (Fig. 8a). The BR_T femora fall within the 95% CI of most groups, with the exclusion of Gravettian and Mesolithic males, which are particularly robust (Sparacello et al. 2018b, 2020). However, plotting the two variables determining size-standardized Zp ($J^{0.73}$ and body mass times femoral mechanical length; Ruff 2002) allows for a better discrimination of groups based on size and mechanical loading (Fig. 8b). Although only the Gravettian males do not overlap with any other group, the BR_T femora fall closer to the centroid of the spread of Pleistocene

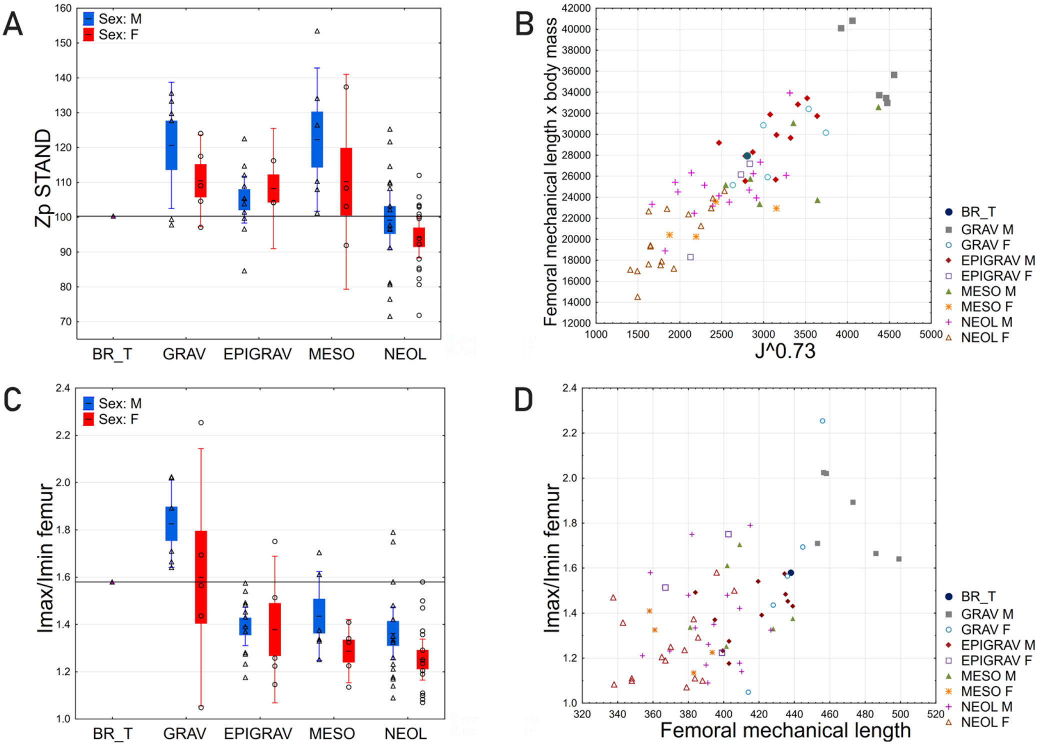


***Fig. 8** – A) Robusticity (mechanical rigidity scaled to body size) of the BR_T femora (BR 6 and BR 7) as by standardized Z_p (see text); B) The same variable displayed as a scatterplot of its factors, using the same individuals grouped by period and sex; C) Cross-sectional shape index I_{max}/I_{min} of the BR_T femora (BR 6 and BR 7); D) I_{max}/I_{min} plotted on femoral mechanical length, using the same individuals grouped by period and sex. BR_T femora are compared to Italian Gravettian, Epigravettian, Mesolithic, and Ligurian Neolithic individuals. The box/whisker indicates the mean, the standard error, and the 95% confidence interval.*

(Epigravettian males and Gravettian females) rather than Holocene individuals (Fig. 8b).

Conversely, the shape indices show a clearer pattern by period and sex, and the high value of I_{max}/I_{min} shown by BR_T femora is at the upper end of the variability of most groups, with the exclusion of Gravettian males (Fig. 8c). Given the correlation observed between shape indices and femoral length in prehistoric, highly-mobile groups (Sparacello et al. 2018b), I_{max}/I_{min} was plotted against femoral mechanical length (Ruff 2002); again, BR_T falls closer to the center of the spread of Pleistocene rather than Holocene groups (Fig. 8d).

The "Conio's finds" and the 19th century excavations in Liguria

To provide some background to the origin of the "Conio's finds", donated in 1908, we focus below on the Paleolithic sites discovered and in existence during that time at Balzi Rossi, which is mentioned in the accompanying note, as well as in Liguria and Piedmont, where the donor had been active (see also Supplementary Material 6).

The Balzi Rossi is a beautiful cliff oriented east-west, with the cave entrances facing south, which provides ideal insolation for human occupation. However, the sea rise after the Last Glacial Maximum left only a narrow strip of land, a few tens meters wide, between the caves and the Mediterranean shore. Human activity focused on this narrow passage and heavily impacted on the *talus* extending in front of the caves, i.e. on the extensive accumulation of deposits which normally develops outside a cave. The Romans first encroached on the archaeological *talus* when they traced the Via Aurelia at the foot of the cliff. However, the major devastation was the outcome of the railway line linking Genoa to Nice after 1870. This implied quarrying away the archaeologically-rich deposits down to ten meters from the original surface. Rivière (1887), attracted by the abundance of archaeological remains, closely followed the railway construction but the *talus* was almost totally destroyed without any proper investigation (Supplementary Material 6, Fig. S1).

The railway did not impact directly on the caves themselves, which have been the focus of most subsequent archaeological research. However, industrial activities were also established in some of them, i.e. lime kilns which directly took advantage of the limestone at the site. At Grotta dei Fanciulli (Grotte des Enfants in the French literature) a kiln, already recorded by de Saussure visiting the area in 1786, eventually took up two thirds of the surface and was deepened down to 7 meters and to *foyer* G, now recognized as Gravettian (Figure S3 in Supplementary Material 6). It was filled by loose redeposited sediments, which were described as rich in remains (De Villeneuve 1906, p. 17-18). At Grotta del Caviglione (Grotte du Cavillon in the French literature), another kiln was already in existence at the beginning of the 19th century (Rivière 1887, p. 127). At the entrance, an enormous carob tree had been uprooted to establish the kiln, assumedly further damaging the archaeological layers.

When archaeological investigations started, possibly in the thirties of the 19th century (Moullé and Arellano 2008), it most often consisted of burrowing and looting (Supplementary Material 6). The quality of research improved in the last quarter of the century. By then, Rivière (1887) hired local people to dig in the caves, removing the sediment by artificial horizontal cuts, and had it sieved. However, it was the team of Albert I of Monaco (De Villeneuve et al. 1906-1919) who first introduced proper scientific methods, albeit using the limited technology of the times. Francesco Abbo, a local entrepreneur who had quarried away half of the Barma Grande, and eventually had Baousso da Torre blown up in 1901 (De Villeneuve 1906), was the last non-professional active on the archaeological scene (Mussi et al. 2008). Eventually understanding that culture and archaeology were profitable, he was also behind the construction of the Museum Praehistoricum funded by Lord Hanbury in 1898.

At the end of the 19th century, however, not much subsisted of the layers with Final Epigravettian industries, i.e. those of the end of the Late Pleistocene, assumedly the most relevant here as compatible in age with the Conio's dated skeletal remains. A hint is currently available of the original extension and altitude of those layers. A kind of freeze of deeply engraved vertical lines stretches over most of the cliff from Grotta dei Fanciulli to Grotta del Caviglione at 27-28m asl, and down to 20-21m asl at the Barma Grande (Vicino and Mussi 2011). This is several meters higher up than the known Gravettian levels at Grotta dei Fanciulli and Grotta del Caviglione. The deeply-cut engraving could only have been produced by means of standing at level with the Final Epigravettian, which is fully recorded only at Grotta dei Fanciulli (Rivière 1887; De Villeneuve et al. 1906-1919), and later at Riparo Mochi (Blanc 1938), while it was completely removed elsewhere. The freeze proves that extensive layers deposited at the end of the Pleistocene once existed along the Balzi Rossi cliffs and its caves.

In order to evaluate the sites known at the time as yielding human remains of Upper Palaeolithic age in the rest of Liguria, we searched the detailed accounts by Issel (1908), which constitute the state of the art around the time of Conio's donation. Notwithstanding the amount of information accurately assembled by Issel, there is almost no possibly relevant Paleolithic site. Issel lists Grotta dei Colombi with some human remains and lithic implements of undefined age, but otherwise focuses on the Balzi Rossi that he describes extensively. The Neolithic burials are much better documented at Grotta di Bergeggi, Caverna Pollera and Caverna delle Arene Candide. However, they are not compatible with Conio's finds in age and in morphometric characteristics, as explained above. In Piedmont, the Upper Paleolithic record is extremely scarce. Relevant sites had not been discovered one century ago (Radmilli 1975). All things considered, we propose that Stefano Conio should be taken seriously when he declares that his finds are from the Balzi Rossi.

Discussion

Direct dating

Unfortunately, radiocarbon dating could not be accomplished in this study due to inadequate amount of collagen in the samples that could be collected. Bad preservation was also noted in an attempt to perform a DNA extraction (A. Mittnik, personal communication). Although negative results are rarely published, skeletal material from Grimaldi caves tend to yield little or no collagen (e.g. Formicola et al. 2004; Benazzi et al. 2015; Pothier Bouchard et al. 2020), especially when compared to the good preservation of skeletal material from other sites in western Liguria, e.g. the Finalese area (Sparacello et al. 2019a,b).

The mean direct dates obtained using the U/Pa method chronologically frame cranium BR 1 within the Early (or Greenlandian) Holocene (from 11,700 to 8,200 cal BP), and BR 2 within the Late Glacial time interval, particularly the Younger Dryas cold event, dated to between ca. 12,900 and 11,700 cal BP (Muscheler et al. 2008; Walker et al. 2009b). However, given the large uncertainty in the determination, the 95% confidence intervals of the dates largely overlap, and span a large portion of Late Glacial and Early/Middle Holocene. Large confidence intervals have been obtained when applying this method to other Italian Late Pleistocene and Holocene specimens (Sineo et al. 2002; D'Amore et al. 2007), and are unfortunately unavoidable when applying U-series dating to relatively recent remains.

When taking into account the chrono-cultural sequences of northern Italy (e.g. Mussi 2001), results from the direct dating suggest that the presumed Balzi Rossi specimen from Torino may chronologically overlap with the Upper Paleolithic cultures of Liguria, i.e. the Late/Final Epigravettian, which span the end of the Pleistocene (Mussi 2001; Formicola et al. 2005; Sparacello et al. 2018a), and are most likely older than the earliest diffusion of Neolithic cultural complexes in Liguria (e.g. Sparacello et al. 2019a,b). An Epigravettian attribution would be compatible with burials found at Balzi Rossi, such as Grotte des Enfants 1-3 (Henry-Gambier 2001). Although the range of the dates overlaps with the Early/Middle Holocene, little evidence for Mesolithic (Sauveterrian or Castelnovian) cultural assemblages is present in western Liguria, and none was reported from Balzi Rossi; few lithic assemblages mainly come from open-air sites at hilltops and mountain passes (Maggi and Negrino 2016).

Cranial morphology

The uncertainty on the absolute chronology of the Balzi Rossi skulls can be at least partially reduced in light of the results obtained through their morphological comparison. Many of the analyses we performed show that the two skulls appear morphologically closer to the Upper Paleolithic and Mesolithic comparative samples than to those of the Neolithic or post-Neolithic. Multivariate comparison carried out on 10 linear measurements produced results showing for BR skulls clearer morphological affinities to Upper Paleolithic and Mesolithic comparative samples, although only BR 1 seems a "typical" specimen, whereas BR 2 appears as a morphological "outlier". A possible explanation for the morphological peculiarity of BR 2 can be found in its extremely tall orbits, with a value well above the Upper Paleolithic and Mesolithic averages. Orbit height M52 is a craniofacial trait showing a diachronic trend toward taller orbits from Early Upper Paleolithic to recent populations (D'Amore et al. 2010, p. 397-400), and its value in BR 2 is quite high, both absolutely

(35 mm) and after size-adjustment (0.458). The raw measurement is constantly more than one standard deviation above the averages of the four comparative samples HG-M, HG-F, EF-M and EF-F, and the size-adjusted value is more than one standard deviation above the average of the HG-M group only, and at the upper limit of the variation for HG-F, EF-M and EF-F; both values are higher than all the averages of the 39 Upper Paleolithic and Mesolithic sub-samples (Supplementary Material 3, Figs. S5-S8). On the contrary, BR 1 has a very low orbit, with values (29 mm and 0.407 after size-adjustment) much closer to the averages of the Upper Paleolithic samples and well below the averages of Mesolithic and Neolithic samples.

It seems unlikely that the peculiar height of BR 2's orbit could be due to taphonomic deformations or an inaccurate restoration: Masali (1967, 1971), who studied the remains when BR 2 was still intact and with the craniofacial region well preserved (see Masali 1967, p. 180 Fig. 3), detected an even higher value for M52 (37 mm), and therefore even more outlier. However, we considered advisable to repeat the two PCAs after excluding this measure. The results show that the general pattern changes, with a less clear distinction between groups; however, the two skulls BR 1 and BR 2 maintain their mutual distance, and BR 2 still continues to be a morphological outlier (Supplementary Material 3, Figs. S9-S12).

Apart from the orbit height, several other morphological and morphometric features of BR 2 are consistent with the Upper Paleolithic/Mesolithic range of variation and provide support to its morphological assessment as a pre-Neolithic specimen.

Overall, the results of the GMM analysis on the 3D sample agree with the morphometric analysis based on linear measurements. Albeit an overlapping between groups has been observed (i.e., Upper Palaeolithic, Mesolithic, Neolithic and recent populations), the 3D analysis on BR 1 emphasize its cranial architecture characterized by an antero-posterior elongation of the neurocranium and a general gracile morphology of the skull, which is in agreement with a female attribution. BR 2 falls on neutral values of both PC1 and PC2. The comparison of BR 2 cranial morphology with those calculated on the average female and male groups belonging to Upper Palaeolithic, Mesolithic and Neolithic, confirms the classification as a male individual (Fig. 6b).

Since our results describe a picture of clear morphological distinction between the BR 1 and BR 2 skulls, it would be interesting to understand what produced it. Paleoanthropological evidence supports the hypothesis of a biological distinction of pre-LGM, Early Upper Paleolithic peoples, and a Late Upper Paleolithic-Mesolithic continuity: this picture was convincingly demonstrated by the results of a craniometric analysis carried out on the most extensive European Upper Paleolithic and Mesolithic database studied so far, where a clear morphological discontinuity was found only between pre-Last Glacial Maximum and later (Late Glacial, Early and Middle Holocene) groups (Brewster et al. 2014). Our results obtained with the second PCA on linear measurements showed a clear separation along PC1 axis between the oldest groups, dated to the Pre-LGM/Early Upper Paleolithic period, and all other (Late Upper Paleolithic and Mesolithic) more recent groups, in agreement with the results obtained by Brewster et al. (2014) who used a different approach and a smaller sample size. Evidence from paleogenomic studies demonstrated clearly not only a genetic bottleneck during the Last Glacial Maximum, but also a consistent population turnover in Europe in conjunction with a climatically unstable period around 14,500 year ago, suggesting the replacement of the post-LGM population by another population with different origins (Posth et al. 2016). On the contrary, no population turnover is detectable between the hunter-gatherers who lived before and after the transition from the Late Glacial to the Early Holocene. Unfortunately, our attempt to obtain a paleogenomic assessment for BR specimens has failed, as has the attempt to obtain radiocarbon dating results, certainly more reliable than the gamma-ray spectrometry ones. Therefore, at the moment it is very difficult to decide whether the evident morphological differences between the BR 1 and BR 2 skulls should be attributed to diachronic inter-population differentiation rather than to intra-population variability coupled with sexual dimorphism.

Although the size of the prehistoric sample is small, it should be noted that the presence of an external auditory exostosis in BR 1 (EAE, grade 2; Supplementary Material 2 and figures in Supplementary Material 1) is more compatible with an Upper Paleolithic attribution, particularly Gravettian (Trinkaus et al. 2019) than a Ligurian Neolithic one (Varalli et al. 2020).

Postcranial morphology

Results from the osteometric and functional morphology analysis of the coupled femora are consistent with direct dating and cranial morphology. Specifically, several variables have values that make a Neolithic attribution unlikely, while earlier attributions are more plausible. Most notably femoral length, a proxy for stature, is above the range shown by Ligurian Neolithic individuals, which, as demonstrated in previous studies, are significantly shorter than Late Pleistocene groups, and especially Gravettian individuals (Formicola and Franceschi 1996; Formicola and Giannecchini 1999; Holt and Formicola 2008). Interestingly, when a correlate of body mass (femoral head diameter) is plotted against stature, obtaining a rough proxy for body proportions, BR_T femora appear most compatible with Gravettian females. Indeed, for most of the variables, BR_T femora overlap with Gravettian females, although it should be noted that the sample size is very small for this group. Given the archaeological context of the Balzi Rossi caves, and our hypothesis regarding the provenience of the Conio's finds (see above), the attribution to the Gravettian would not be implausible. Although the femora have been associated with pelvic fragments attributed to a male (Masali 1967), the attribution cannot be certain, and problematic sex determination of Upper Paleolithic individuals is not uncommon, especially when, as in this case, the pubic region is damaged (Formicola et al. 1990; Mallegni and Fabbri 1995; Trinkaus et al. 2001; Henry-Gambier 2002; Messina et al. 2013; De Lumley 2016; Mittnik et al. 2016). As discussed above, although the direct date centers around the Pleistocene-Holocene transition, the wide confidence interval does not exclude an earlier attribution. Further studies may explore this possibility, which remains open until a more precise absolute age determination, possibly coupled with a reliable genetic test, will be available.

The BR femora overlap with Upper Paleolithic individuals for other osteometric variables that discriminate between Pleistocene and Holocene individuals, such as the femoral torsion angle (see also Trinkaus et al. 2001; Shackelford and Trinkaus 2002), and the femoral neck-shaft angle, which sets apart the Neolithic sample from the others. Both variables may be correlated with mobility levels (Anderson and Trinkaus 1998; Wescott 2014). Other indicators of mobility levels, consisting of femoral CSG shape indices, show a pattern of decrease from Upper Paleolithic hunters to Neolithic agriculturalists (review in Holt 1999, 2003; Marchi et al. 2006, 2011). In our diachronic samples, the decrease is present but less marked, possibly due to continuing terrestrial hunting in the Mesolithic sample (Sparacello et al. 2018b, 2020) and pastoral activities in the Ligurian Neolithic sample (Marchi et al. 2006, 2011). Still, the value shown by BR femora is well above the 95% CI of Ligurian Neolithic people, and is more compatible with Pleistocene levels of mobility (see also Villotte et al. 2017). Overall, both the osteometric and functional anatomy analysis agree in suggesting that a Neolithic attribution of the remains is unlikely.

Taphonomic and funerary remarks

Due to the nature of Conio's finds, no direct information on the depositional context of the remains is available. However, some inferences can be made on the basis of the pattern of ochraceous staining and concretion. Given the absence of complete skeletons, and the orientation of the speleothem that developed on BR 1, the assemblage probably resulted from remains in secondary deposit, which were manipulated or disturbed in ancient times. Given the extreme friability of the bones, which are virtually devoid of collagen (see above), most of the margin of the fractures have recently degraded (and some fractures are indeed recent), but several show a patina, and a few are stained with ochre. The pattern seems compatible with disturbances in prehistoric times, and with recent disturbance of the deposit during excavations unrelated to archaeological research at Balzi Rossi.

The use of ochre is abundant in both Upper Paleolithic and Neolithic burials in Liguria. However, the symmetry in the ochraceous staining in the pair of femora suggest that they were originally deposited with similar orientations, most likely as part of a supine inhumation (Masali 1967). Similarly, the pattern of staining in the fragments of two crania (Individual 3 and 4, i.e. BR 5 and 12) is compatible with a supine inhumation, i.e. the staining is abundant in the endosurface of the occipital, and virtually absent in the endosurface of the frontal. Although the Gravettian and Epigravettian chrono-cultural complexes displayed a variety of inhumation modalities, the supine position with limb extended is predominant (e.g. Mussi 1986; Riel-Salvatore and Gravel-Miguel 2013; Formicola and Holt 2015; Sparacello et al. 2018a), while in the Neolithic of Liguria the crouched inhumation on the left side is virtually exclusive (Sparacello et al. 2019a,b).

Secondary manipulation of the dead has been proposed in Liguria for both Late Upper Paleolithic (Epigravettian) funerary sites (intentional manipulation of burials at Arene Candide; Sparacello et al. 2018a; manipulation/disturbance of Grotte des Enfants 3) and Neolithic (unintentional, due to re-use of funerary spaces, at Arma dell'Aquila; Sparacello et al. 2019a). In addition, commingled assemblages of human remains dating back to the Copper and Bronze Ages are known in Liguria, especially in the Finalese and Imperiese areas (Sparacello et al. 2019b). For the Gravettian, the non-contemporaneous burial of two individuals, crouched in the same grave, has been proposed at Balzi Rossi (Grotte des Enfants 5 and 6; De Villeneuve et al. 1906-19). For the Gravettian of the Perigord region (Cussac Cave), complex secondary manipulation of the dead has been recently described (Kacki et al. 2020). Therefore, although the secondary deposit of the remains does not aid in the determination of their chronology, it does not exclude a Paleolithic origin.

Provenance

Excavations at Balzi Rossi began well before the modern conceptualization of the disciplines of archaeology and paleoethnology, and before the recognition of the Paleolithic as a cultural phase by the Société d'Anthropologie de Paris in 1859 (Rivière 1887, p. 85). The whereabouts of most of the material unearthed from these early excavations are unknown. But ever since 1872, when Rivière found the "homme du Cavillon" (now sexed as female and dated around 24,000 cal BP, suggesting that it was associated with Gravettian industries - De Lumley 2016), the most coveted material were human skeletons. This can be well understood considering that the Cro-Magnon burials had been discovered just a few years earlier, in 1868, and that the question of Paleolithic burials was hotly debated. There was even a proper fight over one of the skeletons from the Barma Grande, which was eventually dismembered and is now kept in two different museums (Mussi et al. 2008). Not only Stefano Conio is never mentioned by Rivière (1887) and by the team of the Prince of Monaco (De Villeveuve et al. 1906-1919), and his name is not entered in the Livre d'Or kept by Bonfils for the visitors of his museum (Supplementary Material 6), but it would have been nonsensical to give away prized human remains to an outsider who, "several years before 1908", probably was very young and had no scientific recognition.

The results discussed in the previous paragraphs suggest for the remains an age within the final millennia of the Pleistocene, which is in line with osteometrics differentiating the "Conio's finds" from the Neolithic sample. The enquiry on the sites available before 1908 in Liguria and over north-western Italy leaves the Balzi Rossi as the most probable and reasonable option. The deeply-engraved freeze along the cliff, together with the evidence surviving at Grotta dei Fanciulli and at Riparo Mochi, provides evidence of once extensive deposits of the final Pleistocene. In the former site a double child burial was discovered in those layers by Rivière (1887), while more child fragments were found by De Villeneuve et al. (1906-1919). Conio's grouped human remains (if they were originally such) of 3 adults and a 6-8 years-old child suggest burials of final Pleistocene age, as those of the Final Epigravettian "necropolis" of Arene Candide, rather than Gravettian ones, albeit a Triple adult burial was unearthed at the Barma Grande (Mussi 1986; Sparacello et al. 2018a). The ochre stain points to burial, while the stalagmite concretions are evidence that the remains were originally in a cave or rockshelter.

Conio's exploration at the Balzi Rossi, most probably after the Museum Praehistoricum was built (Supplementary Material 6 for more detail), happened when the final Pleistocene deposits had almost disappeared. Riparo Mochi (devoid of human remains) had not yet been detected, while it can be ruled out that Conio participated to the excavations at Grotta dei Fanciulli. However, we know that large lime kilns had been previously dug at the entrance of both this cave and of Grotta del Caviglione – which, as Grotta dei Fanciulli, must have once included levels with Final Epigravettian lithic industries, reaching the engraved "freeze". In the 18th century, the removed sediment could not have been dumped too far away, and most probably was stockpiled near the entrance (Supplementary Material 6, Fig. S1).

In De Villeneuve's words (1906, p. 18), who refers to the two kilns, « Il est impossible qu'en creusant la terre, on n'ait pas trouvé des quantités considérables d'ossements d'animaux et peut-être aussi humains, ainsi que des silex et des outils en os, qu'on rejeta avec les déblais à l'entrée de la grotte, ce qui expliquerait comment, aux abords des cavernes des Enfants et du Cavillon, tant de récoltes ont pu être faites à fleur de sol et au prix de léger grattages. »

["It is impossible that during the excavation of the soil a considerable amount of animal and possibly human bones was not found, as well as flint and bone tools, which were thrown with the debris at the entrance to the cave, which would explain why, near the Grotta dei Fanciulli and the Grotta del Caviglione, so many finds were made at surface level, or through some light scraping of the soil". Our translation]

Intriguingly, De Villeneuve not only points to the entrance of the two caves, but also underlines that human remains could well have been found, simply scratching the redeposited soil. Casual findings apparently still happened in his times at the end of the 19th century, when Conio would have possibly been around. This scenario fits with Conio's reconstruction, i.e. a casual finding while strolling around the caves and the museum – the museum being adjacent to Grotta del Caviglione. However, it is quite improbable that he just "collected" surfacing bones – he must rather have "scratched" the ground, a behaviour not surprising in a young boy thrilled by the prehistoric atmosphere of the Balzi Rossi, who was assisted by the beginner's luck.

Regarding the possibility that the origin from Balzi Rossi is fictitious, it would have been rather illogical to give the name of such a famous site, at the center of bitter quarrels for the possession of skeletal materials, if the purpose was to cover their real origin. Furthermore, if Stefano Conio was a mythomaniac, he should have exploited his invention for notoriety, instead of disappearing from the record.

Still, further research is needed to uncover more information about the provenience and the history of the Conio's finds, and to elevate our hypotheses from the realm of speculation. We hope that our contribution will stimulate the debate, and possibly help retrieving pieces of evidence scattered in local archives and in pieces of literature that we could not access at this stage.

Conclusions

The human skeletal remains housed in Torino and dubbed "Conio's Finds" – attributed to the Balzi Rossi sites by a signed note from 1908 – have been the subject of a multidisciplinary analysis aimed at making inferences on their chronology and provenience. Direct dating was attempted via AMS, unsuccessfully due to low collagen content, and via a non-destructive method ($^{231}Pa/^{235}U$ gamma-ray spectrometry). The latter method returned two Late Pleistocene/Early Holocene dates, although with a high error. A likely Late Pleistocene attribution is suggested also by the comparative morphometric analysis of the two better preserved crania, and osteometric and biomechanical analysis of two almost complete femora. All the data we examined appear coherent with an attribution to an Upper Paleolithic population of Western Europe. However, there are some contrasting results: while the direct date centers around a Final Paleolithic attribution (Final Epigravettian), postcranial body proportions are more compatible with an earlier, Gravettian, origin of the remains. Human groups producing both Gravettian and Final Epigravettian lithic tools buried their dead at Balzi Rossi.

Our review of the literature suggests a possible provenience of Conio's finds from the Balzi Rossi complex, possibly from the sediment dumped when deep lime kilns were quarried at the site in the 18th century. At Grotta dei Fanciulli, which yielded Gravettian and Final Epigravettian burials, both layers belonging to these chrono-cultural period had been previously damaged by quarrying activities, which would allow for remains of these two periods to have been redeposited in the soil dumped externally. These hypotheses will be directly tested in the future through the comparative analysis of the speleothem attached to one of the crania, and of the ochre and soil residues.

Our analysis therefore is not conclusive, but has demonstrated that these interesting paleoanthropological finds deserve additional investigations (further historical reconstructions, new attempts to get more precise absolute dating and paleogenomic/paleoproteomic results, X-ray and CT examination for paleopathology and health status, dental wear and stable isotopes analysis for diet and subsistence, speleothem and ochre/soil analyses), and have the potential to provide further insights on the paleobiology of Late Pleistocene people, and on the exceptional richness of the Ligurian paleoanthropological record.

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Author Contribution

Conceptualization: M. Micheletti Cremasco, G. D'Amore, M. Masali, L. Sineo; Methodology: G. D'Amore, V.S. Sparacello, M. Galland, A. Profico, S. Di Marco; Formal analysis: G. D'Amore, V.S. Sparacello, M. Galland, A. Profico, S. Di Marco; Investigation: M. Micheletti Cremasco, G. D'Amore, M. Masali, V.S. Sparacello, M. Mussi; Resources: M. Micheletti Cremasco, V.S. Sparacello, M. Mussi, A. Profico, M. Galland, M. Friess; Data Curation: V.S. Sparacello., M. Galland, M. Friess, R. Micciché; Writing - Original Draft: M. Micheletti Cremasco, G. D'Amore, V.S. Sparacello; Writing – Review and Editing: All authors; Supervision: M. Micheletti Cremasco, L. Sineo; Funding acquisition: M. Micheletti Cremasco, V.S. Sparacello, L. Sineo.

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Appendix 1 – List of skeletal elements belonging to the "Conio's finds" and their possible association.

LABEL	ELEMENTS PRESENT	ATTRIBUTION TO INDIVIDUAL AND MNI	ARTICULATION AND ASSOCIATION OF ELEMENTS	N° FRAGMENTS	AGE CLASS
BR 1	Cranium	Individual 1		1	Adult
BR 2	Cranium	Individual 2		5	Adult
BR 5	Temporal L, fragments of calotte, maxilla R/L	Individual 3		> 10	Adult
BR 12	Temporal R, frontal, fragments of calotte and basicranium	Individual 4 (juvenile)		> 30	Infans Ib-II[1] (c. 6-9 y.o.)
BR 3	Sacrum	Pelvis 1, may belong to individual 1, 2, or 3	BR 3 + BR 9 + BR 13 + BR 15	1	Adult
BR 13	Os coxae R fragment			1	Adult
BR 9	Os coxae L fragment			1	Adult
BR 15	Os coxae L fragment			1	Adult
BR 4	Sacrum fragment	Pelvis 2, may belong to individual 1, 2, or 3	BR 4 + BR 4/bis + BR4/bis2	1	Young adult (visible fusion line of the iliac crest)
BR 4/bis	Os coxae L fragment			1	
BR 4/bis2[2]	Os coxae R fragment			1	
BR 16[3]	Os coxae L fragment	Pelvis 3, may belong to individual 4 (juvenile)		1	Infans Ib-II (c. 6-9 y.o.)
BR 17[3]	Rib fragment	May belong to individual 1, 2, or 3		1	Adult
BR 18[3]	Rib fragment	May belong to individual 4 (juvenile)		1	Infans Ib-II (c. 6-9 y.o.)
BR 6	Femur R	Paired femora, may belong to individual 1, 2, or 3	Femoral head diameter compatible with Pelvis 1	3	Adult
BR 7	Femur L			2	Adult

[1] Scheuer and Black, 2004:7

[2] Present in Masali, 1967 but could not be retrieved

[3] Bone not labeled; label assigned in this study

Appendix 2 - A) List of Upper Paleolithic and Mesolithic samples (hunter-gatherers: HG) considered in the PCA and DFA based on linear measurements, with subdivision among 39 sub-samples (groups) and 10 macro-groups (abbreviation in parentheses). Main sources of data were Brewster et al. (2014), Cheronet et al. (2016), Denisova (1975), Yakimov (1960); a complete list of sources is provided in the Supplementary Material 3, Table S3-1. B) List of Neolithic samples (early farmers: EF) considered in the PCA and DFA based on linear measurements. Main sources of data were Bach (1978), Kővári (2008), Cheronet et al. (2016), Parenti and Messeri (1962), Riquet (1970, 1972); a complete list of sources is provided in the Supplementary Material 3, Table S3-1.

A. UPPER PALEOLITHIC AND MESOLITHIC COMPARATIVE SAMPLE

SAMPLE #	GROUP/SUB-SAMPLE DESCRIPTION	ABBR.	COUNTRY	CHRONO-CULTURAL ATTRIBUTION	DATE KA BP	PERIOD & REGION	ABBR.	M	F	TOT.
1	Balzi Rossi, Liguria, Pre-Last Glacial Maximum	BR	Italy	Gravettian	25-23	Pre-Last Glacial Maximum / Early Upper Paleolithic Europe and West Asia	EUP	3	2	5
2	West Europe Pre-Last Glacial Maximum	WEUP	France, Italy	Gravettian, Proto-Magdalenian	28-22			2	4	6
3	Predmostí	PR	Czech Rep.	Gravettian	27-26			3	2	5
4	Dolní Vestonice	DV	Czech Rep.	Gravettian	27-25			4	1	5
5	East Europe and Levant Pre-Last Glacial Maximum	EEUP	Czech Rep., Israel, Romania, Russia	Aurignacian, Gravettian	36-27			6	2	8
6	Arene Candide Late Epigravettian	AC	Italy	Late Epigravettian	12-11	Late Glacial / Late Upper Paleolithic Europe	LUP	5	0	5
7	Late Epigravettian Italy	EG	Italy	Late Epigravettian	13-11			5	5	10
8	Late Glacial Central Europe	MAG	Czech Rep., France, Germany, Slovakia, Switzerland	Magdalenian and others	17-11			6	5	11
9	Natufian Middle East	NAT	Iran, Israel	Natufian	13-11	Epi-Paleolithic / Natufian West Asia	WAP	8	1	9
10	Fallah- Nahal Oren Natufian	FAL	Israel	Natufian	11-10			7	1	8
11	Cabeço da Arruda	ARR	Portugal	Mesolithic	7-6	Mesolithic Iberia	IBM	1	2	3
12	Moita do Sebastiao	MOIT	Portugal	Mesolithic	7-6			5	6	11
13	Iberian Mesolithic	SPM	Spain	Mesolithic	9-6			2	2	4
14	Mesolithic North-Western Europe	NWM	Belgium, England, France, Luxemburg	Mesolithic	10-8	Mesolithic West-Central Europe	WCM	7	3	10
15	Hoëdic	HOE	France	Mesolithic	7-6			2	2	4
16	Téviec	TEV	France	Mesolithic	7-6			7	8	15
17	Mesolithic Central Europe	CEM	Germany, Italy, Switzerland	Mesolithic	8-6	Mesolithic South-Central Europe	SCM	5	3	8
18	Ofnet	OFN	Germany	Mesolithic	9-8			4	10	14

Appendix 2A - continued.

A. UPPER PALEOLITHIC AND MESOLITHIC COMPARATIVE SAMPLE										
SAMPLE #	**GROUP/SUB-SAMPLE DESCRIPTION**	**ABBR.**	**COUNTRY**	**CHRONO-CULTURAL ATTRIBUTION**	**DATE KA BP**	**PERIOD & REGION**	**ABBR.**	**M**	**F**	**TOT.**
19	Early Holocene Mesolithic Sicily	SICM	Italy	Mesolithic	10-8	Mesolithic South-Central Europe	SCM	5	3	8
20	Vlasac	VLAS	Serbia	Mesolithic	9			7	10	17
21	Early Holocene Mesolithic Greece	GRM	Greece	Mesolithic	0-8			2	1	3
22	Mesolithic Northern Europe (Scandinavia)	SCM	Denmark, Norway, Sweden	Mesolithic	9-6	Mesolithic North-East Europe	NEM	13	3	16
23	Skateholm	SKAT	Sweden	Mesolithic	7-6			2	3	5
24	Zvejnieki	ZVEJ	Latvia	Mesolithic	7-6			8	8	16
25	North Russia Mesolithic	RUSM	Russia (Northern)	Mesolithic	9-7			2	2	4
26	Yuzhnyi Olenii Ostrov	YOO	Russia	Mesolithic	7-6			21	10	31
27	Mesolithic Ukraine	UKM	Ukraine	Mesolithic	10-8	Mesolithic South-East Europe	SEM	4	3	7
28	Vasilevka 1	VAS1	Ukraine	Mesolithic	10			6	0	6
29	Vasilevka 2	VAS2	Ukraine	Mesolithic	8			7	5	12
30	Vasilevka 3	VAS3	Ukraine	Mesolithic	10			13	5	18
31	Dereivka	DER	Ukraine	Dnieper-Donets	6	Ceramist Mesolithic (Ukraine Ceramist HG) South-East Europe	SECM	10	4	14
32	Nikolskoje	NIK	Ukraine	Dnieper-Donets	6			6	3	9
33	Vovnigi	VOV	Ukraine	Dnieper-Donets	6			30	6	36
34	Volnoje	VOLN	Ukraine	Dnieper-Donets	6			12	7	19
35	Aleksandrja	ALEK	Ukraine	Dnieper-Donets	6			11	2	13
36	Bolshoy Olenii Ostrov	BOO	Russia (Northern)	Comb Ceramic	4	Ceramist Mesolithic (Baltic Ceramist HG) North-East Europe	NECM	5	4	9
37	Eastern Baltic Ceramist Hunther-Fisher-Gatherers	EBHG	Estonia, Latvia, Lettland, Poland, Russia	Comb Ceramic	5-4			10	9	19
38	Vaesterbjers	VAES	Sweden	Comb Ceramic	4			9	7	16
39	Ostorf	OST	Germany	Late hunter-fisher Neolithic	4			11	5	16
TOTAL HG								**276**	**159**	**435**

Appendix 2B - continued.

B. NEOLITHIC COMPARATIVE SAMPLE						
GROUP/SUB-SAMPLE DESCRIPTION	**COUNTRY**	**CHRONO-CULTURAL ATTRIBUTION**	**DATE KA BP**	**M**	**F**	**TOT.**
Liguria Neolithic	Italy (Liguria)	ICC, SMP, Chassey	7.0-6.0	18	8	26
West Asia Neolithic	Israel, Lebanon, Syria, Iran, Iraq	PPNB, PN	11.0-8.0	12	5	17
Çatal Höyük	Turkey	Çatal Höyük, Early Neolithic	9.0-8.5	13	14	27
Greece Early Neolithic	Greece	Proto-Sesklo	8.5-8.0	4	11	15
Starcevo-Körös-Cris-Karanovo 1-3 Early Neolithic cultures	Serbia, Hungary, Romania, Bulgaria	Starcevo-Körös-Cris-Karanovo 1-3	8.5-7.5	14	12	26
Linearbandkeramische	Austria, Czech Rep., France, Germany, Hungary, Slovakia	LBK, AVK	7.5-7.0	57	44	101
Italy Neolithic (other than Liguria)	Italy	ICC, SMP, Chassey-Lagozza, Painted Pottery, Catignano, Passo di Corvo, Sasso-Fiorano, Serra d'Alto, Diana-Bellavista	7.5-6.5	23	21	44
France Middle/Late Neolithic	France	Chassey, Rossen, Megalithic	6.5-5.5	23	23	46
Germany Middle/Late Neolithic	Germany	SBK, Rossen, Michelsberg	6.5-5.5	21	11	32
Switzerland Middle/Late Neolithic	Switzerland	Egolzwill, Cortaillod/ Chambandes	6.5-5.5	22	31	53
Hungary Middle/Late Neolithic	Hungary	Tiszai, Lengyel	6.5-5.5	15	10	25
Poland Middle/Late Neolithic	Poland	Lengyel	6.5-5.5	16	4	20
Ukraine Middle/Late Neolithic	Ukraine	Tripolje	6.0-5.5	20	8	28
Spain Middle/Late Neolithic	Spain	Sepulcros de Fosa, Almeria, Neolitico antiguo, medio y final	6.5-4.5	33	8	41
Portugal Middle/Late Neolithic	Portugal	Almeria, Neolitico antiguo, medio y final	6.5-4.5	30	24	54
Greece Middle/Late Neolithic	Greece	Middle and Late Neolithic (Tsangli, Dimini?)	6.5-5.5	6	2	8
TOTAL EF				**327**	**236**	**563**

Appendix 3 - Upper Paleolithic, Mesolithic, Neolithic and recent comparative samples used in the morphometric geometric analysis.

SITE AND SPECIMENS	GEOGRAPHICAL PROVENIENCE	CHRONO-CULTURAL ATTRIBUTION	DATE YEARS BP [A]	REFERENCE FOR CHRONO-CULTURAL ATTRIBUTION	N. CRANIA
Abri Pataud 1	France	Upper Paleolithic	20,535	Brewster et al. 2014	1
Arene Candide 2, 3, 4	Italy (Liguria)	Upper Paleolithic	between 10,735±55 and 9,925±50	Formicola et al. 2005	3
Brno 3	Czech Republic	Upper Paleolithic	Gravettian, 23,680±200 as Brno 2?	Brewster et al. 2014	1
Bruniquel 24	France	Upper Paleolithic	15,290±150	Brewster et al. 2014	1
Chancelade 1	France	Upper Paleolithic	Magdalenian, 12-11,000 as Oberkassel?	Brewster et al. 2014	1
Cro-Magnon 1, 2	France	Upper Paleolithic	27,680±270	Brewster et al. 2014	2
El Wad 10256, 10260	Israel	Upper Paleolithic	Natufian, 12,950-10,700	Bocquentin, 2003; Cheronet et al. 2016	2
Kebara 10352	Israel	Upper Paleolithic	Natufian, 12,470-11,150	Bocquentin, 2003	1
Mladec 1	Czech Republic	Upper Paleolithic	31,190±400	Brewster et al. 2014	1
Ohalo II H2	Israel	Upper Paleolithic	19,000	Hershkovitz et al. 1995	1
Predmost 3	Czech Republic	Upper Paleolithic	26,595	Brewster et al. 2014	1
Rond-du-Barry 1	France	Upper Paleolithic	17,100±150	Brewster et al. 2014	1
San Teodoro 1, 2	Italy (Sicily)	Upper Paleolithic	12,580±130	Mannino et al. 2011	2
Villabruna 1	Italy	Upper Paleolithic	12,140±70	Vercellotti et al. 2010	1
Oberkassel 1, 2	Germany	Upper Paleolithic	11,570±110; 12,180±110	Brewster et al. 2014	2
Grotta d'Oriente B	Italy (Sicily)	Mesolithic	9,377±25	Mannino et al. 2012	1
Molara 2	Italy (Sicily)	Mesolithic	8,600±100	Gowlett et al. 1987	1
Mondeval de Sora 1	Italy	Mesolithic	7,425±55	Alciati and Formicola, 2005	1
Uzzo 2, 5, 6	Italy (Sicily)	Mesolithic	9,270±100; 9,365±40; 8,856±37	Belluomini and Delitala, 1983; Mannino et al. 2015	3
Zvejnieki 9, 37, 160, 199, 211, 241, 242, 252, 269	Latvia	Mesolithic	5,480-7,730	Zarina, 2006; Brewster et al. 2014	9
TOTAL UPPER PALEOLITHIC AND MESOLITHIC SKULLS					**36**

(a) Uncalibrated years BP date.

Appendix 3 - continued.

SITE AND SPECIMENS	GEOGRAPHICAL PROVENIENCE	CHRONO-CULTURAL ATTRIBUTION	DATE YEARS BP (A)	REFERENCE FOR CHRONO-CULTURAL ATTRIBUTION	N. CRANIA
Arene Candide 7PE, 8PE, III BB, IV BB, VI BB, VII BB, IX BB, 1 Tiné, 2 Tiné	Italy (Liguria)	Neolithic	5178-5860	Sparacello et al. 2019b	9
Arma del Morto 252	Italy (Liguria)	Neolithic	6230±25	Sparacello et al. 2019b	1
Arma di Nasino 1	Italy (Liguria)	Neolithic	5285±30	Sparacello et al. 2019b	1
Pollera 1 Tiné, 12 Rossi, 13 Morelli, 30 Rossi, 33 Rossi, 6246 Amerano	Italy (Liguria)	Neolithic	5710-5860	Sparacello et al. 2019b	6
TOTAL NEOLITHIC SKULLS FROM LIGURIA					**17**
Czech (Cz) (b)	Czech Republic	Recent			19
French (Fr)	France	Recent			13
Hungarian (Hg)	Hungary	Recent			11
Romanian (Ro)	Romania	Recent			10
Swedish (Sw)	Sweden	Recent			24
TOTAL RECENT SKULLS					**77**

(b) Abbreviation in parentheses.

Appendix 4 - A) Measurements and indices of BR 1 and BR 2 crania (measurements in mm; cranial capacity in cm³); data on the originals collected by M.M and partially published in Masali (1967, 1971), re-checked by M.M.C. and G.D. in 2019. B) Osteometric measurements and cross-sectional geometry variables of the femora BR 6 (right) and BR 7 (left).

A. CRANIOFACIAL MEASUREMENTS	MEASUREMENT #	BR 1	BR 2
Maximum cranial length (gl-op)	1	184	183
Cranial length at inion (gl-in)	2	175	179
Maximum cranial breadth (eu-eu)	8	137	136
Least frontal breadth (ft-ft)	9	95	91
Maximum frontal breadth (co-co)	10	116	115
Basion-bregma height (ba-br)	17	133	(138.2) [a]
Auriculo-bregmatic height (po-br)	20	109	117
Bizygomatic breadth (zy-zy)	45	126 [b]	(137) [c]
Upper facial height (na-pr)	48	65	68
Orbital breadth (mf-ek)	51	41	43
Orbital height	52	29	35
Nasal breadth (al-al)	54	23	28
Nasal height (na-ak)	55	47	55
Internal palatal length (ol-sta)	62	46	47
Internal palatal breadth (enm-enm)	63	36	35
Cranial capacity	38	1470	1422
Indices			
Cranial index	8/1	74.46	74.32
Fronto-parietal index	9/8	69.34	66.91
Height-length index	17/1	72.28	(75.52)
Height-breadth index	17/8	97.08	(101.62)
Auricular height-length index	20/1	59.24	63.93
Auricular height-breadth index	20/8	79.56	86.03
Transversal craniofacial index	45/8	91.97	(100.74)
Upper facial index	48/45	51.59	(49.64)
Orbital index	52/51	70.73	81.40
Nasal index	54/55	48.94	50.91

Appendix 4 - continued.

B. FEMORAL MEASUREMENTS	BR 6 FEMUR R	BR 7 FEMUR L	ESTIMATED (D)
Maximum length M1[e]	464		
Bicondylar length M2			460
Trochanter -bicondylar length M3			452
Midshaft AP diameter M6	32	31	
Midshaft ML diameter M7	26	25	
Pilastric index (midshaft AP/ML diameter) 100*M6/M7	123	124	
Subtrochanteric ML diameter M9		33	
Subtrochanteric AP diameter M10	28	29	
Meric index (subtrochanteric AP/ML diameter) 100*M10/M9		87.9	
Upper epiphyseal length M13	90	91	
Vertical neck diameter M15	31	31	
Sagittal neck diameter M16	23.5	25	
Neck index (M15/M16)	1.32	1.24	
Vertical head diameter M18	45	44.5	
Maximum breadth of the condylar articular surface (F16 Pearson 1997)			73
Distal bicondylar width M21			79 [f]
Torsion angle M28			13
Collo-diaphyseal angle M29	130	127.5	
Condylo-diaphyseal angle M30	9		
Femoral variables for CSG analysis			
Femoral mechanical length (Ruff 2002)			438

(a) Estimated from the auriculo-bregmatic height (#20) using a least square regression based on a pooled sample of Upper Paleolithic and Mesolithic crania (n=76). #17=#20×0.957+26.19, r2=0.482.
(b) Taken on the 3D model with a segmentation tool used to virtually remove the thick encrustation.
(c) Estimated by doubling the measured distance from the reconstructed left zygomatic arch to the midline (average value of four repetitions).
(d) Values that could be approximated by measuring both femora, or by completing the 3D model of one side with the mirrored model of the other side.
(e) Measurements as defined in Braüer 1988.
(f) Calculated via regression equation based on a world-wide sample of humans from the late Pleistocene to modern times (data courtesy of OM Pearson; Pearson 1997): $M18 = 9.3203 + 0.9527 \times F16$; $r = 0.9103$, $p < 0.0001$; $r2 = 0.8287$ n=437

Appendix 4 - continued.

B. FEMORAL MEASUREMENTS	BR 6 FEMUR R	BR 7 FEMUR L	ESTIMATED (D)
Body mass (equation from Ruff 1991)	66.7	65.6	
Body mass (equation from Grine 1995)	65.6	64.4	
BM (equation from McHenry 1994)	60.9	59.7	
Body Mass estimate (Trinkaus and Ruff 2012)	64.4	63.2	
Ix(g)	33854.89	28313.29	
Iy(g)	22258.4	21262.64	
Imax	34550.93	30189.18	
Imin	21562.35	19386.74	
J	56113.28	49575.92	
Ix/Iy(g)	1.52	1.33	
I_{max}/I_{min}	1.60	1.56	

(g) CSG variables requiring a precise orientation along the longitudinal axis of the diaphysis (Ix, Iy, and Ix/Iy) are approximated using the 3D model described above.