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To cite this version:
Sandrine Prat, Stéphane Péan, Laurent Crépin, Dorothée G. Drucker, Simon Puaud, et al.. The Oldest Anatomically Modern Humans from Far Southeast Europe: Direct Dating, Culture and Behavior. PLoS ONE, 2011, 6 (6), pp.e20834. 10.1371/journal.pone.0020834. hal-00839163

HAL Id: hal-00839163
https://hal.science/hal-00839163
Submitted on 28 Oct 2020

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The Oldest Anatomically Modern Humans from Far Southeast Europe: Direct Dating, Culture and Behavior

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Abstract

Background: Anatomically Modern Humans (AMHs) are known to have spread across Europe during the period coinciding with the Middle to Upper Paleolithic transition. Whereas their dispersal into Western Europe is relatively well established, evidence of an early settlement of Eastern Europe by modern humans is comparatively scarce.

Methodology/Principal Finding: Based on a multidisciplinary approach for the study of human and faunal remains, we describe here the oldest AMH remains from the extreme southeast Europe, in conjunction with their associated cultural and paleoecological background. We applied taxonomy, paleoecology, and taphonomy combined with geomorphology, stratigraphy, archeology and radiocarbon dating. More than 160 human bone remains have been discovered. They originate from a well documented Upper Paleolithic archeological layer (Gravettian cultural tradition) from the site of Buran-Kaya III located in Crimea (Ukraine). The combination of non-metric dental traits and the morphology of the occipital bones allow us to attribute the human remains to Anatomically Modern Humans. A set of human and faunal remains from this layer has been radiocarbon dated by Accelerator Mass Spectrometry. The direct-dating results of human bone establish a secure presence of AMHs at 31,900±240/−220 BP in this region. They are the oldest direct evidence of the presence of AMHs in a well documented archeological context. Based on taphonomical observations (cut marks and distribution of skeletal elements), they represent the oldest Upper Paleolithic modern humans from Eastern Europe, showing post-mortem treatment of the dead as well.

Conclusion/Significance: These findings are essential for the debate on the spread of modern humans in Europe during the Upper Paleolithic, as well as their cultural behaviors.

Introduction

The timing of the appearance of early Anatomically Modern Humans (AMHs) in Europe, their hypothesized biological and cultural interactions by replacement or admixture with local populations (Neanderthals or other hominins [1,2]), and their association with Upper Paleolithic industries are issues subject to continuous debate [3–14] despite the increasing number of human fossils, archeological sites and new dates from previously discovered sites.

Whereas the arrival and dispersal of modern humans into Western Europe is relatively well established, data related to their early settlement in Eastern Europe is relatively scarce [15,16]. Buran-Kaya III and Siuren I [17] in Crimea (Ukraine) are the only sites in the northern Black Sea region where a Middle to Upper Paleolithic archeological sequence is well preserved. Crimea is particularly rich in Middle Paleolithic industries and Neanderthal remains (e.g. Kiik Koba [Kiik Koba 1 and 2 [18–20]], Zaskaľnaya V and VI [21]) (Figure 1). However, with the exception of one molar discovered in Unit G from Siuren I [22], dated to 30–28 ka BP [11], no Upper Paleolithic AMH remains have been reported in this region.

We report here the discovery and subsequent first scientific investigation of the human remains from the Buran-Kaya III site. This shelter-cave, overhanging the Burulcha river in the Belogorsk region (N45°00’10.5”; E34°24’16.3”) (Figure 2), was discovered in 1990 by A. Yanevich and excavated up to 2001 by a team under the direction of A. Yanevich and A. Marks, with the participation of V. Chabai, Y. Demidenko, K. Monigal, M. Otte and Y. Yamada. Nineteen cultural layers have been identified spanning a period stretching from the Middle Paleolithic to the Middle Ages [26–28]. The site was reopened for excavation in 2009 under the direction of A. Yanevich and S. Péan. The excavation and detailed analyses of the human and faunal remains are still continuing.
The 2001 and 2009–2010 excavations were focused on nine archeological layers that generated Middle and Upper Paleolithic artefacts: Szeletian (layer C), Micoquian (layer B), Aurignacian (layers 6-5, 6-4, 6-3), Gravettian (layers 6-2, 6-1, 5-2) and Final Upper Paleolithic (layer 4) (Figure 3, Figure 4). A multidisciplinary approach was used to study the following layers: all layers [29,30], layer C [31–33], layer B [34–39], layers 6-2, 6-1 and 5-2 [40,41]. This research demonstrates that Buran-Kaya III is a key site for the understanding of the Middle to Upper Paleolithic transition since it is characterized by the peculiar presence of a Middle Paleolithic layer (Micoquian) situated between two Early Upper Paleolithic layers (Szeletian and Aurignacian).

In 2001 A. Yanevich discovered 162 human remains in 6 m² (lines A and B, columns 9, 10 and 11) of Buran-Kaya III (Figure 5). These remains were found in a well-documented Upper Paleolithic stratum (layer 6-1) with no evidence of an intentional burial pit. In the same layer, 11 remains were found in 1994 (squares 9B, 10 B, 11 B and 9G) and 8 new ones were recently discovered during the 2009 and 2010 field seasons (square 9Z).

Layer 6-1 has yielded the richest assemblage of lithic and bone industries, body ornaments (Figure 6), ochre fragments, and faunal, human and paleobotanical remains [41] from the site. Lithic artefacts have been attributed to the Gravettian cultural tradition [26,40] (Figure 7). The bioarchaeological features of the layer 6-1 enabled us to investigate the taxonomical attribution of these anthropological finds as well as the relevant cultural behavior in their paleoenvironment context.

Results and Discussion

Geomorphological data, paleoenvironmental and archeological contexts

The Buran-Kaya III shelter-cave is a “differential gelification balm” [42] due to erosion of the cretaceous limestone banks of the cliffs by frost breaking processes. The sedimentary infilling of this shelter-cave is composed of diamicton layers with angular or slightly rounded autochtonous limestone fragments and a small amount of loamy or sandy matrix. The latter has an aeolian origin but could have been also deposited by water from the overlying plateau. These lithostratigraphic facies suggest that the sequence was formed in a periglacial environment, corresponding to a dry and cold period. However, a thin sandy clay layer between layers 6-2 and 6-1 would indicate more temperate conditions. The results of paleoecological studies, based on pollen [43], microfauna [30], large mammals (see paragraph faunal assemblage) and sediments, indicate an open environment characterised by a reduced tree cover with a cold and arid climate that progressively become more severe from the bottom to the top of layer 6-1.

The abundant lithic assemblage is made up of 23,027 artefacts of which 3.5% are retouched tools, including end-scrapers, burins and numerous backed microliths (84.4% of retouched tools).
Yielded an age of 31,320 ± 160 14C BP (GrA-40485) and 620 ± 20 14C BP (GrA-37938) by Accelerator Mass Spectrometry (AMS) (Table 1). In addition, the AMS dated at 34,050 ± 500 14C BP (GifA-10021/SacA-19018). The chemical quality parameters for the fossil bones (organic content, C/N ratio and stable isotope ratios) are also shown in Table 1. These four new dates are chemically reliable and provide a chronology consistent with the stratigraphic sequence of the samples.

The C/N atomic ratio (3.3) of the dated human fragment is within the acceptable range of 2.9–3.6, expected for well-preserved collagen [45,46]. The δ 15N value on dated collagen of the Buran-Kaya III human bone (15.4%) is similar to the one measured on the Kostenki 8 human fossil from the site of Kostenki 1 (15.3%), a result interpreted as reflecting more than 50% of the diet originating from freshwater-derived protein [47]. Similarly, high consumption of fish is considered the likely explanation for the Oase 1 human mandible’s high δ 15N value (13.3%) [48], which is about 8% higher than those found for the red deer from the same site (5.3 and 5.8% [49]). This exceeds the expected range of 3 to 5% between a consumer and its prey (e.g. [50]). Interestingly, if the human δ 15N value in Buran-Kaya III is about 2% higher than the one found in Oase, the associated red deer are about 4% higher in Buran-Kaya III compared to Oase. As a result of those high 15N abundances, the red deer of layer 6-1 have a similar isotopic signature to those of the wolves of Oase (Figure 8). Thus, we observe different δ 15N values for terrestrial ecosystems in Eastern Europe during the early Upper Paleolithic. The higher 15N amounts found in fauna from Buran-Kaya III in Crimea compared to Oase in Romania could be explained by environmental differences between both regions. However, we should also consider the hypothesis of a chronological increase in δ 15N values between Oase (layer 1 and 2) and red deer, as well as wolves, were older than ca. 45,000 BP [48] and Buran-Kaya III (layer 6-1) for which we obtained AMS dates of 30,500–32,000 BP. Such a shift towards higher δ 15N values in terrestrial food webs was observed around the Middle to Upper Paleolithic transition in western Europe [51]. Analysis of stable isotopes for chronologically and geographically nearby fauna is necessary for thorough assessment of the human diet. The contribution of aquatic resources is needed not only to study the evolution of food patterns, but also to quantify the marine or freshwater reservoir effect for 14C dates [52]. Preliminary biogeochemical results on the coeval mammals from layer 6-1 of Buran-Kaya III suggest a diet composed of mainly terrestrial resources and only a moderate consumption of freshwater food for the dated human. A reservoir correction for the radiocarbon dates is not significant considering the measurement uncertainties.

Stable isotopes and radiocarbon dating

A human parietal fragment from layer 6-1 was radiocarbon dated at 31,900±240/−220 14C BP (GrA-37938) by Accelerator Mass Spectrometry (AMS) (Table 1). In addition, the AMS radiocarbon dating of a red deer metacarpal from layer 6-1 yielded an age of 31,320±820 14C BP (GifA-10021/SacA-19018). Furthermore, one horse metatarsal from layer 6-2, was dated by the two different laboratories independently, and provided comparable results: 34,050±260/−240 14C BP (GrA-40485) and 34,910±950 14C BP (GifA-80181/SacA-12260). The chemical quality parameters for the fossil bones (organic content, C/N ratio and stable isotope ratios) are also shown in Table 1. These four new dates are chemically reliable and provide a chronology consistent with the stratigraphic sequence of the samples.

The C/N atomic ratio (3.3) of the dated human fragment is within the acceptable range of 2.9–3.6, expected for well-preserved
in forest, shrubland and grassland ecosystems [54]. Thus, the burning of the bone material from layer 6-1 is supported to have resulted from human activities rather than natural phenomena.

Cut marks and fracture features due to human activities are observed on 7% of the NISPs of the following 6 taxa: saiga antelope, hare, bovine, horse, fox and wolf (Figure 10). Human modifications of the saiga bone surfaces (on cranial and postcranial remains) mainly reflect disarticulation and defleshing activities, breakage and marrow extraction. Consumption of hares is also evidenced by taphonomical modifications. Foxes exhibit marks of disarticulation and defleshing, and also traces of fur removal on metapodials and tarsals. Saiga antelope represents the main game of the hunter-gatherers in the site.

Human remains: taxonomic attribution, skeletal distribution and human modification

A total of 162 human remains were discovered in layer 6-1 during the 2001 field season. They were spread over 6 m² of the entire excavated area. These remains consist mostly of highly fragmented cranial parts (n = 117) and teeth (n = 29), whereas the postcranial skeleton (n = 16; MNI = 2, juvenile and adult) is barely represented (7 rib fragments, 1 vertebra and 8 hand phalanx fragments). At least 5 individuals were identified from the dental remains. They belong to 3 different developmental age groups: juvenile (n = 1), sub-adult (n = 2) and adult (n = 2). The human skeletal distribution shows a clear lack of anatomical parts (especially long bones from upper and lower limbs) which are usually preserved. This cannot be explained by differential preservation processes since other mammals are conversely represented by most, if not all, skeletal elements.

The taxonomic attribution of the human remains was made possible thanks to the well-preserved cranial bones and teeth (from both 1994 and 2001). The dental remains exhibit traits that occur more frequently in Anatomically Modern Humans (AMHs) than in Neanderthals; namely, the symmetry observed in the occlusal outline, the lack of a well-developed metaconid and a transverse crest on the lower second premolar, the lack of a well-developed mid-trigonid crest and a large anterior fovea on the lower first and second molars, the lack of shovelling, labial convexity and well-developed lingual tubercles on the upper first and second incisors (Figure 11). The combination of these traits taxonomically distinguishes AMHs from Neanderthals [12,55]. Furthermore, the occipital bones and especially the specimen BK3-55 (Figure 12) do not show an occipital “bun” and do not present a bilaterally transverse occipital torus nor a suprainiac fossa which are considered as typical Neanderthal features [56–58]. Therefore, based on this suite of morphological features, the human remains from Buran-Kaya III can be attributed to Anatomically Modern Humans.

Regarding the human modifications, the presence of cut marks on the exocranial surface of 14 remains, especially on one occipital bone (Figure 12), one temporal bone (Figure 13), one fronto-parietal fragment (Figure 14), was confirmed by analyses under a stereomicroscope and Environmental Scanning Electron Microscope (ESEM). The striations are multiple and parallel. Their morphological features include V-shaped cross section, shoulder and splitting effects. No percussion marks, reflecting breakage and marrow extraction, were observed on cranium and mandible, and no taphonomical marks from carnivores were identified. The observed cut marks, according to their morphology, location
and distribution (number and orientation) suggest two different processes: scalping on the fronto-parietal fragment and disarticulation on the occipital and temporal bones.

The taphonomical modifications observed on the Buran-Kaya III early AMHs, along with the over-representation of cranial remains, suggest a post-mortem processing of human body parts, including intentional selection of the skull. Dietary and non-dietary cannibalisms as well as mortuary practices are the most common explanations proposed for anthropic actions on human bodies [59–62]. Dietary cannibalism (“the use of humans by humans as food” [63]) is usually described as either survival (“starvation-induced cannibalism” [60]) or gastronomic [60], gustatory or nutritional (“consumption of human flesh not as a starvation avoidance” [61]). In general, evidence for dietary cannibalism is shown by a similar treatment of animal and human remains, in terms of butchering marks, anatomical element representation, marrow extraction, post-processing discard and cooking [63]. Non-dietary cannibalism is notably called either funerary cannibalism (“cannibalism of deceased, usually within-group members in which affectionate motivation is present” [60]) or ritual cannibalism (“consumption of specific body parts not as food source but as part of mortuary ritual” [61]).

In Buran-Kaya III, the representation of skeletal elements (%NISP and Percentage of element Representation) of the human and faunal remains (illustrated by saiga antelope, predominant prey) are noticeably different: absence of human upper and lower limbs and over-representation of human skulls compared to post-cranial parts (Figure 15). Conversely, all the skeletal elements of saiga antelope are represented. The percentages of bones with cut marks are also different: cut marks are observed on 9.5% of the human skull remains, 1.3% for saiga antelope; on 0% of the human post-cranial remains, 7.7% for saiga antelope. The modification frequencies are significantly different (chi² = 51.65, p<0.05, ddl = 2). Marrow extraction is evidenced only in saiga antelope (mandible, long bones and phalanges). These features suggest that humans and main game of the hunters-gatherers were not processed in a similar way. Thus, the hypothesis of a dietary...
Figure 6. Buran-Kaya III, layer 6-1, body ornaments from mammoth ivory. Scale bar equals 1.0 cm. doi:10.1371/journal.pone.0020834.g006

Figure 7. Buran-Kaya III, layer 6-1, lithic industry. 1–26: microliths; 27: end-scraper; 28: blade with retouch; 29–31: burins; 32: pièces esquillées; 33–34: cores. Scale bar equals 1.0 cm. doi:10.1371/journal.pone.0020834.g007
cannibalism, as defined above [63], does not seem to be supported by evidence based on body treatment. We consider an alternative scenario. The modifications on human remains could be interpreted as a mortuary ritual, either ritual cannibalism or a specific mortuary practice: post-mortem disarticulation processes of corpses for secondary disposal. The primary processing of the deceased body would have occurred in the site, where mainly cranial and dental remains along with a few phalanges, ribs and vertebra were leftover. The remaining parts of the body would have been taken outside the site by humans (at least as far as the excavated part of the site is concerned). Furthermore, the association with imported body ornaments reinforces the hypothesis of symbolic behavior related to the treatment and disposal of the human remains.

Our multidisciplinary research focus of Buran-Kaya III provides a new dataset of early Anatomically Modern Human remains, directly dated by radiocarbon, and securely associated

Table 1. Radiocarbon and stable isotopes results for the human and faunal remains from Gravettian layers 6-1 and 6-2 of Buran-Kaya III, Crimea.

| Laboratory number | Homo sapiens (parietal) | Cervus elaphus (metacarpal) | Equus sp. (metatarsal) |
|-------------------|-------------------------|-----------------------------|-----------------------|
| Layer             | GrA-37938               | GifA-10021/SacA-19018       | GrA-40485             |
| Radiocarbon age (AMS $^{14}$C years BP) | 31,900+240/-220          | 31,320±820                  | 34,050+260/-240       |
| “Calendar” age (cal BP age) based on IntCal09 [44], 95.4% (2 $\sigma$) Cal age ranges | 35,488-35,980             | 36,163-36,912              | 34,744-37,986         |
| Radiocarbon age (AMS $^{14}$C years BP) | 31,900+240/-220          | 31,320±820                  | 34,050+260/-240       |
| “Calendar” age (cal BP age) based on IntCal09 [44], 95.4% (2 $\sigma$) Cal age ranges | 35,488-35,980             | 36,163-36,912              | 34,744-37,986         |
| Relative area under distribution | 0.207                   | 0.793                       | 1.0                   |
| C (%)             | 43.2                    | 43                          | 32.2                  |
| N (%)             | 15.3                    | 15                          | 11.5                  |
| C/N*              | 3.3                     | 3.3                         | 3.3                   |
| $\delta^{13}$C (%) | −19.4                   | −19.1                       | −19.2                 |
| $\delta^{15}$N (%) | 15.4                    | 7.9                         | 9.0                   |

*C/N corresponds to the atomic ratio calculated as follows: (C content/N content)*(14/12). The dates were calibrated using the sofware calibREV6.0.0 based on IntCAl09 calibration dataset [44].

doi:10.1371/journal.pone.0020834.t001
within a well-documented archeological context of the Gravettian cultural tradition.

Our results lead to three major implications for the understanding of the colonization of Europe and related Upper Paleolithic cultural manifestations.

1) The direct date of human bone from Buran-Kaya III (layer 6-1) at 31,900±240–320 BP (GrA-40485) is the oldest one in far southeastern Europe. Buran-Kaya III (layer 6-1) provides one of the oldest direct indications for the presence of Anatomically Modern Humans in Europe and therefore increases the number of European modern human remains directly dated between 40,000 and 29,000 BP. We highlight, in Table 2, the other European Anatomically Modern Human remains directly dated between 40-29 ka BP with a quite secure taxonomical attribution.

2) Layer 6-1 provided lithic artifacts and ivory ornaments securely attributed to the Gravettian cultural tradition [26,40], with unexpected early 

14C dates. This association is free from material sedimentary overlap, as shown by the stratigraphic and sedimentologic work conducted during the 2001 and 2009 field seasons. There is a continuity in the Buran-Kaya III stratigraphical sequence from the lower layers (6-5, 6-4, 6-3) that provided lithic elements consistent with the Aurignacian cultural tradition up to the upper layers (6-2, 6-1, 5-2), where lithic industries exhibited features of the Gravettian technocomplex.

Radiocarbon dates of approximately 31–32 ka BP have been associated mostly with Aurignacian [6,11,12,75], but also with Gravettian settlements: e.g. in Poland (31,000±550 BP (OxA-4586) in Ohlazowa cave, layer VIII [72]), Austria (30,500+900/−800 BP (GrN-11193) in Willendorf II, layer 5 [76]), and Ukraine (29,650±1,320 BP in Molodova V, layer IX [77]). Thus, the new Buran-Kaya III 14C dates confirm the hypothesis of a very early occurrence of Gravettian settlements prior to 30 ka BP in Eastern Europe [78,79].

3) These results also shed new light on the symbolic behavior of early Anatomically Modern Humans, in terms of treatment of corpses. To date, two 14C dated Aurignacian settlements from Western Europe have yielded early modern human remains bearing cut marks: La Crouzade [73] (31-30 ka BP) and Les Rois [80] (28–30 ka BP, taxonomical attribution of the mandible under discussion) in France. Thus, proven by direct dating, Buran-Kaya III seems to represent the oldest evidence in Europe at 32 ka BP of cut mark actions on modern human corpses, which seem to be related rather to ritual cannibalism or mortuary practices than to dietary cannibalism.
Our findings fill an important gap in the study of modern human settlements in Eastern Europe. The human fossils represent the oldest direct evidence of the presence of modern humans in far southeastern Europe. Our multi-disciplinary studies yield new insights into the subsistence and symbolic behaviors of the earliest European AMHs. In particular, anthropogenic modifications of human bones represent the oldest evidence of postmortem treatments of the dead by early modern humans in Europe.

Specific aspects of the Crimean early Upper Paleolithic lithic industries need to be further investigated, especially in the context of this new radiocarbon dated sequence. Crimea and Eastern Europe represent important regions for a better understanding of the dispersal of early AMHs and the diffusion of Upper Paleolithic cultures with their related symbolic behavior.

Materials and Methods

In order to study the Upper Paleolithic layers of Buran-Kaya III, we carried out radiocarbon dating, plus geomorphological, stable isotopes, zooarchaeological, taphonomical and anthropological analyses.

Geomorphological analyses

Geomorphological research on the formation of the shelter-cave and studies of its sedimentary infilling were undertaken to better understand the depositional processes. Sections were drawn and deposits were described macroscopically and microscopically in order to distinguish the different sedimentary layers and establish a stratigraphic sequence. Its detailed description takes into account the texture of the sediment matrix (sand, silt, clay), its color according to the charts of Cailleux [81] and Munsell [82], its composition (quartz, limestone) and porosity. The elements of the coarse fraction (larger than 2 mm) were also described in terms of nature, shape and surface preservation. The synthesis of these first results provides information concerning the origin and the mode of sediment deposition as well as the paleoenvironmental context of the human settlement in Buran-Kaya III.

Stable isotope analysis and radiocarbon dating

Bone samples from the 2001 excavations were radiocarbon dated by Accelerator Mass Spectrometry (AMS) using purified collagen. These analyses were performed at the Center for Isotope Research of Groningen University, Netherlands (GrA), and at the Laboratoire des Sciences du Climat et de l’Environnement (LSCE) and on Artemis at the Laboratoire de Mesure du C-14 (LMC-14, Commissariat à l’Énergie Atomique, Saclay/Gif-sur-Yvette, France) (GifA/SacA).

The AMS 14C dating of human bone was performed from layer 6-1. A red deer specimen (metacarpal, Cervus elaphus) from the same
layer has been also dated. One horse sample (metatarsal, *Equus* sp.) from layer 6-2 was dated at both the Groningen and Gif-sur-Yvette/Saclay laboratories. The dates were calibrated using the software CalibREV6.0.0 based on the IntCal09 calibration dataset [44].

Collagen extraction from the Buran-Kaya III samples was performed following a protocol adapted from Longin [83] at the Center for Isotope Research of Groningen (human bone) and at the Center for Archaeological Science, University of Tubingen (red deer and horse). At the LSCE, bones were prepared by the method proposed by Nelson [84] based on chemical reaction between ninhydrin and the amino-acids of collagen [85]. Measurements of stable isotopes were performed on a continuous-flow isotope-ratio mass spectrometer (Thermo Quest Delta+XL) connected to a NC 2500 elemental analyzer at the Institute of Geoscience, University of Tubingen, Germany. Isotopic abundances are expressed as $\delta$ values as follows: $\delta X = (R_{\text{sample}}/R_{\text{standard}})\times 1000$ %, where X stands for $^{13}$C or $^{15}$N and R is the isotopic ratio $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N. The calibration was based on USGS 24 ($\delta^{13}$C = $-16.0\%_{\text{oo}}$ relatively to the international standard VPDB) for $\delta^{13}$C and AEA 305 A ($\delta^{15}$N = $39.8\%_{\text{oo}}$, relatively to the international standard AIR) for $\delta^{15}$N. The analytical error, based on replicate measurements of

| Site | Country | Specimen No. | Element | $^{14}$C date (BP) and laboratory number |
|------|---------|--------------|---------|-----------------------------------------|
| Kostenki 1 (layer III) [47,64,65] | Russia | Kostenki 8 | Undescribed tibia and fibula | 32,600±1,100 (OxA-7073) |
| Peștera cu Oase [66] | Romania | Oase 1 | Mandible | 34,290±970/−870 (GrA-22810) |
| Peștera Muierii [67,68], Baia de Fier | Romania | Peștera Muierii 1 | Scapula and tibia | 30,150±800 (LuA-5228) |
| Peștera Muierii 1 | Cranium | 29,930±170 (OxA-15529) |
| Peștera Muierii 2 | Temporal | 29,110±190 (OxA-16252) |
| Peștera Cioclovina Uscată [68–70] | Romania | Cioclovina 1 | Temporal | 29,000±700 (LuA-5229) |
| Mladč [71] | Czech Republic | Mladč 1 | Right upper second molar | 31,190+440/−390 (VERA-3073) |
| Mladč 2 | Left upper third molar | 31,320+410/−390 (VERA-3074) |
| Mladč 8 | Left upper second molar | 30,680+380/−360 (VERA-3075) |
| Mladč 9a | Right upper canine | 31,500+420/−400 (VERA-3076-A) |
| Mladč 9a | Right upper canine | 27,370±230 (VERA-3076-B) |
| Mladč 25c | ulna | 26,330±170 (VERA-2736) |
| Oblazowa cave [72] | Poland | Oblazowa | Distal thumb phalanx | 31,000±500 (OxA-4586) |
| La Crouzade [73] | France | La Crouzade VI | Maxilla | 30,640±640 (ERL-9415) |
| Goat’s Hole, Paviland [74] | United Kingdom | Paviland 1 | Rib | 28,870+180 (AF, OxA-16412) |
| Paviland 1 | Rib | 28,400±320 (AG, OxA-16502) |
| Paviland 1 | Scapula | 29,490±210 (AF, OxA-16413) |
| Paviland 1 | Scapula | 28,820±340 (AG, OxA-16503) |

doi:10.1371/journal.pone.0020834.t002
modern collagen, was ±0.1% for δ13C values and ±0.2% for δ15N values. The chemical composition of the collagen is used to assess the reliability of the isotopic measurements. We determined the preservation of the bone collagen using the C/N atomic ratio. Carbon and nitrogen contents (%C and %N) from the collagen of the samples are comparable to those found in modern mammals.

Zoarcheological analyses
The zoarcheological analyses were conducted on the whole faunal assemblage of large mammals: taxonomical and anatomical determination, taphonomical analyses (following the methodology of Villa [63], Bouzouit [86], Lyman [97], Patou-Mathis [98]). Remains were counted using the following units: Number of Identified Specimens (NISP), Combined Minimum Number of Individuals (cMNI), Percentage of element Representation (PR or % survival) defined as PR(i) = (MNE(i)*100)/(N(i)*cMNI); MNE=Minimum Number of Elements and N(i) is defined as the number of time that one element (i) occurs in one skeleton). Palaeocological information was obtained from the distribution of large mammal associations [89].

Anthropological analyses
Regarding the anthropological analyses, the MNI (Minimum Number of Individuals) was based on the dental wear status, the estimation of the dental development, the position of the enamel hypoplasia and the frequency of each tooth. The sex assessment of these individuals was not possible due to the absence of the pelvic bone, which is a good estimator of sex determination [90]. The determination of the dental developmental age stages (juvenile, sub-adult, adult) was based on the degree of occlusal wear and the dental development (cusp and root developments).

The taxonomic assignment was made only on a few complete bones and complete teeth. The dental non-metric traits have been recorded using the Arizona State University Dental Anthropology System (ASUDAS) [91,92] and described in Bailey’s publications [12,55,93].

Areas with striations were replicated by using Coltenese President light body silicone moulds. These were subsequently studied under a stereomicroscope and an Environmental Scanning Electron Microscope (ESEM) at the Muséum National d’Histoire Naturelle de Paris and at the Laboratoire de Micropaléontologie, Université Paris 6, Pierre et Marie Curie, UPMC.

Acknowledgments
We thank the National Academy of Sciences of Ukraine for permission to excavate at Buran-Kaya III and all the team members of the 2001, 2009 and 2010 excavations. We thank Sylvie Crasquin (UPMC) for the access to the E-MEB and Danièle Fouchier (UPR 2147) for artwork. We also wish to thank Evelyn Kalmtecher (LSCE/UVSQ) for her collaboration in the bone sample preparation and Christophe Moreau for the C-14 dating on LMR-14. We are grateful to Miguel Caparros, Frank Steeg and Brigitte Deniau for improving the English text and to Maryléne Patou-Mathis, Hervé Bocherens, Nicholas Conard, Fernando-Ramírez-RoZZi, Christine Verna, Fred Smith and anonymous reviewers for their helpful comments.

Author Contributions
Conceived and designed the experiments: SP SCP LC. Performed the experiments: SP SCP LC DGD SJP HV ML-G JvdP AY. Analyzed the data: SP SCP LC DGD SJP HV ML-G JvdP AY. Contributed reagents/materials/analysis tools: SP SCP LC DGD SJP HV ML-G JvdP AY. Wrote the paper: SP SCP LC DGD SJP HV ML-G JvdP AY.

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