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News and views

# Human remains from a new Upper Pleistocene sequence in Bondi Cave (Western Georgia)

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## The Bondi Cave sequence

A new sequence containing human remains from a previously unstudied cave, Bondi Cave, has been discovered in Georgia, with deposits dating to the Caucasian Upper Pleistocene. This site lies in the basin of Rioni-Kvirila Rivers, in the Imereti region of north-western Georgia. The site has yielded a long sequence with human occupations dated from ~39 ka $^{14}$C (uncalibrated) and thus covers the time span of the Middle Palaeolithic (MP)–Upper Palaeolithic (UP) transition in the region. Changes in the technological features between the lower and upper part of the sequence indicate that Bondi Cave could potentially highlight the tempo and mode of the population replacement. Indeed, recent studies in the southern Caucasus (notably at Ortvale Klde, Western Georgia) suggest a very rapid occupation by modern humans replacing existing Neanderthal populations (Adler, 2002; Meshveliani et al., 2004; Bar-Yosef et al., 2006; Adler et al., 2008). The rich UP levels at the upper and middle parts of the new sequence offer data on modern human subsistence and technological behaviors, and on the humans who occupied this cave, as a human tooth has also been discovered in this part of the sequence.

Bondi Cave is located ~5 km north of the town of Chiatura, near the sites of Ortvale Klde and Dzudzuana, which have yielded sequences of Early Upper Palaeolithic (EUP) and Upper Palaeolithic (UP) materials dated from ~38–32 ka $^{14}$C BP (Adler et al., 2008). It opens to the south onto the slope of a small valley lying approximately 30 m above the Tabagrebi River (Fig. 1). During excavations conducted in 2007 and 2009, six squares (A3-4, B3-4 and C3-4) were opened in the cave entrance (Fig. 1). This excavation has revealed a sedimentary sequence of more than 3 m in thickness. The limestone bedrock has not yet been reached.

Eight distinct lithological layers can be distinguished, with fallen blocks representing major roof collapses, notably those defining layer VI (Fig. 2). We observe two complexes: 1) the upper part (layers I to V, about 150 cm in thickness) that has yielded abundant material from the UP, and 2) the lower part, composed of layers VII (and VIII) (more than 60 cm thick) that has yielded less artifacts. The artifacts from the latter complex differ markedly from those in the upper layers by their typo-technological composition (i.e. less blades and elongated blanks), and relatively larger size.

In total, close to 10,000 well-preserved lithic and faunal remains have been recovered, including close to 3000 macro-faunal remains ($n = 2851$) and more than 7000 lithic artifacts. Layers II, IV and V contain the richest concentration, with nearly 90% of the sample of artifacts recovered within these layers. Evidence of fire has been recovered throughout the sequence (demonstrated by burnt bones and flint, as well as micro-charcoal fragments). A human tooth was recovered from the Upper Paleolithic sub-layer Vb, making this the third Georgian site with human remains of this period; the others are Deviskhvreli and Sakajia, which date to around 12 to 10 ka (Nioradze and Otte, 2000).

## Radiocarbon dating

Twelve samples (bones) associated with various archeological layers were dated using Accelerator Mass Spectrometry (AMS) radiocarbon dating methods (Table 1). The results were calibrated using the Greenland-Hulu U/Th timescale (Weninger and Joris, 2008) to be comparable with other dates reported from this region by Adler et al. (2008). The dates indicate episodes of human

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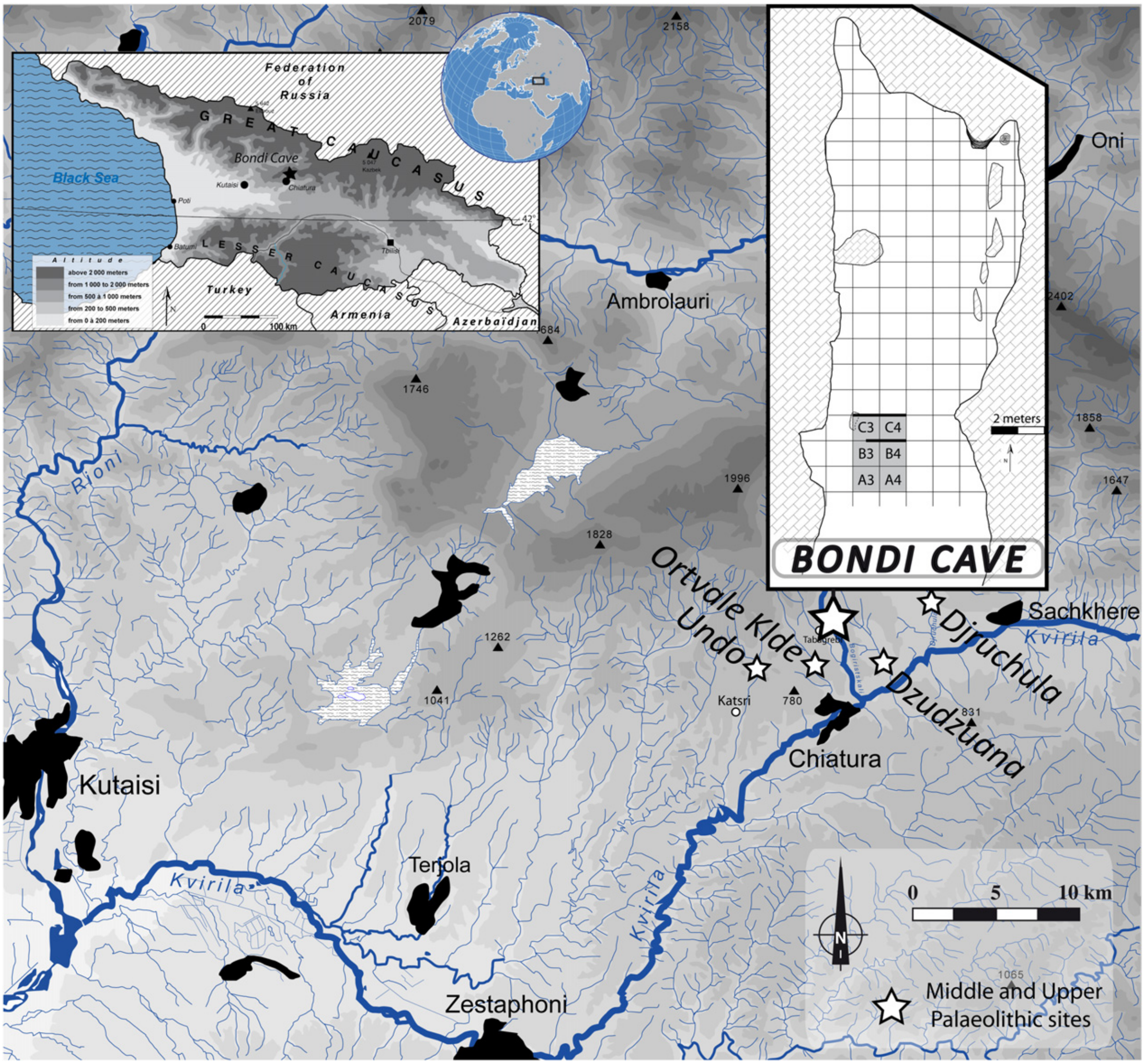


**Figure 1.** Location of Bondi Cave and of some Middle and Upper Palaeolithic sites, Imereti, West Georgia. Plan of the cave and location of the test pit. The bold lines of the grid refer to the stratigraphic section of Fig. 2.

occupation from 38,750 ± 480 ka $^{14}$C BP (43,123 ± 632 ka Cal $BP_{Hulu}$) (layer VII) to 14,050 ± 90 ka $^{14}$C BP (17,295 ± 225 ka Cal $BP_{Hulu}$) (layer III).

There is a clear differentiation between the two cultural complexes, with layer VII (MP affinities) dated to between ~38.7 to 35 ka $^{14}$C BP (43–40 ka Cal $BP_{Hulu}$) and the layers V to III (UP levels) from ~24.6 to 14 ka $^{14}$C BP (29–17 ka Cal $BP_{Hulu}$). These two complexes are separated by a layer of large collapsed blocks (layer VI) dated to 31.2 ka $^{14}$C BP (35.4 ka Cal $BP_{Hulu}$), with certain UP artifacts. This date indicates either: 1) a first UP human occupation in the cave or 2) a hiatus of several thousand years between the bottom layer and the main UP sequence (assuming that certain UP pieces might originally derive from layer V).

The dates of both layers IV and V are within the time range from ~26 to 11 ka $^{14}$C BP (~31–13 ka Cal $BP_{Hulu}$) but some of them appear erroneous. The date of 10,920 ± 40 ka $^{14}$C BP (12,860 ± 81 ka Cal $BP_{Hulu}$) obtained on a bone specimen sampled in layer Va close to the present-day surface of square A4 may have been contaminated. Secondly, one other date of Layer Va (18,010 ± 140 ka $^{14}$C BP; 21,726 ± 395 Cal $BP_{Hulu}$) and the date of layer IV (26,020 ± 170 ka $^{14}$C BP; 30,978 ± 348 ka Cal $BP_{Hulu}$) also appear under- and overestimated respectively, if we consider the age sequence in its entirety (cf. Fig. 3). If we omit these dates, then the ages of layer IV and layer Vb (~40 cm thick; A4 sample near the tooth) are consistent regarding the general sequence (Fig. 3). The dates of layer IV are centered around 23.5 ka Cal $BP_{Hulu}$ and those obtained on samples from sub-layer Vb (the human tooth layer) are between 25.7 and 29.5 ka Cal $BP_{Hulu}$.

## Palaeoenvironmental reconstruction of the sequence

Eleven taxa are identifiable and the faunal assemblage appears homogeneous throughout the sequence. Within the faunal list (including Aves sp., *Felis* cf. *silvestris*, *Canis lupus*, *Ursus* cf. *arcto*, *Equus* sp., *Sus* cf. *scrofa*, cf. *Capreolus capreolu*, *Cervus* cf. *elaphus*, cf. *Rupicapra rupicapra*, *Capra* cf. *caucasica*), *Bison* cf. *bonasus caucasicus* Turkin and Satunin, 1904 is the most common species. Six micromammals species have also been identified, *Microtus arvalis* Pall, 1779, *Arvicola terrestris* Lacepede, 1799, *Prometheomys*

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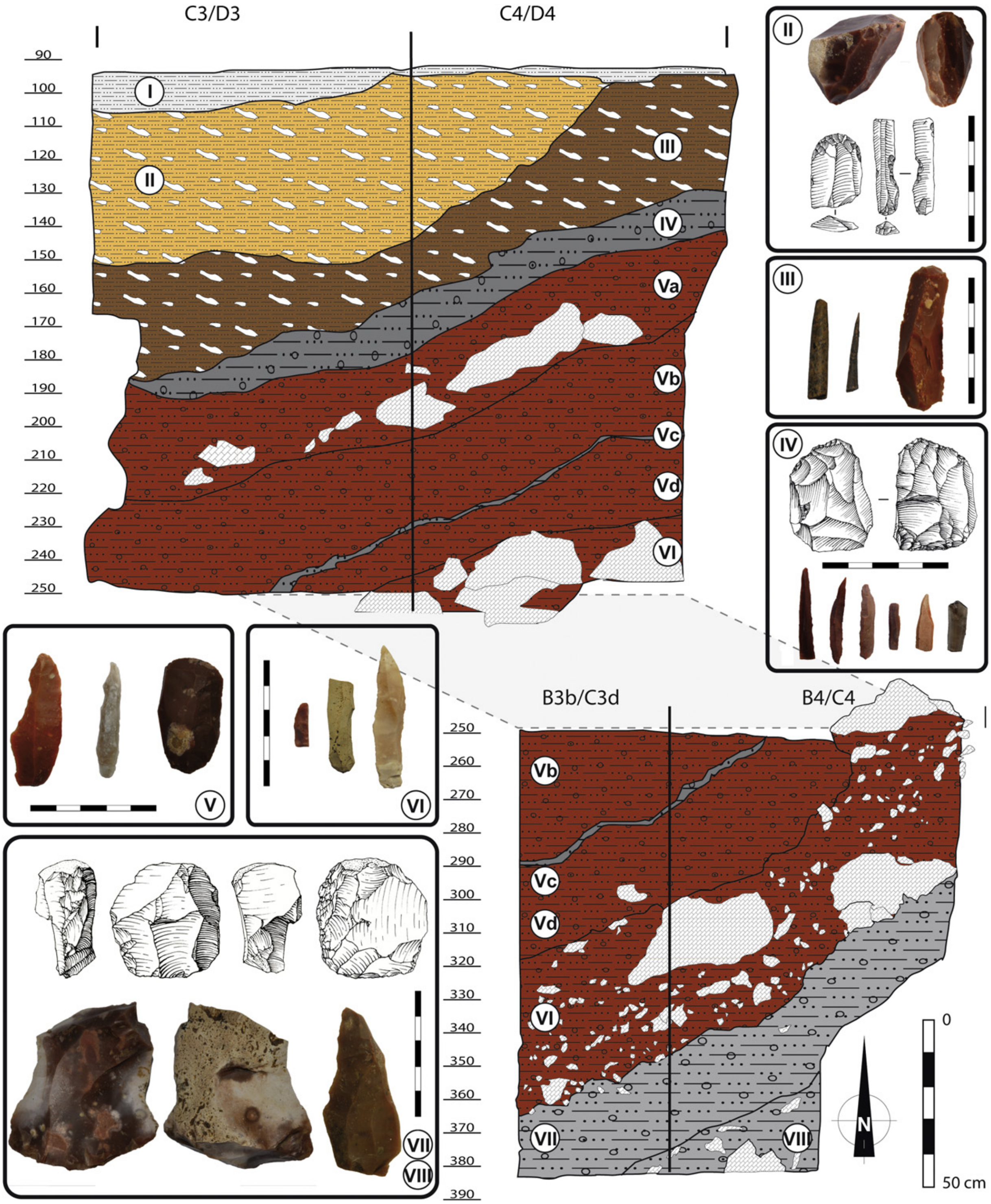


**Figure 2.** Synthetic stratigraphic section E–W (transversal) of 4/5 and 3/4 bands of Bondi Cave. Examples of Upper Palaeolithic artefacts of layers II–VI (flint (backed) blades and bladelets; endscrapers, flint carenated core, obsidian broken bladelet, polished pointed bone tools) and of Middle Palaeolithic affinity artefacts of layers VII–VIII (flint Levallois point and cores). The known sequence consists of eight lithological layers, with phases of blocks representing major collapses of the porch of the cave: – I: surface sediments with average thickness of 10–15 cm – II: orange-brown clay with many small pebbles and with thickness of about 60 cm. The sediment was deposited between the collapsed blocks. – III: gravelly brown clay, with a maximum thickness of 45 cm – IV: black layer markedly different from the other levels by its colour and the richness of the archaeological material. The average thickness of this layer is 20–30 cm (40 cm maximum). – V: dark brown and red coloured clay. This layer (~60 cm of thickness) can be divided into four sub-layers, with the same clayey matrix. Collapsed blocks are at the top (sub-layer Va). The sub-layer Vc is a pellicular blackish layer in the middle. Sub-layers Vb and Vd are identical and differentiated by the presence of small limestone blocks and gravels. – VI: major phase of the roof collapse of about 50 cm in thickness, marked by numerous indurated blocks. Sediments of layer V are included among the blocks. – VII: brown-greenish clay more than 60 cm thick, with blunt gravel. Its base has not been yet reached. – VIII: brown red-greenish clay, with small blocks (~20 cm). Its summit currently just appears in the north-eastern corner of the excavation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
$^{14}C$ dates at Bondi Cave (Cal. HULU http://www.calpal-online.de/).

| Lab# | Square | Layer | Depth (cm) | Conventional radiocarbon age BP | Age Cal BP 1σ |
|---|---|---|---|---|---|
| SacA-12064 | C3 | III | 130–150 | 14,330 ± 90 | 17,504 ± 257 |
| SacA-12065 | C3 | III | 150–160 | 14,050 ± 90 | 17,295 ± 225 |
| Beta 2392225 | B4 | IV | 110–140 | 19,360 ± 120 | 23,124 ± 286 |
| SacA-12066 | C3 | IV | 170–190 | 20,080 ± 170 | 24,005 ± 349 |
| Beta 270160 | C3 | IV | 178 | 26,020 ± 170 | 30,978 ± 348 |
| Beta 239226 | A4 | Va | 145–165 | 10,920 ± 40 | 12,860 ± 81 |
| SacA-12067 | C3 | Va | 200–210 | 18,010 ± 140 | 21,726 ± 395 |
| Beta 270161 | A4 | Vb | 185–205 | 21,550 ± 120 | 25,668 ± 405 |
| SacA-12068 | C3 | Vb | 203–230 | 24,620 ± 300 | 29,462 ± 580 |
| SacA-12069 | C3 | VI | 240–250 | 31,270 ± 640 | 35,438 ± 683 |
| Beta 2392227 | B4 | VII | 270–280 | 35,070 ± 340 | 40,082 ± 867 |
| Beta 270162 | A4 | VII | 315–325 | 38,750 ± 480 | 43,123 ± 632 |

*schaposchnikovi* Sat., *Cricetulus migratorius* Pall, 1773, *Pitymys* sp. and *Chionomys ex. gr. gud-roberti* (Meshveliani et al., 1990).

The composition of the faunal assemblage indicates the presence of montane environments, as well as forested and open grasslands near the cave, which agrees well with other studies from the area (Bar-Oz et al., 2002, 2004, 2008; Bar-Oz and Adler, 2005). Pollen and spores of 32 herbaceous and 11 arboreal species (Khvavadze and Tushabramishvili, 2008) indicate three periods of cooling (layers VII, VI, Vb-c-d and IV) and two warming periods (layer Va and bottom of layer II). During cold and dry climatic conditions, pine (*Pinus*) open woodland and various small bushes with elements of upland steppes were widespread. In the warm periods, there were forests with hornbeam, maple and elm trees present. In the river flood-plain, alder (*Alnus*) forests were present.

## Evidence of human occupations

Cut-marked bones and artifacts are associated within each lithological layer, attesting that the cave has been inhabited during the period bracketed by the radiocarbon dates. The artifacts from

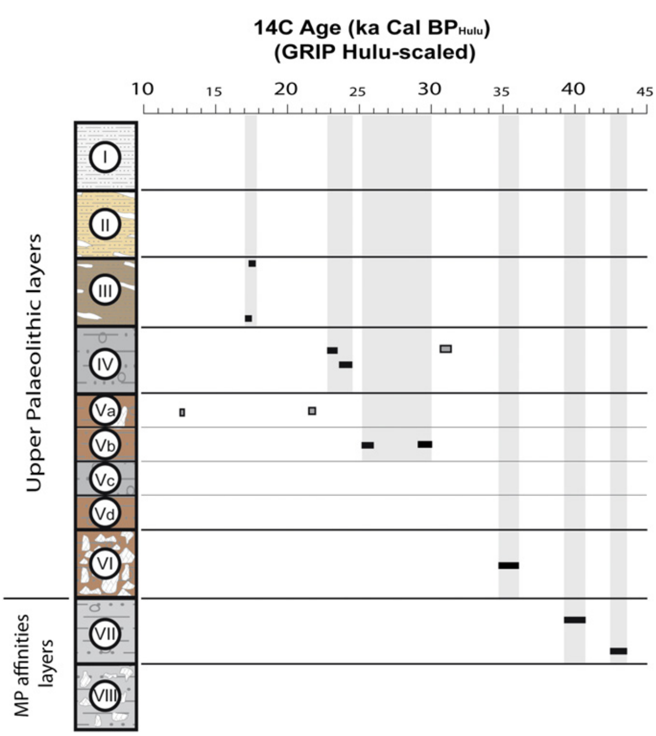


**Figure 3.** Radiocarbon data of Bondi Cave by stratigraphic layer. Ages are plotted with 1σ (ka BP, GRIP Hulu-scaled).

above layer VI (Table 2), are mainly composed of local flint blades and bladelets. The higher proportion of the bladelets at the top of the sequence with more numerous blades at the bottom indicates a slight, but continuous cultural change over time. The retouched products (on flakes, blades and bladelets) account for only ∼4% of the total amount of the lithics collected from layers I to V (Table 2). Microlithic tools are less abundant than in sites such as Dzudzuana (Epi-Gravettian from 17 to 16 to 15–13 ka BP, Meshveliani et al., 2007; Bar-Yosef et al., 2011), Gwardzilas Klde (15 ka BP), Deviskhvreli (10 ka BP) or Sakazhia (11 ka BP) (Nioradze and Otte, 2000). Flint knapping took place on the site (unipolar convergent or *semi-tournant* cores for blades; discoid, Kombewa and Levallois cores for flakes). Obsidian pieces (0.9%) are quite rare, occurring only in layers II, IV and V, and mainly composed of unretouched pieces, blades, bladelets, small flakes and a few tools (scrapers, burins, burin spalls, retouched blades). Obsidian sources are not present in this area. The closest identified outcrops are on the Chikiani volcanoes near Lake Paravani, more than 100 km south of the site. In addition, some broken bone points have also been discovered in layer II (Fig. 2), while a cockle-shell bead (3 mm wide and 1 mm in thickness) has also been found in layer Vb in the vicinity of the human tooth.

Layers VII and VIII, under the main collapse phase of the cave (layer VI), yielded 278 pieces (Table 2). The artifacts show techno-morphological characteristics that clearly distinguish them from the UP material recovered in layers VI and II. All are unretouched and made of local flint. They are mainly small and large flakes, with unipolar or centripetal negative removals. Some thick or thin blades and pointed elongated flakes are also present. The cores are Levallois (preferential, unipolar and centripetal recurrent), and discoidal. The flaking is oriented towards short or elongated flakes on one or two faces (Fig. 2). Some Middle Palaeolithic features common in the Caucasian area are thus clearly visible (Liubin, 1977, 1989; Tushabramishvili, 1984, 1994, 2002; Nioradze, 1992; Meignen, 1994, 2000; Liubin and Bosinski, 1995; Tushabramishvili et al., 1999, 2007; Golovanova and Doronichev, 2003; Adler and Tushabramishvili, 2004; Golovanova et al., 2006; Meignen and Tushabramishvili, 2006; Adler et al., 2006, 2008; Pleurdeau et al., 2007; Doronichev, 2008).

## The human tooth from sub-layer Vb

A hominin tooth (Fig. 4) was excavated in the sub-layer Vb. The tooth could be either a lower right permanent first molar ($M_1$ dextra) or lower right deciduous second molar ($m_2$). The tooth is fairly well-preserved; however some enamel is chipped off the mesio-buccal corner and along the cervical margin of the buccal side, and presents, at the disto-buccal angle, a small missing flake above the cervix. The advanced attrition of the crown, stage 5 of Molnar's classification (1971), further complicates its anatomical determination. Nevertheless, the height of the preserved crown, the rectangular shape, its still bulbous morphology, the size of the pulp chamber and the preserved parts of the roots support its identification as a second deciduous molar (Al Qahtani et al., 2010).

The tooth displays an ovoid contour, with clear evidence of all five cusps. The wear degree of this surface increases from the disto-lingual to the mesio-buccal direction. Despite the heavy wear, a part of the mesial fossa can still be observed.

Viewed buccally, the length decreases towards the cervix (a classical trait for a deciduous tooth). Just after its discovery, it was very clear that this surface was divided into three parts by two grooves (the mesial one has disappeared because of a recent enamel chip), again normal morphology considering a five-cusped molar. At the cervix, the enamel dips slightly with its lowest part not at the mid-diameter but in a more mesial position.

**Table 2**
Stratigraphical distribution of the lithic artefacts at Bondi Cave.

| Layer | Flakes | | Blades | | Bladelets | | Small flakes (>20 mm) | | Debris | | Cores | | Retouched tools | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I | 60 | 18% | 69 | 21% | 33 | 10% | 134 | 40% | 18 | 5% | 8 | 2% | 10 | 3% | 332 |
| II | 451 | 31% | 273 | 19% | 134 | 9% | 454 | 31% | 60 | 4% | 35 | 2% | 63 | 4% | 1470 |
| III | 33 | 47% | 14 | 20% | 6 | 9% | 9 | 13% | | 0% | 4 | 6% | 4 | 6% | 70 |
| IV | 628 | 26% | 445 | 19% | 193 | 8% | 892 | 37% | 78 | 3% | 38 | 2% | 115 | 5% | 2389 |
| V | 381 | 16% | 326 | 13% | 147 | 6% | 1431 | 59% | 57 | 2% | 28 | 1% | 73 | 3% | 2443 |
| VI | 26 | 40% | 15 | 23% | 2 | 3% | 8 | 12% | 5 | 8% | 4 | 6% | 5 | 8% | 65 |
| VII | 33 | 13% | 20 | 8% | | 0% | 185 | 74% | 5 | 2% | 6 | 2% | | 0% | 249 |
| VIII | 4 | 14% | | 0% | | 0% | 24 | 83% | | 0% | 1 | 3% | | 0% | 29 |
| *Total* | 1616 | | 1162 | | 515 | | 3137 | | 223 | | 124 | | 270 | | 7047 |


**Figure 4.** The human tooth of Bondi Cave (layer V). a) occlusal (mesial border = top), b) mesial (buccal border = left) and c) buccal (mesial border = right).

In the lingual view, again the bulbous morphology of the crown can be noted with the MD length decreasing as one approaches the cervix. On this surface, a classic shallow groove, separating metaconid and entoconid, is observed, and between the two roots, the enamel of the cervix dips clearly into the bifurcation.

When viewed mesially and distally, the cemento-enamel junction appears straight. The interproximal contact facets have an oval shape in distal view and half-ellipsoid when viewed mesially. The longest margin of each of these facets is probably reduced at the occlusal border, due to attrition of the crown. Still, the facets have different sizes – with the mesial one being wider (5.73 mm versus 4.1 mm). Note that there are no subvertical grooves on both interproximal facets as can be observed on some Neanderthal permanent molars.

The roots are resorbed (or broken, if the specimen is a permanent molar, but the regularity of the border of the dentine is very similar to the one that can be observed on an antemortem shed milk molar) almost up to the cervix and the pulp chamber is open, revealing a small, rhomboid cavity. If the specimen is an antemortem lost $m_2$, then the age of the juvenile specimen could be around 11.5 years, when compared to modern human samples (Al Qahtani et al., 2010).

**Table 3**
The human tooth (Bondi 1) of Bondi Cave (Layer Vb). Bondi 1 crown diameters (mm) and variability of deciduous teeth from different extant samples (B.M. personal data and data compilation; Maureille, 2001). Bondi 1 diameters (especially MD diameter) are minimal ones considering the degree of interproximal wear.

| | Bondi 1 | Extant human variability | Neanderthal variability |
|---|---|---|---|
| Mesio-distal diameter | (9.4) | $m = 10.02$<br>$s = 0.587$<br>$n = 350$ | $m = 10.46$<br>$s = 0.65$<br>$n = 37$ |
| Bucco-lingual diameter | (8.5) | $m = 9.01$<br>$s = 0.507$<br>$n = 350$ | $m = 9.33$<br>$s = 0.47$<br>$n = 37$ |

The Bondi Cave specimen is small relative to a sample of deciduous extant human teeth and Neandertal ones (Table 3). For both crown diameters, significant overlap between modern humans and Neanderthal samples makes it difficult to assign the Bondi tooth to either species, based solely on crown size. All the observed traits could equally be found within the extant or any Upper Palaeolithic human group, or within a Neanderthal population. Presently, we prefer to attribute this tooth to *Homo sapiens* sp. and await further hominin material that will clarify the exact taxonomic position of the Bondi Cave hominin.

## Discussion and conclusion

The Bondi Cave sequence complements recent research in the southern Caucasus (Fourbouley et al., 2003; Adler et al., 2008; Pinhasi et al., 2008; Fernandez-Jalvo et al., 2010). Several Upper Palaeolithic occupations seem to have occurred at this site and date to between ~31/24.5[1] and 14 ka $^{14}$C BP. These layers would be contemporaneous in part with the Dzudzuana UP (Units D at 32–26 ka, C at 23–19 ka and B at 13–11 ka) and the Ortvale Klde UP (38 ka BP for layer 4d and 34 ka BP for layer 4c) (Meshveliani et al., 1999, 2004; Adler and Tushabramishvili, 2004; Bar-Yosef et al., 2006, 2011; Adler et al., 2008; Kvavadze et al., 2009).

[1] Depending on the status of layer VI: it is either the first UP occupation or a major roof collapse in which some UP artifacts from layer V were displaced into the underlying layer.

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The base of the sequence (~38.7–35 ka $^{14}$C) has yielded occupation levels with affinities to the MP of the region. Due to the dating hiatus between layer VII and layer VI/V, we cannot assess whether or not a rapid transition from MP to UP and replacement of populations around 35–31 ka occurred, as has been observed for Ortvale Klde (~34–38 ka) and Mesmaiskaya (~36–32 ka) (Cohen and Stepanchuk, 1999; Golovanova et al., 1999, 2006, 2010; Ovchinnikov et al., 2000; Bar-Yosef et al., 2006; Bar-Oz et al., 2008; Adler et al., 2008).

Several aspects of the archeology, the paleontology and the paleoenvironmental data from the upper part of Bondi Cave sequence resemble those observed in the UP of Dzudzuana and Ortvale Klde. Specifically, these aspects relate to the raw material exploitation (with local flint predominating and exogenous obsidian used in the UP levels), the laminar and bladelet production, and finally, the presence of microlithic tools. The absence of Aurignacian components is also common to these sites (only few carinated cores have been recovered from the upper layers of Bondi as in Dzudzuana unit C; Meshveliani et al., 2004; Bar-Yosef et al., 2006, 2011), while they appear to be a local development from MP in certain neighbouring areas, for instance in Zagros and Taurus in Iran, which date to between 35 and 23 ka BP (e.g. Meignen, 2006; Otte et al., 2007; Otte and Kozlowski, 2007). The observed differences between sites could relate to different management of the environment and the territory, to different seasons of occupation, or to the wide variety of ecological niches evident at these different sites: for instance dominant *Capra caucasica* at both the MP and UP levels at Ortvale Klde and *Bison bonasus caucasicus* at Bondi Cave and Dzudzuana (Bar-Oz et al., 2002, 2004; Adler et al., 2006). Moreover, bone tools are rare in Bondi Cave while they have been recovered at Dzudzuana (Bar-Yosef et al., 2006, 2011), and in the final UP of Sakajia and Gvardjilas Klde (Nioradze and Otte, 2000) and in the later EUP of Mezsmaiskaya (Golovanova et al., 2010).

The lower layers VII and VIII, although providing fewer artifacts, contain material with very different technical features. Indeed, the presence of thick elongated lithic products contrasts markedly with the thin and elongated blades found in layers VI and V, and the presence of Levallois cores is also remarkable. Further work and excavation of the Layers VII and VIII (bedrock has not yet been reached) will help to provide more techno-cultural features in order to assess whether the layers are transitional MP/UP or strictly LMP.

Finally, although it is widely accepted that the EUP occupations in the region are those of early modern humans, this hypothesis remains tentative since there are few or no remains of *H. sapiens* definitively associated with the EUP. So far, only two sites in Georgia have yielded *H. sapiens* remains within an Upper Paleolithic context: Devishkhvreli, with a fragment of mandible, and Sakajia with some cranial remains. At both sites, human remains have been unearthed in recent levels dated ~12–10 ka (Nioradze and Otte, 2000). The lack of sites preserving human remains underlines the importance of the Bondi Cave in the archaeological landscape of Georgia. The human tooth has been discovered in the UP context of the sub-layer Vb, dated to between 21.5 and 24.6 ka $^{14}$C BP. These ages provide the oldest date range for human remains in UP context in Georgia, presuming its attribution to *H. sapiens* is correct. Unfortunately, a precise taxonomic attribution of the Bondi tooth must await the recovery of further remains, both in UP and MP affinity levels, to shed further light on the question of the transition between Neanderthals and the first *H. sapiens* in the Caucasus (Skinner et al., 2005; Golovanova et al., 2006).

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## References

Adler, D.S., 2002. Late Middle Palaeolithic patterns of lithic reduction, mobility, and land use in the southern Caucasus. Ph.D. Dissertation, Harvard University.

Adler, D.S., Bar-Oz, G., Belfer-Cohen, A., Bar-Yosef, O., 2006. Ahead of the Game. Middle and Upper Palaeolithic behaviors in the southern Caucasus. Curr. Anthropol. 47, 89–118.

Adler, D.S., Tushabramishvili, N., 2004. Middle Paleolithic patterns of settlement and subsistence in the southern Caucasus. In: Conard, N.J. (Ed.), Settlement Dynamics of the Middle Paleolithic and Middle Stone Age, vol. II. Tübingen, pp. 91–133.

Adler, D.S., Bar-Yosef, O., Belfer-Cohen, A., Tushabramishvili, N., Boaretto, E., Mercier, N., Valladas, N., Rink, W.J., 2008. Dating the demise: Neandertal extinction and the establishment of modern humans in the southern Caucasus. J. Hum. Evol. 55, 817–833.

Al Qahtani, S.J., Hector, M.P., Liversidge, H.M., 2010. Brief communication: the London atlas of human tooth development and eruption. Am. J. Phys. Anthropol. 142, 481–490.

Bar-Oz, G., Adler, D.S., Meshveliani, T., Tushabramishvili, N., Belfer-Cohen, A., Bar-Yosef, O., 2002. Middle and Upper Palaeolithic foragers of the southwest Caucasus: new faunal evidence from western Georgia. Archaeology, Ethnology and Anthropology of Eurasia 4, 45–52.

Bar-Oz, G., Adler, D.S., Vekua, A., Meshveliani, T., Tushabramishvili, N., Belfer-Cohen, A., Bar-Yosef, O., 2004. Faunal exploitation patterns along the southern slopes of the Caucasus during the Late Middle and Early Upper Palaeolithic. In: Mondini, M., Muñoz, Wickler, S. (Eds.), Colonisation, Migration, and Marginal Areas: A Zooarchaeological Approach. Oxbow Books, Oxford, pp. 46–54.

Bar-Oz, G., Adler, D.S., 2005. Taphonomic history of the Middle and Upper Palaeolithic faunal assemblage from Ortvale Klde, Georgian Republic. J. Taphonomy 3, 185–211.

Bar-Oz, G., Belfer-Cohen, A., Meshveliani, T., Djakeli, N., Bar-Yosef, O., 2008. Taphonomy and zooarchaeology of the Upper Palaeolithic Cave of Dzudzuana, Republic of Georgia. Int. J. Osteoarchaeol. 18, 131–151.

Bar-Yosef, O., Belfer-Cohen, A., Adler, D.S., 2006. The implications of the Middle–Upper Palaeolithic chronological boundary in the Caucasus to Eurasian Prehistory. Anthropologie XLIV, 49–60.

Bar-Yosef, O., Belfer-Cohen, A., Mesheviliani, T., Jakeli, N., Bar-Oz, G., Boaretto, E., Goldberg, P., 2011. Dzudzuana: an Upper Palaeolithic cave site in the Caucasus foothills (Georgia). Antiquity 85, 331–349.

Cohen, V., Stepanchuk, V.N., 1999. Late Middle and Early Upper Palaeolithic evidence from the East European plain and the Caucasus: a new look at variability, interactions and transitions. J. World Prehist. 13, 265–319.

Doronichev, V., 2008. The Lower Paleolithic in eastern Europe and the Caucasus: a reappraisal of the data and new approaches. PaleoAnthropology, 107–157.

Fernandez-Jalvo, Y., King, T., Andrews, P., Yepiskoposyan, L., Moloney, N., Murray, J., Domınguez-Alonso, P., Asryan, L., Ditchfield, P., van der Made, J., Torres, T., Sevilla, P., Nieto Dıaz, M., Caceres, I., Allue, E., Marın Monfort, M.D., Sanz Martın, T., 2010. The Azokh Cave complex: Middle Pleistocene to Holocene human occupation in the Caucasus. J. Hum. Evol. 58, 103–109.

Fourbouley, C., Beauval, C., Colonge, D., Liagre, J., Ollivier, V., Chataigner, C., 2003. Le Paléolithique en Arménie: état des connaissances acquises et données récentes. Paléorient 20, 5–18.

Golovanova, L.V., Hoffecker, J.F., Kharitonov, V.M., Romanova, G.P., 1999. Mezmaiskaya Cave: a Neandertal occupation in the northern Caucasus. Curr. Anthropol. 40, 77–86.

Golovanova, L.V., Cleghorn, N., Doronichev, V.B., Hoffecker, J.F., Burr, G.S., Sulergizkiy, L.D., 2006. The early Upper Paleolithic in the northern Caucasus (New data from Mezmaiskaya Cave, 1997 excavation). Eurasian Prehist. 4, 43–78.

Golovanova, L.V., Doronichev, V.B., 2003. The Middle Palaeolithic of the Caucasus. J. World Prehist. 17, 71–140.

Golovanova, L.V., Doronichev, V.B., Cleghorn, N.E., 2010. The emergence of bone-working and ornamental art in the Caucasian Upper Palaeolithic. Antiquity 84, 299–320.

Khvavadze, E., Tushabramishvili, N., 2008. Л.В. КВАВАДЗЕ1, Н.Д. ТУШАБРАМИШВИЛИ2. МИКРООСТАТКИ ВОЛОКОН ЛЬНА И ШЕРСТИ В ЦАЛИНОЛОГИцЕСКОМ МАТЕРИАЛЕ ВЕРЧНЕЦА ЛЕОЛИТИцЕСКИЧ СЛОЕВ ЦЕЩЕРЫ БОНДИ. (Microremains of Flax and Wool Fibers in the Palynological Material of Upper Paleolithic Layers of Bondi Cave). Georgian National Museum. Problems of Paleobiology III.

Kvavadze, E., Bar-Yosef, O., Belfer-Cohen, A., Boaretto, E., Jakeli, N., Matskevich, Z., Meshveliani, T., 2009. 30 000-years-old Wild Flax Fibers. Science 325, 1359.

Liubin, V.P., 1977. Mustierskie kul'turi Kavkaza. (Mousterian Cultures of the Caucasus). Nauka, Leningrad.

Liubin, V.P., 1989. Paleolit Kavkaza. (Palaeolithic of the Caucasus). In: Boriskovski, P.I. (Ed.), Paleolit Kavkaza I Sredney Azii (The Palaeolithic of the Caucasus and Northern Asia). Nauka, Leningrad, pp. 9–144.

Liubin, V.P., Bosinski, G., 1995. The earliest occupation of the Caucasus region. In: Roebroeks, W., Van Kolfschoten, T. (Eds.), The Earliest Occupation of Europe, Proceedings of the European Science Foundation Workshop at Tautavel, France, 1993. University of Leiden, pp. 207–235.

Maureille B., 2001. Variabilité dans le genre Homo: les mensurations des couronnes dentaires déciduales et permanentes. Synthèse de l'activité scientifique pour l'obtention de l'Habilitation à Diriger des Recherches (UMR 5809), Université de Bordeaux 1, unpublished.

Meignen, L., 1994. Le Paléolithique moyen au Proche-Orient: le phénomène laminaire. In: Révillion, S., Tuffreau, A. (Eds.), Les Industries Laminaires au Paléolithique Moyen. Dossier de Documentation archéologique 18. CNRS, Paris, pp. 125–161.

Meignen, L., 2000. Early Middle Palaeolithic blade technology in Southwestern Asia. Acta Anthropol. Sinica 19, 158–168.

Meignen, L., Tushabramishvili, N., 2006. Paléolithique moyen laminaire sur les flancs sud du Caucase: productions lithiques et fonctionnement du site de Djurchula, Géorgie. Paléorient 32, 81–104.

Meignen, L., 2006. From the late middle Palaeolithic to the early upper Palaeolithic, between the Adriatic and the Caspian Sea: continuity or discontinuity? An introduction. Anthropologie XLIV, 1–7.

Meshveliani, T., Tvalchrelidze, M.G., Lordkipanidze, D.O., 1990. Dzudzuana cave. In: Chronostratigraphy of the Paleolith of North, Central, East Asia and America. Novosibirsk, pp. 231–234.

Meshveliani, T., Bar-Yosef, O., Belfer-Cohen, A., Djakeli, N., Kraus, A., Lordkipanidze, D., Tvalchrelidze, M., Vekua, A., 1999. Excavations at Dzudzuana Cave, western Georgia (1996–1998): preliminary results. Préhistoire Européenne 15, 79–86.

Meshveliani, T., Bar-Yosef, O., Belfer-Cohen, A., 2004. The Upper Paleolithic of western Georgia. In: Brantigham, P.J., Kuhn, S.L., Kerry, K.W. (Eds.), The Early Upper Paleolithic beyond Western Europe. University of California Press, Berkeley, pp. 129–143.

Meshveliani, T., Bar-Oz, G., Bar-Yosef, O., Belfer-Cohen, A., Boaretto, E., Jakeli, N., Koridze, I., Matskevich, Z., 2007. Mesolithic hunters at Kotias klde, western Georgia: preliminary results. Paléorient 33, 47–58.

Molnar, S., 1971. Human tooth wear, tooth function and cultural variability. Am. J. Phys. Anthropol. 34, 175–190.

Nioradze, M., 1992. Paleolit Kavkasa I sopredel'nikh Territory. (Palaeolithic Caves Sites of the Tskaltsitela River Gorge). Metsniereba, Tsibili.

Nioradze, M., Otte, M., 2000. Paléolithique supérieur de Géorgie. L'Anthropologie 104, 265–300.

Otte, M., Biglari, F., Flas, D., Shidrang, S., Zwyns, N., Mashkour, M., Naderi, R., Mohaseb, A., Hashemi, N., Darvish, J., Radu, V., 2007. The Aurignacian in the Zagros region: new research at Yafteh Cave, Lorestan, Iran. Antiquity 81, 82–96.

Otte, M., Kozlowski, J.K., 2007. L'Aurignacien du Zagros, ERAUL 118. Université de Liège, 203 pp.

Ovchinnikov, I.V., Götherström, A., Romanova, G.P., Kharitonov, V.M., Liden, K., Goodwin, W., 2000. Molecular analysis of Neanderthal DNA from the northern Caucasus. Nature 404, 490–493.

Pinhasi, R., Gasparian, B., Wilkinson, K., Bailey, R., Bar-Oz, G., Bruch, A., Chataigner, C., Hoffmann, D., Hovsepyan, R., Nahapetyan, S., Pike, A.W.G., Schreve, D., Stephens, M., 2008. Hovk 1 and the Middle and Upper Paleolithic of Armenia: a preliminary framework. J. Hum. Evol. 55, 803–816.

Pleurdeau, D., Tushabramishvili, N., Nioradze, M., de Lumley, H., Lordkipanidze, D., 2007. Les industries lithiques du Paléolithique moyen de Géorgie. L'Anthropologie 111, 400–431.

Skinner, A.R., Blackwell, B.A.B., Martin, Sara, Ortega, A., Blickstein, J.I.B., Golovanova, L.V., Doronichev, V.B., 2005. ESR dating at Mezmaiskaya Cave, Russia. Appl. Radiat. Isot. 62, 219–224.

Tushabramishvili, D., 1984. Paleolit Gruzii. (Palaeolithic of Georgia). Newsletter of the Georgian State Museum 37B, 5–27.

Tushabramishvili, N., 1994. Srednii Paleolit Zapadnoi gruzii I etapy ego perekhoda k verkhnemu paleolitu po materialam Ortvala Klde. (The Middle palaeolithic of Western Georgia and the Stages of its Transition to the Upper Palaeolithic based on the material from Ortvala Klde). PhD dissertation, University of Tbilisi.

Tushabramishvili, N., 2002. Les Cavernes de la Géorgie – Les Sites de l'Homme préhistoriques Le Guide, Tbilisi (géorgien, anglais, français).

Tushabramishvili, N., Lorkipanidze, D., Vekua, A., Tvalcherlidze, M., Muskhelishvili, A., Adler, D.S., 1999. The Middle Palaeolithic rockshelter of Ortvala Klde (Imereti region), the Georgian Republic. Préhistoire Européenne 15, 65–77.

Tushabramishvili, N., Pleurdeau, D., Moncel, M.-H., Mgeladze, A., 2007. Le complexe Djruchula-Koudaro au sud Caucase (Géorgie). Remarques sur les assemblages lithiques pléistocènes de Koudaro I, Tsona et Djruchula. Anthropologie XLV, 1–18.

Weninger, Joris, 2008. A 14C age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in western Eurasia. J. Hum. Evol. 55, 772–781.