Morphological description and morphometric analyses of the Upper Palaeolithic human remains from Dzudzuana and Satsurblia caves, western Georgia

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Introduction

While paleoanthropologists and archaeologists agree that western Georgia was used as a thoroughfare of human movements to and from the Caucasus (Pinhasi et al., 2012; 2014), the paleoanthropological fossil record of the local Middle and Upper Palaeolithic in this key region is currently limited to scanty human remains. For the Late Pleistocene, the Middle Palaeolithic (MP) Georgian human fossil record consists of a partial maxilla from the site of Sakajia and some isolated teeth from the sites of Bronze Cave, Djruchula, Ortvala and Ortvale Klde, which were all classified as Neandertals (Pinhasi et al., 2012). The Upper Palaeolithic (UP) fossil record consists of a modern human tooth from Bondi cave (Tushabramishvili et al., 2012), recently dated between 39,000 and 35,800 cal. BP (Pleurdeau et al., 2016), and cranial fragments from Sakajia, dated between 12,000-10,000 cal. BP (Nioradze and Otte, 2000) (Fig. S1). Therefore, even though some author suggests that Caucasus represents a sort of *cul de sac* for Neandertal survival, and that modern humans arrived in this area much later compared to other regions (Bar-Yosef and Pilbeam 2000), the paucity of human remains prevents any conclusive assessment.

Here we report additional Upper Palaeolithic human remains from the Imereti region, western Georgia (Fig. S1; see SOM): two isolated teeth from Dzudzuana cave (Bar-Yosef et al., 2011), one isolated tooth and a hemi-mandible bearing teeth from Satsurblia cave (Pinhasi et al., 2014). In particular, the human remains from Dzudzuana cave, dated between 27,000–24,000 cal. BP, fill a huge gap in the Upper Palaeolithic Georgian fossil record and play an important role in the debate about modern human peopling of the Caucasus.

Materials and methods

Micro-CT

High-resolution µCT images of the teeth from Dzudzuana (Dzu 1 and Dzu 2; Fig. 1) and the isolated tooth from Satsurblia (SATP5-2) (Fig. 2) were obtained with a XALT microtomographic system (Institute of Clinical Physiology, Pisa, Italy) (Panetta et al., 2012). The Satsurblia mandible

(Fig. 3) was scanned with a Birscan microtomographic system (Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany) (Scan parameters and processing procedures are described in the SOM).

Morphological description

Terminology for the morphological description of the mandible and the teeth follows White et al. (2012) and Scott and Turner (1997), respectively. Nonmetric traits were evaluated according to standards outlined by the Arizona State University Dental Anthropology System, ASUDAS (Turner et al.,1991), Bailey (2002), Bailey et al. (2011) and Martìnez de Pinillos and colleagues (2014). Occlusal wear stage was assessed based on Molnar (1971). For deciduous teeth, the age at death was estimated using the sequences provided by AlQahtani and colleagues (2010).

Morphometric analyses

Height and breadth of the mandibular corpus were measured in the digital model at the level of both the mental foramen (Buikstra and Ubelaker, 1994) and the lower first molar (Rosas and Bermùdez de Castro, 1999).

In addition to MD and BL crown diameters (Benazzi et al., 2011a; 2013a; Margherita et al., 2016) for the deciduous molars we used crown (for Dzu 1, Dzu 2 and SATP5-5) and cervical outline analyses (for Dzu 2 and SATP5-5), following methods provided by Benazzi et al. (2011b; 2012a; 2014a) and Bailey et al. (2014). For the permanent teeth we have computed the 3D enamel thickness following guidelines provided by Benazzi and colleagues (2014b). Finally, to assess whether Dzu 1 and Dzu 2 belong to the same individual, both teeth were analysed using the Occusal Fingerprint Analyser (OFA) software package (2008-2014 ZiLoX-IT GbR) (see e.g., Benazzi et al., 2012b; 2013b, c; 2015; 2016; Kullmer et al., 2013; Fiorenza et al., 2015) (for more details about methods see SOM).

Metric comparison

Whereas no metric comparison was undertaken for the mandibular corpus owing to its subadult age, the BL diameters of the deciduous teeth were compared with a sample of Neandertal (N), Upper Palaeolithic *H. sapiens* (UPHS) and recent *H. sapiens* (RHS) teeth collected from the scientific literature (Hillson and Trinkaus, 2002; Henry-Gambier et al., 2004; Hershkovitz et al., 2011). The MD diameter was not considered owing to the interproximal wear. For the permanent dentition, comparative dataset for MD and BL diameters were created *ex novo* and include N, Early *H. sapiens* (EHS) and RHS (Table S1).

The shape variables (Dzu 1 crown outline; Dzu 2 and SATP5-5 crown and cervical outlines) were projected into the shape-space obtained from a principal component analysis (PCA) of the comparative sample used by Bailey et al. (2014) and Benazzi et al. (2012a), respectively. We used cross-validation linear discriminant analysis (LDA) of the Principal Components that account for about 90% of the total variability to assess the closest taxa affiliated with the Dzu 1, Dzu 2 and SATP5-5 specimens.

Comparative data for 3D enamel thickness were created *ex novo* and include N, EHS and RHS with different wear stages (Table S1). The only UPHS specimen available for enamel thickness analysis (Villabruna, lower left first molar; Vercellotti et al., 2008; Oxilia et al. 2015) was included in the RHS sample. To discern differences in enamel thickness between N and RHS, 3D AET and 3D RET indices were tested using the Mann-Whitney *U* test ($\alpha = 0.05$; two-tailed) with a Monte Carlo permutation. Standardized scores (Z-score) were computed to establish the group means closest to the values of Dzudzuana and Satsurblia specimens. The data were processed and analysed using R v. 2.15.1 (R Development Core Team, 2012).

Results

Dzudzuana – morphological description

Dzu 1 is an upper right second deciduous molar (Rdm^2), with a complete crown and a cervical quarter of the root (Fig. 1A). The tooth has several visible fractures on the enamel-dentine junction (EDJ; Fig. S3A). While it is heavily worn (wear stage 5) (Fig. 1A), the remnants of four principal cusps, a weak Cusp 5 (ASUDAS grade 1), accessory crests and a small Carabelli's trait are still visible on the EDJ (Fig. S3A). The hypocone is small, giving to the crown a sub-square shape. Dzu 1 has a distal interproximal facet larger (length=5 mm; height=1.6 mm) than the mesial one (length=3.7 mm; height=1 mm). On the buccal wall of the crown there is a large wear facet with dentine exposure, probably related to para-masticatory activities. Root resorption at the R¾ stage suggests that the tooth had been lost ante-mortem and corresponds to an age ranging from nine to 12 years old. The tooth crown has a MD diameter of 9.9 mm and a BL diameter of 10.5 mm (Table 1). At the cervix, the MD diameter is 7.4 mm and BL diameter is 9.9 mm.

Dzu 2 is a worn (wear stage 4) lower right second deciduous molar (Rdm$_2$) with a complete crown and a cervical quarter of the root (Fig. 1B). The tooth has several visible fractures, the main one is oriented bucco-lingually and divides the tooth into two parts (see Fig. S2 for the virtual restoration). It is worn (wear stage 4). From the occlusal view the crown outline shows a bucco-distal reduction and a straighter lingual side (Fig. 1B). On the EDJ, five principal cusps, a weak anterior fovea bordered distally by a weak mesial trigonid crest (MeTC), and potentially the remnant of a distal trigonid crest (DTC), almost entirely removed by tooth wear, can be observed (Fig. S3B). Interproximal facets are evident both mesially (length=3.7 mm; height=1.7 mm) and distally (length=5.1 mm; height=2.5 mm). Root resorption is at a Res ¾ grade suggesting that the tooth had been lost ante-mortem, at an age ranging from nine to 12 years old. The tooth crown has a MD diameter of 10.3 mm and a BL diameter of 9.5 mm (Table 1). At the cervix, the MD diameter is 8.6 mm and BL diameter is 7.9 mm.

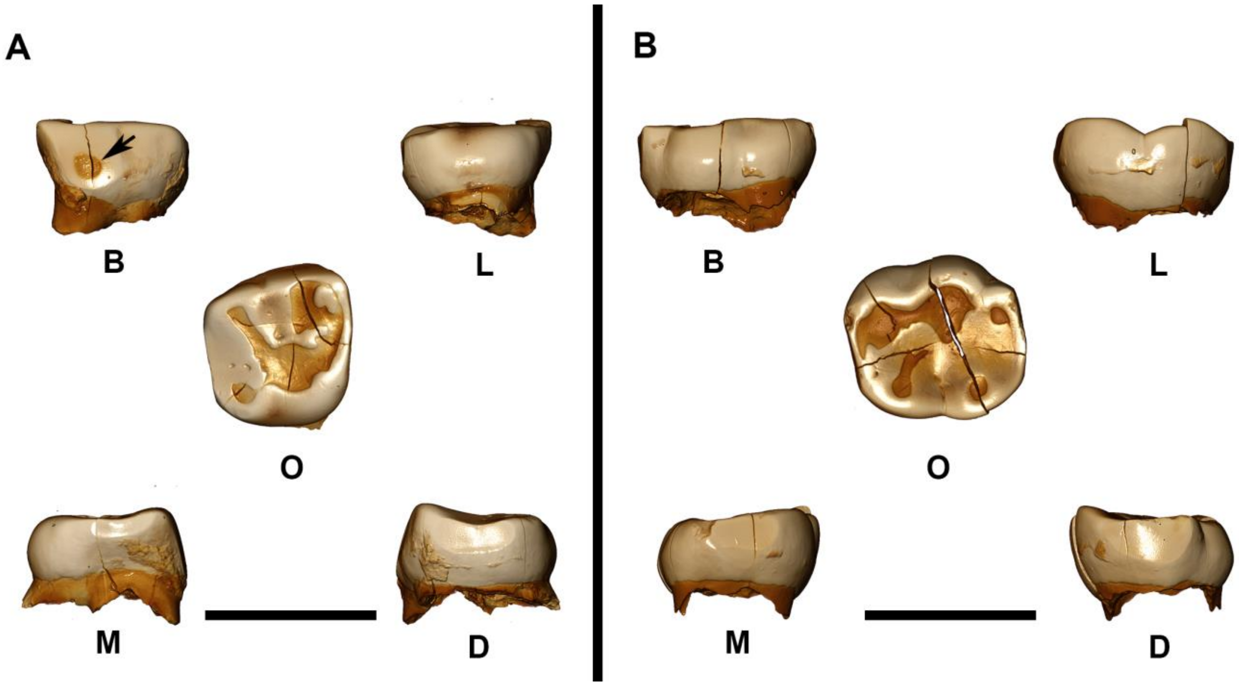

Figure 1. A) Three-dimensional digital models of Dzu 1 (upper right second deciduous molar, Rdm2); B) Three-dimensional digital model of Dzu 2 (lower right second deciduous molar, Rdm2). The black bar is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal.

Testing occlusal contacts between Dzu 1 and Dzu 2

Only three occlusal contacts are detected during maximum intercuspation in the OFA software, this suggests that the teeth do not belong to the same individual (Fig. S4; see SOM).

Satsurblia – morphological description

SATP5-2 is an upper right central deciduous incisor (Rdi^1), worn (wear stage 4), with the enamel on the mesial side chipped off and the cervical quarter of the root preserved. A longitudinal fracture, bucco-lingually directed, separates a distal portion of the tooth. (Fig. 2). From the labial view, the crown has moderate labial convexity (ASUDAS grade 3), that becomes less pronounced distally. The lingual surface is concave, and shows a distal marginal ridge (the mesial one is not visible, maybe removed by wear) and a faint median ridge, which disappears as it reaches the cervical eminence (Fig. 2). The stage of resorption is at Res ½ (the preserved portion is 3.5 mm) and suggests that the tooth had been lost ante-mortem through dental development, at an age estimated to be between six and seven years. The tooth crown has a MD diameter of 6.8 mm (minimum estimation due to wear) and a BL diameter of 5.6 mm (Table 1). At the cervix, the MD diameter is 5.5 mm and BL diameter is 4.9 mm.

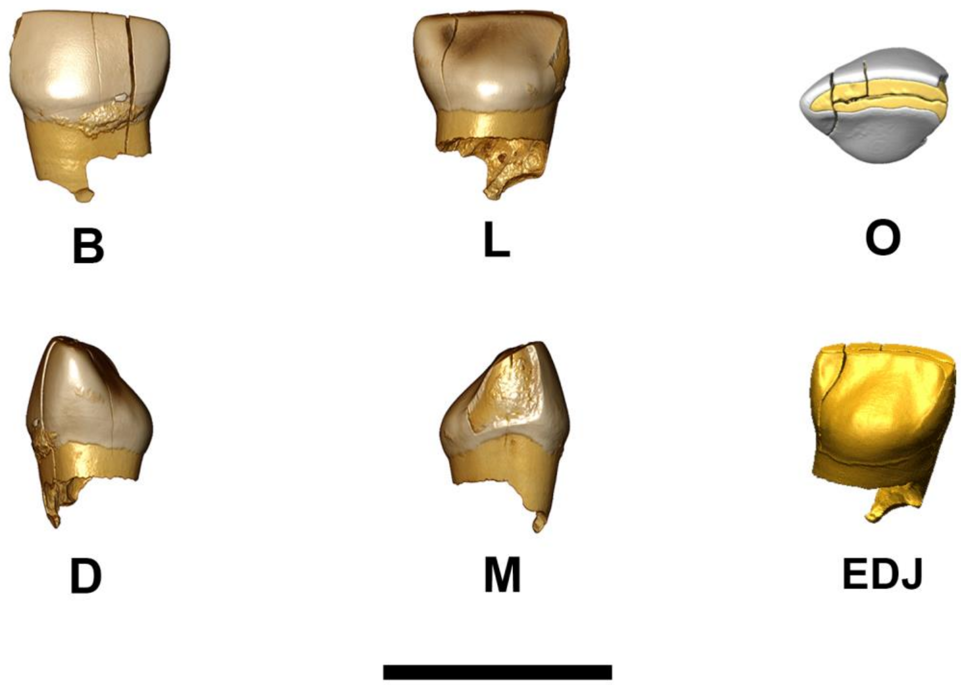

Figure 2. Three-dimensional digital model of SATP5-2 (upper right central deciduous incisor, Rdi1). The black bar is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal; EDJ, enamel-dentine junction.

Mandible

SATP5 is an incomplete left hemi-mandible with part of the body and the ramus preserved (Fig. 3A-C). In detail, the gonial region and the condyle process are missing, as well as the portion of the mandibular body in front of an imaginary line that connects the mental foramen and the alveolus of the left first incisor.

In SATP5, only the second deciduous molar (dm_2; SATP5-5) and the first molar (M_1; SATP5-6) are visible, while premolars (P_3 and P_4, respectively SATP5-3and SATP5-4) and second molar (M_2; SATP5-7) are unerupted (Table 1). The teeth are well-preserved, except for a small fracture in the P_3. The P_4 is turned upside down, probably from post-depositional repositioning that occurred within the tooth socket. Since the degree of mineralization of teeth, dental development and eruption stages correspond to an age ranging from six to seven years. On the lingual side of the hemi-mandible (Fig. 3A), the mylohyoid line runs from the unerupted M_2 till the anterior fracture. On the buccal side (Fig. 3C), the mental foramen is positioned between the interalveolar septa of the deciduous canine and the first deciduous molar.

The maximal height of the corpus is 45.7 mm and its maximal length is 69.8 mm. The height of the corpus at the level of the mental foramen is 21.4 mm, with a thickness of 5.3 mm. At the level of the M_1, the corpus height is 19 mm, with a thickness of 4.8 mm.

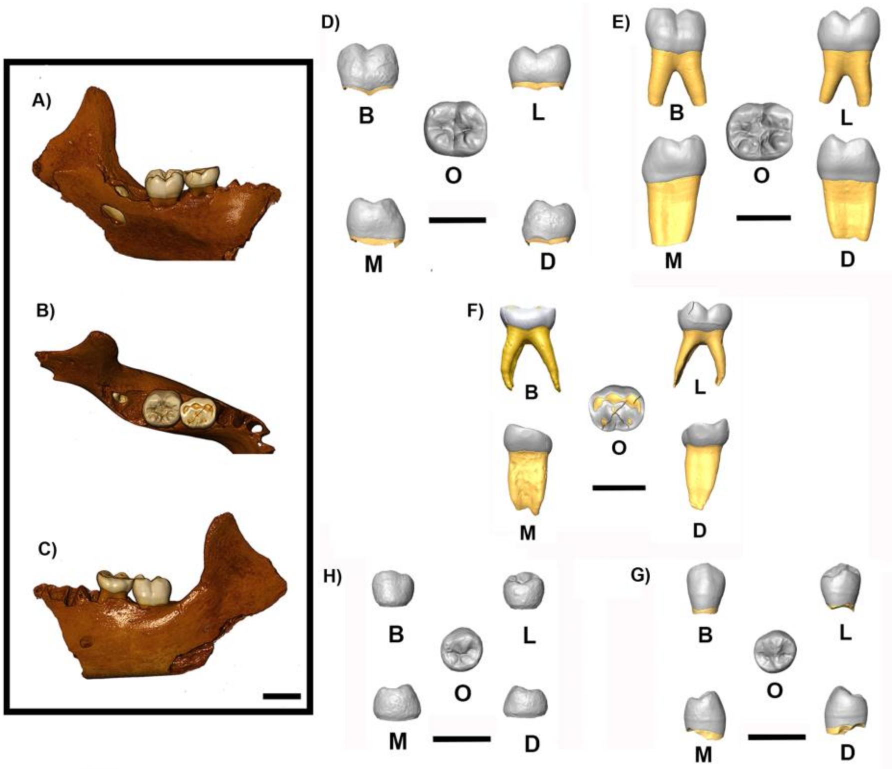

Figure 3. On the left three-dimensional digital model of Satsurblia mandible (SATP5): A) Lingual side; B) Occlusal side; C) Buccal side. On the right three-dimensional digital models of: D) SATP5-7 (lower left second molar, LM2); E) SATP5-6 (lower left first molar, LM1); F) SATP5-5

(left second deciduous molar, Ldm2); G) SATP5-3 (lower left third premolar, LP3); H) SATP5-4 (lower left fourth premolar, LP4). The black bar is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal.

SATP5-3 is a lower left third premolar (LP_3) with a complete, unerupted crown and root in earliest formation, at the Ri developmental stage (Fig. 3G). The crown is sub-circular and shows two main cusps, the protoconid larger than the metaconid, separated by a mesio-distal groove. On the EDJ, two further small dentine horns (hypoconid and entoconid) and a moderate transverse crest connecting the protoconid and metaconid (grade 2, Bailey, 2002) are visible (Fig. S5A).

The tooth crown has a MD diameter of 6.9 mm and a BL diameter of 7.5 mm (Table 1). At the cervix, the MD diameter is 4.7 mm and BL diameter is 6.5 mm.

SATP5-4 is a lower left fourth premolar (LP_4) with a complete, unerupted crown but without the root, at the Crc developmental stages (Fig. 3H). The crown has a circular occlusal outline and shows four cusps, with the metaconid equal in size to the entoconid (ASUDAS grade 4). The mesio-distal groove separates the main cusps. On the EDJ a mesial accessory ridge (MAR) borders an anterior fovea distally (Fig. S5B). The tooth crown has a MD diameter of 7.2 mm and a BL diameter of 7.9 mm (Table 1). At the cervix, the MD diameter is 4.5 mm and the BL diameter is 6.4 mm.

SATP5-5 is a lower left second deciduous molar (Ldm_2) with both crown and root preserved (Fig. 3F). The tooth shows several fractures (see SOM). While it is very worn (wear stage 4), the five principal cusps forming a Y groove pattern can be recognized, as confirmed by the EDJ. A moderate shoulder on the distal side of the metaconid (Fig. S5C) is identified as C7 (ASUDAS grade 1A). The mesial interproximal wear facets are smaller (length=1.5 mm; height=1.1 mm) than the distal one (length=1.9 mm, height=2.1 mm). On the lingual side, traces of calculus are present (Fig. 3F). The tooth crown has a MD diameter of 10 mm and a BL diameter of 8.7 mm (Table 1). At the cervix, the MD diameter is 8.3 mm and BL diameter is 7 mm. Root morphology suggests cynodontism, with root bifurcation placed at 2.7 mm from the cervix. The distal root, longer than the mesial one, measures 11.8 mm.

SATP5-6 is a lower left first molar (LM_1) with crown and root well-preserved (Fig. 3E), at the R ½ developmental stage. The tooth is slightly worn (category 2), with a weak interproximal facet on the mesial side (length=1.8 mm; height=3.4). In occlusal view, the crown has a rectangular outline and has four main well-developed cusps, an entoconulid (C6) and a faint C7 (ASUDAS grade 1A), also visible on the EDJ (Fig. S5D). The metaconid is in contact with the hypoconid, confirming the classic 4-Y groove pattern. The tooth crown has a MD diameter of 10.8 mm and a BL diameter of 10.3 mm (Table 1). At the cervix, the MD diameter is 8.3 mm and the BL diameter is 8.4 mm. The root length measures 9.5 mm on the mesial side, while 8.81 mm on the distal side.

SATP5-7 is an unerupted lower left second molar (LM_2) with a well-preserved crown and cervical quarter of the root, at the Ri development stage (Fig. 3D). The tooth has four well-developed main cusps arranged in an + pattern, and a faint shoulder identified as a C7 (ASUDAS grade 1A). From this latter develops a weak (grade 1 of Bailey et al., 2011) and continuous DTC (Type 3 following Martìnez de Pinillos et al., 2014), visible on the EDJ (Fig. S5E). The tooth crown has a MD diameter of 10.4 mm and a BL diameter of 9.7 mm (Table 1). At the cervix, the MD diameter is 8.7 mm and the BL diameter is 7.8 mm.

Table 1. Inventory of the human remains from Dzudzuana (Dzu) and Satsurblia (SATP5) caves.

Inventory no.	**Tooth class**	**MD**	**BL**	**Wear stag**	**Estimated age (years)[b]**	**Stratigraphic Unit**	**Culture**
Dzu 1	Rdm^2	9.9	10.5	5	9-12	Layer C3	Upper Palaeolithic
Dzu 2	Rdm_2	10.3	9.5	4	9-12	Layer C4	Upper Palaeolithic
SATP5-2	Rdi^1	6.8	5.6	4	6-7	Area B	Upper Palaeolithic
Mandible SATP5					6-7	Area B	Upper Palaeolithic
SATP5-3	LP_3	6.9	7.5	1			
SATP5-4	LP_4	7.2	7.9	1			
SATP5-5	Ldm_2	10.0	8.7	4			
SATP5-6	LM_1	10.8	10.3	2			
SATP5-7	LM_2	10.4	9.7	1			

[a] Molnar, 1971.

[b] AlQahtani et al., 2010.

Metric comparison

The Z score computed for the BL diameter of Dzu 1 is closer to the UPHS mean, while for Dzu 2 the Z-score is equally close to Neandertals and UPHS. The BL diameter of SATP5-2 is closer to UPHS mean while the BL diameter of SATP5-5 is closer to the RHS variability (Table 2). The permanent teeth of Satsurblia are small, falling in the range of modern humans (Fig. S6).

Table 2. BL diameters (in mm) of Dzudzuana and Satsurblia's deciduous teeth standardized to Z-scores of the hominin samples used in this study. N, Neandertal; UPHS, Upper Palaeolithic *H. sapiens*; RHS, recent *H. sapiens*.

	Dzu 1 (Rdm^2)		**Dzu 2 (Rdm_2)**		**SATP5-2 (Rdi^1)**		**SATP5-5 (Ldm_2)**	
	BL Mean (SD/*n*)	Z-score	BL Mean (SD/*n*)	Z-score	BL Mean (SD/*n*)	Z-score	BL Mean (SD/*n*)	Z-score
	10.54		9.53		5.62		8,70	
N	10.2 (0.7/13)[a]	0.48	9.4 (0.5/34)[b]	0.26	6.13 (0.35/23)[b]	-1.45	9.4 (0.5/34)[b]	-1.4
UPHS	10.4 (0.7/11)[a]	0.2	9.44 (0.35/8)[c]	0.26	5.42 (0.35/18)[b]	0.57	9.44 (0.35/8)[c]	-2.11
RHS	9.5 (0.5)[a]	2.08	8.3 (0.6/57)[b]	2.05	4.87 (0.35/47)[b]	2.14	8.3 (0.6/57)[b]	0.67

[a] Hillson and Trinkaus, 2002.

[b] Hershkovitz et al., 2011.

[c] Henry-Gambier et al., 2004.

Dzu 1 crown outline was projected into the shape-space PCA computed by Bailey and colleagues (2014) and is positioned in PCA space (first two components) within recent and the UPHS variability (Fig. 4A, B). The cross-validation LDA of the first four PCs attributes the tooth to modern human with a P_{post}=0.99. Dzu 2 and SATP5-5 crown and cervical outlines were projected in the shape-space computed by Benazzi and colleagues (2014a). Both outlines of SATP5-5 plots within *H. sapiens* variability (Fig. 4C, D). Whereas, Dzu 2 crown outline falls within *H. sapiens*

(Fig. 4C), but falls within the Neandertals variability for the cervical outline due to its bucco-distal enlargement (Fig. 4D). The cross-validation LDA of the first five PCs shows that SATP5-5 is attributed to modern human with a P_{post}=1, while Dzu2 is attributed to modern human based on its crown outline (P_{post}=1), but to Neandertals based on its cervical outline (P_{post}=0.99).

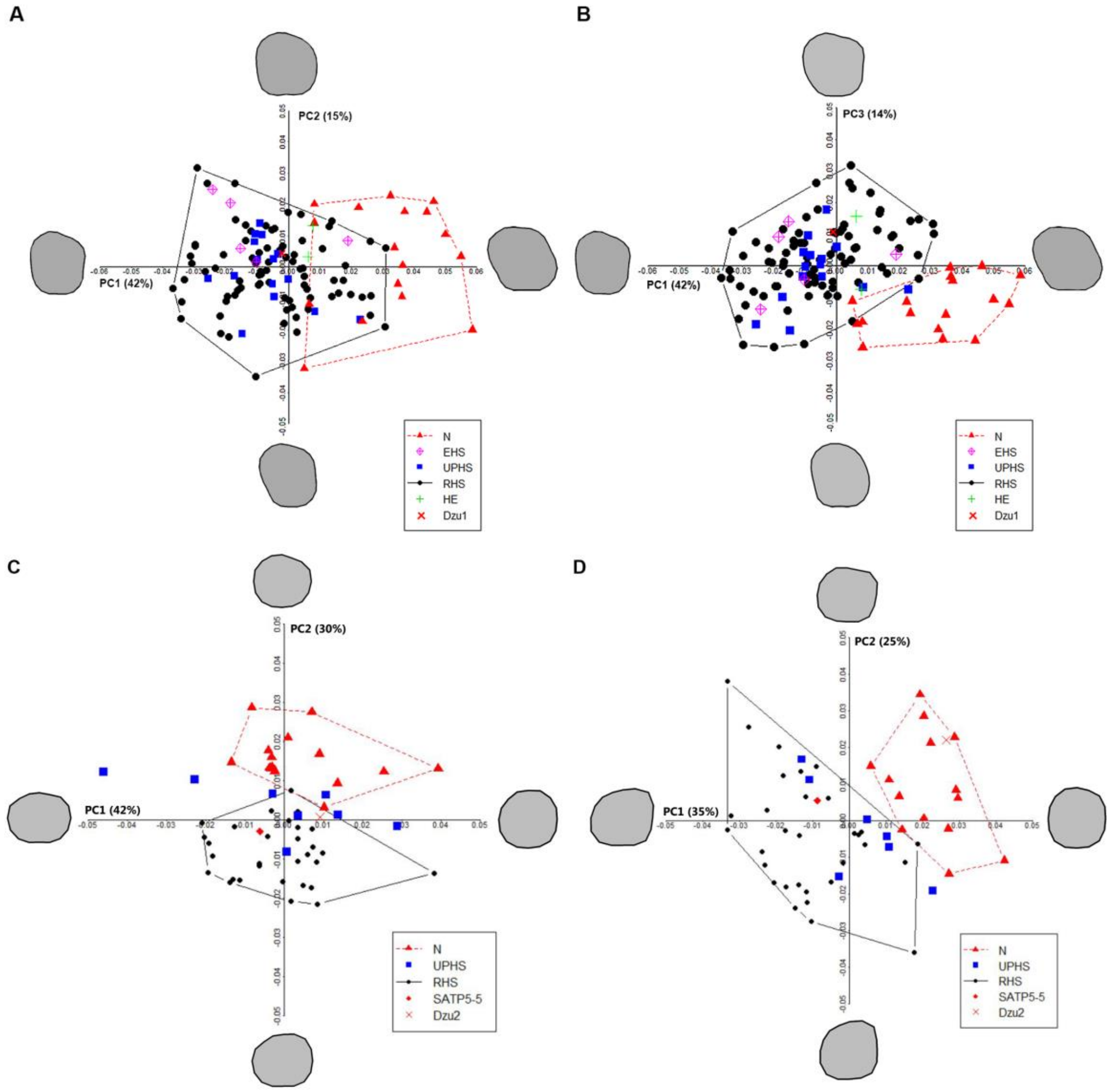

Figure 4. A, B) Shape-space PCA plots of *Homo erectus*, Neandertal and *H. sapiens* (EHS; UPHS; RHS) dms2 crown outlines. A) PC1 plotted against PC2; B) PC1 plotted against PC3. The deformed mean outlines in the four directions of the PCs are drawn at the extremity of each axis. HE, *H. erectus*; N, Neandertal; EHS, Early *H. sapiens*; UPHS, UP *H. sapiens*; RHS, recent *H. sapiens*; C, D) Shape-space PCA plots of Neandertal and *H. sapiens* (RHS and UPHS) dm2 crown

outlines (C), and cervical outlines (D). The deformed mean outlines in the four directions of the PCs are drawn at the extremity of each axis. N, Neandertal; UPHS, UP *H. sapiens*; RHS, recent *H. sapiens*.

For the 3D RET of Satsurblia permanent posterior teeth the Z-scores computed are always closer to the *H. sapiens* mean than to Neandertal ones (Table 3 and Table S2).

Table 3. Three-dimensional (3D) relative enamel thickness (RET). Satsurblia specimens are standardized to Z-scores of the Neandertals (N)and Recent *H. sapiens* (RHS) sample in different wear stages.

Taxon (n)	**n**	**Wear**[a]	**3D RET Mean (SD)**	**Z-score**
SATP5-3 (LP$_3$)		1	26.75	
N	8	1-2	18.55 (1.60)	5.12
RHS	11	1-2	24.39 (2.38)	0.99
RHS	4	3	19.60 (0.93)	7.69
SATP5-4 (LP$_4$)		1	41.46	
N	11	1-2	20.62 (2.37)	8.79
RHS	8	1-2	25.69 (2.22)	7.10
RHS	4	3	25.01 (4.46)	3.69
SATP5-6 (LM$_1$)		2	20.47	
N	8	1-2	18,61 (1.59)	1.17
N	6	3	15,86 (1.33)	3.47
N	9	4	12,21 (1.66)	4.97
RHS	8	1-2	20.17 (3.50)	0.29
RHS	8	3	16.16 (1.98)	2.18
RHS	5	4	14.30 (2.34)	2.64
SATP5-7 (LM$_2$)		1	23.7	
N	9	1-2	17.42 (2.60)	2.41
RHS	9	1-2	21.61 (1.73)	1.20

[a] Molnar, 1971.

Discussion and Conclusion

Morphological features and morphometric analyses support the attribution of the human remains from Satsurblia cave and the dm^2 from Dzudzuana cave (Dzu 1) to modern humans. Dzu 2 is more ambiguous, because though the general crown morphology aligns with modern human, the cervical outline plots within the Neandertals variability. Moreover, the evaluation of the occlusal contacts (i.e., OFA software) excludes the attribution of Dzu 1 and Dzu 2 to the same individual. Although it is more likely that Dzu 2 belongs to a modern human, further work is needed (e.g. ancient DNA) to assess the combination of modern human and Neandertal traits, probably a case of interbreeding, reported based on morphometric analysis for this specimen. It is important to note that there is no indication in the relevant archaeological contexts to suggest any 'transitional' (MP-UP) techno-cultural elements. Starting with the earliest remains uncovered in Dzudzuana, Unit D (dated to ca. 33,000 cal. BP, see SOM), there are no traces of any attributes of MP cultures. Moreover, the lithic assemblages of Unit C can be considered as a variant of the "Eastern Gravettian" and "Epi-Gravettian" complexes as the lithic industry from the Area B layers, Satsurblia, from which the human remains described here were recovered (Bar-Yosef et al., 2011; Pinhasi et al. 2014).

This particular case study has provided the opportunity to emphasize the potential of the OFA software to associate isolated teeth. In a previous contribution, two isolated teeth from Taddeo Cave (Italy) were attributed to the same individual by matching the interproximal facets in the OFA software (Benazzi et al., 2011c). This is the first study to use the OFA software for matching isolated antagonistic teeth, even though recent studies suggest that antagonists show close correspondence in macrowear pattern (Kullmer et al., 2012).

Our results also show that even though both SATP5-2 and SATP5 derive from the same layer and share the same age estimate, they should be attributed to different individuals.

In sum, the analyses of the modern human remains from Dzudzuana and Satsurblia caves provide a major addition to the UP human fossil record of Georgia and indicate the unequivocal presence of modern humans in Georgia during the Upper Palaeolithic, supporting the idea that modern humans reached the Caucasus earlier than previously thought, an assumption that until now was supported only by the tooth from the Bondi Cave (Pleurdeau et al., 2016). Even though this region is characterized by several Palaeolithic sites, only two other cave sites (Bondi cave and Sakajia) have yielded human remains from UP deposits. It is important to note that the chronological age of the teeth from Dzudzuana cave (27,000–24,000 cal. BP) falls between the currently oldest modern human tooth Bondi I (Pleurdeau et al., 2016) and the most recent human remains from Sakajia (Nioradze and Otte, 2000), filling the huge gap of more than 20,000 years.

Finally, we provide new information on the 3D enamel thickness of Neandertal and modern human lower molars and premolars at different wear stages following recent guidelines (Benazzi et al., 2014b) taking into consideration the current lack of comparative data for lower (and upper) premolars. Our results confirm that Neandertal M_2s have significantly lower RET indices than modern humans (Olejniczak et al., 2008; Smith et al., 2012). However, contrary to our expectations and previous contributions (Macchiarelli et al., 2006; Olejniczak et al., 2008; Bayle et al., 2010; Smith et al., 2012), the results do not support the same discriminatory power for the M_1, as differences between the two groups did not reach the significant level. Differences between the two groups appear pronounced in the premolars, ultimately suggesting that P_3s and P_4s represent valuable tooth classes to discriminate between Neandertals and modern humans. Interestingly, even though the small sample size prevents statistical tests, differences seem to persist at least in wear stage 3, rendering the lower post-canine dentition, and particularly the premolars, useful tooth classes even when affected by moderate dental wear.

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References

AlQahtani, S.J., Hector, M.P., Liversidge, H.M., 2010. Brief communication: The London atlas of human tooth development and eruption. American Journal of Physical Anthropology. 142, 481–490.

Bailey, S.E., 2002. A Closer Look at Neanderthal Postcanine Dental Morphology: The Mandibular Dentition. Anatomical Record. 269, 148–156.

Bailey, S.E., Skinner, M.M., Hublin, J.J., 2011. What lies beneath? An evaluation of lower molar trigonid crest patterns based on both dentine and enamel expression. American Journal of Physical Anthropology. 145, 505–518.

Bailey, S.E., Benazzi, S., Souday, C., Astorino, C., Paul, K., Hublin, J.J., 2014. Taxonomic differences in deciduous upper second molar crown outlines of *Homo sapiens*, *Homo* *neanderthalensis* and *Homo erectus*. Journal of Human Evolution. 72, 1–9.

Bar-Yosef, O., Pilbeam D., (Ed.), 2000. The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean. Volume Bulletin No. 8. Peabody Museum Press, Harvard University, Cambridge.

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

Bayle, P., Macchiarelli, R., Trinkaus, E., Duarte, C., Mazuriere, A., Zilhão, J., 2010. Dental maturational sequence and dental tissue proportions in the early Upper Paleolithic child from Abrigo do Lagar Velho, Portugal. PNAS. Vol. 107, no. 4, 1338-1342.

Benazzi, S., Coquerelle, M., Fiorenza, L., Bookstein, F., Katina, S., Kullmer, O., 2011a. Comparison of Dental Measurement Systems for Taxonomic Assignment of First Molars. American Journal of Physical Anthropology. 144, 342-354.

Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J.J., Pap, I.I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011b. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. Nature. 479, 525-528.

Benazzi, S., Viola, B., Kullmer, O., Fiorenza, L., Harvati, K., Paul, T., Gruppioni, G., Weber, G.W., Mallegni, F., 2011c. A reassessment of the Neanderthal teeth from Taddeo cave (southern Italy). Journal of Human Evolution. 61, 377-387.

Benazzi, S., Fornai, C., Buti, L., Toussaint, M., Mallegni, F., Ricci, S., Gruppioni, G., Weber, G.W., Condemi, S., Ronchitelli, A., 2012a. Cervical and crown outline analysis of worn Neanderthal and modern human lower second deciduous molars. American Journal of Physical Anthropology. 149, 537–546.

Benazzi, S., Kullmer, O., Grosse, I., Weber, G., 2012b. Brief communication: comparing loading scenarios in lower first molar supporting bone structure using 3D Finite Element Analysis. American Journal of Physical Anthropology. 147, 128-134.

Benazzi, S., Bailey, S.E., Mallegni, F., 2013a. Brief communication: A morphometric analysis of the Neandertal upper second molar Leuca I. American Journal of Physical Anthropology. 152, 300-305.

Benazzi, S., Nguyen, H.N., Schulz, D., Grosse, I.R., Gruppioni, G., Hublin, J.J., Kullmer, O., 2013b. The Evolutionary Paradox of Tooth Wear: Simply Destruction or Inevitable Adaptation? PLoS One 8, e62263.

Benazzi, S., Nguyen, H.N., Kullmer, O., Hublin, J.J., 2013c. Unravelling the functional biomechanics of dental features and tooth wear. PLoS One 8, e69990.

Benazzi, S., Bailey, S.E., Peresani, M., Mannino, M.A., Romandini, M., Richards, M.P., Hublin, J.J., 2014a. Middle Paleolithic and Uluzzian human remains from Fumane cave, Italy. Journal of Human Evolution. 70, 61-68.

Benazzi, S., Panetta, D., Fornai, C., Toussaint, M., Gruppioni, G., Hublin, J.J., 2014b. Technical

Note: Guidelines for the digital computation of 2D and 3D enamel thickness in hominoid teeth. American Journal of Physical Anthropology. 153, 305-313.

Benazzi, S., Nguyen, H.N., Kullmer, O., Hublin, J.J., 2015. Exploring the biomechanics of taurodontism. Journal of Anatomy. 226, 180-8.

Benazzi, S., Nguyen, H.N., Kullmer, O., Kupczik, K., 2016. Dynamic Modelling of Tooth Deformation Using Occlusal Kinematics and Finite Element Analysis. PLoS One 11, e0152663.

Buikstra, J.E., Ubelaker, D.H., (Ed.), 1994. Standards for data collection from human skeletal remains: procedings of a seminar at the field Museum of Natural History. Arkansas Archeological Survey Research Series No. 44.

Fiorenza, L., Nguyen, H.N., Benazzi, S., 2015. Stress Distribution and Molar Macrowear in *Pongo pygmaeus*: A New Approach through Finite Element and Occlusal Fingerprint Analyses. Human Evolution. 30, 215-226.

Henry-Gambier, D., Maureille, B., White, R., 2004. Vestiges Humains Des Niveaux De L ’ Aurignacien Ancien Du Site De Brassempouy (Landes). Bulletins et mémemoires de la Société d’Anthropologie de Paris. 16, 49-87.

Hershkovitz, I., Smith, P., Sarig, R., Quam, R., Rodríguez, L., García, R., Arsuaga, J.L., Barkai, R., Gopher, A., 2011. Middle Pleistocene dental remains from Qesem Cave (Israel). American Journal of Physical Anthropology. 144, 575-592.

Hillson, S.W., Trinkaus, E., 2002. Comparative Dental Crown Metrics. In: Zilhão, J.,Trinkaus, E.

(Eds.), Portrait of the Artist as a Child. The Gravettian Human Skeleton from the Abrigo do Lagar Velho and its Archeological Context. Trabalhos de Arqueologia Vol. 22, Instituto Português de Arqueologia, Lisboa, pp. 356-364.

Kullmer, O., Schulz, D., Benazzi, S., 2012. An experimental approach to evaluate the correspondence between wear facet position and occlusal movements. Anatomical Record. 295, 846-852.

Kullmer, O., Benazzi, S., Schulz, D., Gunz, P., Kordos, L., Begun, D.R., 2013. Dental arch restoration using tooth macrowear patterns with application to *Rudapithecus hungaricus,* from the late Miocene of Rudabánya, Hungary. Journal of Human Evolution. 64, 151-160.

Macchiarelli, R., Bondioli, L., Debenath, A., Mazurier, A., Tournepiche, J.F., Birch, W., Dean, M.C., 2006. How Neanderthal molar teeth grew. Nature. 444, 748-751.

Margherita, C., Talamo, S., Wiltschke-Schrotta, K., Senck, S., Oxilia, G., Sorrentino, R., Mancuso, G., Gruppioni, G., Lindner, R., Hublin, J.J., Benazzi, S., 2016. A reassessment of the presumed Torrener Bärenhöhle's Paleolithic human tooth. Journal of Human Evolution. 93, 120-125.

Martìnez de Pinillos, M., Martinón-Torres, M., Skinner, M.M., Arsuaga, J.L., Gracia-Téllez, A., Martínez, I., Martín-Francés, L., Bermùdez de Castro, J.M., 2014. Trigonid crests expression in Atapuerca-Sima de los Huesos lower molars: Internal and external morphological expression and evolutionary inferences. Comptes Rendus - Palevol. 13, 205-221.

Molnar, S., 1971. Human tooth wear, tooth function and cultural variability. American Journal of

Physical Anthropology. 34, 175-189.

Nioradze, M.G., Otte, M., 2000. Paleolithique superieur de Georgie. Anthropologie. 104, 265-300.

Olejniczak, A.J., Smith, T.M., Feeney, R.N.M., Macchiarelli, R., Mazurier, A., Bondioli, L., Rosas, A., Fortea, J., de la Rasilla, M., Garcia-Tabernero, A., Radovčic, J., Skinner, M.M.,Toussaint, M., Hublin, J.J., 2008. Dental tissue proportions and enamel thickness in Neandertal and modern human molars. Journal of Human Evolution. 55, 12-23.

Oxilia, G., Peresani, M., Romandini, M., Matteucci, C., Debono Spiteri, C., Henry, A.G., Schulz, D., Archer, W., Crezzini, J., Boschin, F., Boscato, P., Jaouen, K., Dogandzic, T., Broglio, A., Moggi-Cecchi, J., Fiorenza, L., Hublin, J.J., Kullmer, O., Benazzi, S., 2015. Earliest evidence of dental caries manipulation in the Late Upper Palaeolithic. Scientific Reports. 5, 12150.

Panetta, D., Belcari, N., Del Guerra, A., Bartolomei, A., Salvadori, P.A., 2012. Analysis of image sharpness reproducibility on a novel engineered micro-CT scanner with variable geometry and embedded recalibration software. Physica Medica. 28, 166-173.

Pinhasi, R., Nioradze, M., Tushabramishvili, N., Lordkipanidze, D., Pleurdeau, D., Moncel, M.-H., Adler, D.S., Stringer, C., Higham, T.F.G., 2012. New chronology for the Middle Palaeolithic of the southern Caucasus suggests early demise of Neanderthals in this region. Journal of Human Evolution. 63, 770-780.

Pinhasi, R., Meshveliani, T., Matskevich, Z., Bar-Oz, G., Weissbrod, L., Miller, C.E., Wilkinson, K., Lordkipanidze, D., Jakeli, N., Kvavadze, E., Higham, T.F.G., Belfer-Cohen, A., 2014. Satsurblia: New insights of human response and survival across the last glacial maximum in the southern caucasus. PLoS ONE. 9, e111271.

Pleurdeau, D., Moncel, M.-H., Pinhasi, R., Yeshurun, R., Higham, T., Agapishvili, T., Bokeria, M., Muskhelishvili, A., Le Bourdonnec, F.-X., Nomade, S., Poupeau, G., Bocherens, H., Frouin, M., Genty, D., Pierre, M., Pons-Branchu, E., Lordkipanidze, D., Tushabramishvili , N., 2016. Bondi Cave and the Middle-Upper Palaeolithic transition in western Georgia (south Caucasus). Quaternary Science Reviews. 146, 77-98.

Rosas, A., Bermùdez de Castro, J.M., 1999. The ATD6-5 mandibular specimen from Gran Dolina (Atapuerca , Spain). Morphological study and phylogenetic implications. Journal of Human Evolution. 37, 567-590.

Scott, R.G., Turner, C.I., 1997. The anthropology of modern human teeth. Dental morphology and its variation in recent human population. Cambridge University Press, Cambridge.

Smith, T.M., Olejniczak, A.J., Zermeno, J.P., Tafforeau, P., Skinner, M.M., Hoffmann, A., Radovcic, J., Toussaint, M., Kruszynski, R., Menter, C., Moggi-Cecchi, J., Glasmacher, U.A., Kullmer, O., Schrenk, F., Stringer, C., Hublin, J.J., 2012. Variation in enamel thickness within the genus *Homo*. Journal of Human Evolution. 62, 395-411.

Turner II, C.G., Nichol, C.R., Scott, G.R., 1991. Scoring Procedures for Key Morphological Traits of the Permanent Dentition: The Arizona State University Dental Anthropology System. In: Kelley, M.A., Larsen, C.S. (Eds.), Advances in Dental Anthropology. Wiley-Liss, New York, pp. 13-31.

Tushabramishvili, N., Pleurdeau, D., Moncel, M.H., Agapishvili, T., Vekua, A., Bukhsianidze, M., Maureille, B., Muskhelishvili, A., Mshvildadze, M., Kapanadze, N., Lordkipanidze, D., 2012. Human remains from a new Upper Pleistocene sequence in Bondi Cave (Western Georgia). Journal of Human Evolution. 62, 179-185.

Vercellotti, G., Alciati, G., Richards, M., Formicola, V., 2008. The Late Upper Paleolithic skeleton Villabruna 1 (Italy): A source of data on biology and behavior of a 14.000 year-old hunter. Journal of Anthropological Sciences. 86, 143–163.

White, T.D., Black, M.T., Folkens, P.A., (Ed.), 2012. Human Osteology, Third. ed. Elsevier. London.