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News and Views

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

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1. 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 scant 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 (calibrated years before present; Pleurdeau et al., 2016), and cranial fragments from Sakajia, dated between 12,000 and 10,000 cal. BP (Nioradze and Otte, 2000) (Supplementary Online Material [SOM] Fig. S1). Therefore, even though some authors suggest that the 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 (SOM Fig. S1): two isolated teeth from Dzudzuana cave, Dzu 1 and Dzu 2 (both deciduous; Bar-Yosef et al., 2011), and one isolated tooth (SATP5-2, deciduous) and a hemi-mandible (SATP5) bearing permanent and deciduous teeth (SATP5-3 – SATP5-7) from Satsurblia cave (Pinhasi et al., 2014). In particular, the human remains from Dzudzuana cave, dated between 27,000 and 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.

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2. Materials and methods

2.1. 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 (SOM Fig S2, S3).

2.2. 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; Martìnez de Pinillos et al., 2014). Occlusal wear stage was assessed based on Molnar (1971). For deciduous teeth, the age at death was estimated combining different observations, such as stages of tooth formation, dental eruption and root resorption using the sequences provided by Moorrees (1963) and Al Qahtani and colleagues (2010).

2.3. 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 Bermúdez de Castro, 1999). For the deciduous molars, we measured mesiodistal (MD) and buccolingual (BL) crown diameters (Benazzi et al., 2011a, 2013a; Margherita et al., 2016), and we used crown (for Dzu 1, Dzu 2 and SATP5-5) and cervical outline analyses (for Dzu 2 and SATP5-5), following methods described in Benazzi et al. (2011b; 2012a; 2014a) and Bailey et al. (2014). For the permanent teeth (but not for the deciduous teeth, which are heavily worn), we computed three-dimensional (3D) enamel thickness following guidelines provided by Benazzi et al. (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).

2.4. Metric comparison

Height and breadth of the mandibular corpus at the level of the mental foramen were compared to data gathered from the scientific literature (see SOM Table S1). The BL diameters of the deciduous teeth were compared with a sample of Neandertal, Upper Palaeolithic *Homo sapiens* (UPHS) and recent (i.e., post-Neolithic) *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 interproximal wear. For the permanent dentition, comparative datasets for MD and BL diameters were created ex novo and include Neandertal, early (i.e., pre-Upper Palaeolithic) *H. sapiens* (EHS) and RHS (SOM Table S2).

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-validated linear discriminant analysis (LDA) of the principal components, which accounted for about 90% of the total variability, to assess the taxa most closely affiliated with the Dzu 1, Dzu 2 and SATP5-5 specimens.

Comparative data for 3D enamel thickness were created ex novo and include Neandertal, EHS and RHS with different wear stages (SOM Table S2). 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 Neandertal and RHS, 3D average enamel thickness (AET) and 3D relative enamel thickness (RET) indices were analyzed using the Mann–Whitney *U* test ($\alpha = 0.05$; two-tailed) with a Monte Carlo permutation. For sample size >3 individuals, standardized scores (Z-scores) 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).

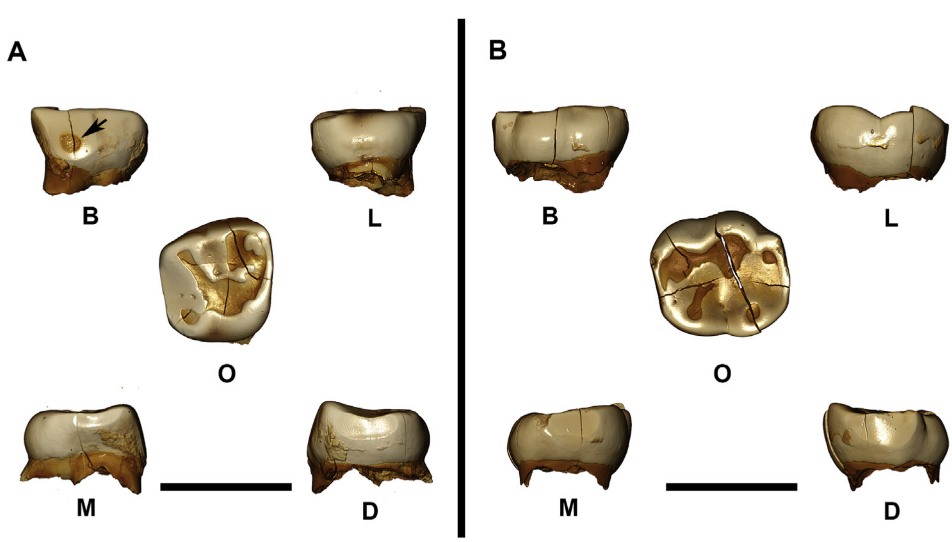

Figure 1. A) Three-dimensional digital models of Dzu 1 (upper right second deciduous molar, Rdm^2); B) Three-dimensional digital model of Dzu 2 (lower right second deciduous molar, Rdm$_2$). The horizontal black bars are equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal.