# Human deciduous teeth from the Middle Stone Age layers of Sibudu Cave (South Africa).

Alessandro Riga [1,2], Gregorio Oxilia [1,3], Daniele Panetta [4], Piero A. Salvadori [4], Stefano Benazzi [3,5], Lyn Wadley [6], Jacopo Moggi-Cecchi [1*].

*Corresponding author, e-mail: iacopo.moggicecchi@unifi.it

[1] Laboratory of Anthropology, Department of Biology, University of Florence, Via del Proconsolo 12, Firenze 50122, Italy

[2] Laboratory of Archaeoanthropology, SABAP-FI, Via de'Rossi 26/A, Scandicci (FI) 50018, Italy

[3] Department of Cultural Heritage, Laboratory of Anthropology, University of Bologna, Via degli Ariani 1, Ravenna 48121, Italy

[4] Institute of Clinical Physiology, IFC-CNR, Via G. Moruzzi 1, Pisa 56124, Italy

[5] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany

[6] Evolutionary Studies Institute, University of the Witwatersrand, PO WITS 2050, South Africa

**Abstract**

In the African Pleistocene, the fossil evidence for early *Homo sapiens* populations is still relatively limited. Here we present two additional specimens (two deciduous teeth) recovered from the Middle Stone Age (MSA) deposits of Sibudu Cave (KwaZulu-Natal, South Africa). We describe their morphology and metrics, using three-dimensional models of the teeth obtained from high-resolution micro-CT images. The first specimen is a $Ldm_1$ (HUM. TO 1) recovered in the BS5 layer dated 77.3 ± 2.7 ka, and associated with stone tools assigned to the “pre-Still Bay” assemblage. The other specimen is a $Rdi_1$ (HUM. TO 2) coming from the Pinkish Grey Sand (PGS) layer, dated 64.7±2.3 ka, and associated with a Howieson’s Poort industry. Both teeth are well preserved, with minor post mortem cracks not affecting the overall morphology, and they comprise the intact, worn crown and the remnants of the roots, naturally resorbed. A large carious lesion occupies most of the distal face and part of the occlusal surface in the $Ldm_1$; also a chip of enamel is missing from the disto-buccal corner. In the $Rdi_1$ average enamel thickness and relative enamel thickness values have been measured. For both teeth, we compared mesio-distal (MD) and bucco-lingual (BL) diameters with those of other Late Pleistocene deciduous teeth and extant *Homo sapiens*. The analysis has shown that the teeth are comparable in size with the other MSA specimens described in the literature.

**Keywords:** Sibudu Cave, deciduous teeth, Middle Stone Age, South Africa

**Short heading:** Deciduous teeth from Sibudu Cave

## Introduction

In the African Pleistocene, the fossil evidence of early *Homo sapiens* populations is still relatively limited, with specimens from 52 sites and 12 countries covering a long time span (see Grine, 2016 for a systematic review). In this scenario, South Africa contributes a fairly good record, with human fossils deriving from 15 sites. In most cases, however, the evidence is represented by isolated specimens, sometimes without good contextual data – although sites do exist where the fossil evidence is more abundant and/or particularly significant. As such, any new discovery represents an important addition to the record of the anatomy of these populations and of their variability. Among the South African sites is Sibudu Cave, near the east coast of South Africa, where a few human fossils were recorded years ago from the uppermost Middle Stone Age (MSA) layers (Plug, 2004). More recent excavations led to the recovery of two additional specimens – two deciduous teeth. Here, we describe these two teeth (a lower dm1 and a lower di1), recovered from the MSA deposits of the site. Then their measurements are compared with those of other Late Pleistocene deciduous teeth and extant *Homo sapiens*.

## Sibudu Cave

Sibudu was excavated by Lyn Wadley and a University of the Witwatersrand team between 1998 and 2011; since 2011 the site has been excavated by a team from the University of Tübingen under the direction of Nicholas Conard.

Sibudu Cave (29°31'S, 31°05'E) is a site located in the province of KwaZulu-Natal (South Africa), about 40 km north of Durban and 15 km inland from the Indian Ocean coast. It is a rock shelter above the uThongathi River, which has a deep sequence of sediments with traces of occupation from the Iron Age above the extensive MSA occupations (Wadley & Jacobs, 2004). The MSA layers offer a spectacular archaeological record, documenting a variety of innovation typical of the African MSA, among which is possibly the earliest use of bow and arrow and the use of bone needles (Backwell et al., 2008; Lombard & Phillipson, 2010; Lombard, 2011; Rots et al. 2017); the placement of medicinal plants in bedding construction (Wadley et al., 2011); the use of ornaments in the form of perforated shells beads (d'Errico et al., 2008); and the widespread use of ochre (over 9000 pieces recovered) for a variety of different tasks (Lombard, 2007; Hodgskiss, 2012; Hodgskiss, 2013; Wadley & Langejans, 2014; Soriano et al., 2009; Wadley, 2015).

In the MSA, Sibudu was occupied discontinuously, either due to environmental conditions or as a result of small populations paying infrequent visits to the area (Jacobs et al., 2008 a; Chase, 2010; Wadley, 2012; Wadley, 2015). Nonetheless, repeated site visits in the MSA produced many technocomplexes: pre-Still Bay, Still Bay, Howiesons Poort, post-Howiesons Poort, late and final MSA assemblages from about 77,000 years (77 ka) ago to 38 ka ago (Jacobs et al., 2008 a,b; Wadley, 2012). Two layers and technocomplexes excavated by Wadley are highlighted in this paper. These layers are BS5 from the Brown Sand (BS) member with a pre-Still Bay stone tool assemblage, and layer Pinkish-Grey Sand (PGS) with a Howiesons Poort Industry. On the one hand, the pre-Still Bay lithic assemblage at the base of the sequence is rather difficult to define typologically for it lacks bifacial points and there are only rare retouched tools. The Howiesons Poort Industry, on the other hand, is blade-rich, has many backed tools, like segments and other geometric pieces. The backed tools were hafted and probably used in innovative ways as hunting weapons (Backwell et al. 2008).

*Stratigraphy*

Fine-resolution excavation was carried out so the teeth examined here have secure contexts. Site sediments were distinguished by colour (using the Munsell Colour chart) and texture. Where members had fairly homogeneous strata in terms of colour and texture, they were subdivided into centimetre-thick layers based on superimposed 'pavements' of lithics. Member BS is an example. It was divided into sixteen layers, BS1 to BS16, and the relevant layer here is BS5. BS is loose, brown sand (7.5YR 4/3 brown on the Munsell chart) with rock spalls and many encroaching rocks. PGS is loose, pinkish-grey sand (5 YR 5/2 pinkish grey on the Munsell chart), with few rock spalls. Layers BS5 and PGS are separated by at least 50 cm of intervening sediment (Fig. 1) and the ages for each layer imply that the occupations were about 12 ka apart. The stratigraphic observations are important for understanding the integrity of the fossil contexts, and the relationship between the human teeth described here.

*Age*

Sediment samples were collected from the site and quartz grains taken from these were processed in the University of Wollongong laboratory for single grain optically stimulated luminescence (OSL) dating. Extraction, processing and statistical calculation are described elsewhere (Jacobs et al., 2008a, Jacobs & Roberts, 2017).

OSL sample SIB 23 (77.3 ± 2.7 ka) is from BS; OSL sample SIB 19 (64.7 ± 2.3 ka) is from PGS (Jacobs et al., 2008a).

*Human fossils*

Plug (2004) conducted a faunal analysis of Sibudu Cave materials excavated in the first few years of the Wadley excavation. She reported two human remains (a lateral malleolus of a fibula and the distal phalanx of an adult hand) from the final MSA sediments (49 ka). Slightly earlier MSA sediments (58 ka) yielded a toe phalanx and a fragment of a putative human sternum (Plug, 2004). Plug recorded that the human bone looks more recent than animal bones in the same layers and she thought that it might be intrusive from the overlying Iron Age occupation. Wadley acknowledges this likelihood, but has not discounted the possibility that the remains may be of MSA origin (Grine, 2016) because the Iron Age pits into the final MSA layers were carefully excavated before taking out MSA material. In the absence of chemical tests, the issue cannot be resolved.

Subsequently, during continued excavations, the two deciduous human teeth presented here were recovered from older, much deeper MSA layers where no Iron Age contamination could have occurred. The first (catalogue number 2931CA 15 HUM. TO 1, hereafter HUM. TO 1) is a lower left first molar ($Ldm_1$), deriving from the pre-Still Bay BS member (Square B4b, layer Brown Sand 5 base), with an age of 77.2 ± 2.2 ka. The second tooth (catalogue number 2931CA 15 HUM. TO 2 hereafter HUM. TO 2) is a lower right central incisor ($Rdi_1$), from the Howiesons Poort PGS layer (Square C4a, layer Pinkish Grey Sand), with an estimated age of 64.7 ± 2.3 ka (Wadley, 2015).

## Methods

### *Acquisition of virtual images*

High-resolution micro-CT images of all the teeth were obtained with the Xalt micro-CT scanner (Panetta et al., 2012). The most relevant scanning parameters were 50 kVp, 2 mm Al filtration, 960 projections over 360°, 0.9 mAs/projection for a total scan time of 50 minutes per sample. All the tomographic images were reconstructed using a modified Feldkamp algorithm with embedded correction for geometric misalignment (Feldkamp et al., 1984; Panetta et al., 2008) and raw data pre-correction for beam-hardening and ring artefacts reduction. All images were reconstructed on a volume dataset of 600x600x1000 cubic voxels, each with a size of 18.4 $\mu m^3$.

### *Measurements*

Mesio-Distal (MD) and Bucco-Lingual (BL) crown diameters of both teeth were measured using a digital caliper. Whereas the $Ldm_1$ is heavily worn, for the $Rdi_1$ it has been possible to compute enamel thickness following the guidelines provided by Benazzi *et al.* (2014). We measured enamel volume, dentine volume (including also the volume of the crown pulp chamber), and Enamel-Dentine Junction (EDJ) surface; then, we computed both the Average Enamel Thickness index (AET = volume of enamel divided by the EDJ surface) and the Relative Enamel Thickness index (RET = AET divided by the cubic root of dentine volume).

*Comparisons and statistical analyses*

We compared the crown diameters of the Sibudu teeth with those of other Pleistocene fossil specimens and extant *Homo sapiens* (EHS) (Tab. 1, Tab. 2 and Appendix).

The RET value obtained for the $Rdi_1$ was compared with those of Neandertals, Pleistocene *Homo sapiens* and EHS published by Fabbri et al. (2016).The wear stage was assessed following Molnar (1971): it ranges from 1 to 2 (unworn-wear facets minimal in size), 3 (cusp pattern partially or completely obliterated), 4 (dentine patch-minimal) and 5 (dentine patch-extended).

The significance of the differences among groups in the MD and BL diameters was tested through multivariate analysis of variance (MANOVA), using the Pillai-Bartlett statistic (as suggested by Hand & Taylor, 1987). For the RET comparisons we calculated the standard score (Z score) of the $Rdi_1$ with respect to the other samples, and used that score to assess the similarities. All statistical analyses were performed using R (R Core Team 2017).

## Anatomical description

*Abbreviations*

In describing the dental morphology the following abbreviations have been used: Orientation: bucco-lingual (BL), mesio-distal (MD), occlusal-cervical (OC), inciso-cervical (IC). Cusps: protoconid (PR), entoconid (EN), metaconid (ME), hypoconid

(HY), hypoconulid (HYPL). Other features: marginal ridge (MR), interproximal contact facet (ICF), cervical enamel line (CEL).

*2931CA 15 HUM. TO 1 (Ldm$_1$)*

The specimen comprises the intact crown and the remnants of the roots that have been resorbed (Fig. 2a). Preservation is very good, with minor post mortem cracks across the surface not affecting the overall morphology. The occlusal wear is marked, however, with large, confluent areas of dentine exposed on the PR, HY, HYPL and EN, and, to a lesser extent, on the ME. Dentine is also exposed at the level of the mesial MR. The mesial ICF is very faint. A large carious lesion occupies most of the distal face, also extending to the most distal part of the occlusal surface. A chip of enamel is missing from the disto-buccal corner; flaking must have occurred *in vitam*, since the edges of the enamel are smooth. The occlusal outline is oval, with some degree of MD compression and mesio-buccal extension. The fissures among the five cusps are still evident. Although worn, PR must have been the largest cusp, followed by the EN, HY and HYPL. Distal to the ME tip, dentine exposure and enamel thickening are suggestive of the occurrence of a postmetaconulid. The PR is mesially placed in relation to the ME. Although worn, the mesial MR must have been very thick. The anterior fovea, lingually placed to the midline, is reduced to a fissure that opens lingually just in front of the ME. Remnants of what must have been a deep central fovea are evident, mesial to the EN. On the buccal face the *tuberculum molare* is fairly well developed, with a notable mesio-buccal extension. The CEL curves around the *tuberculum molare*, climbing distally at the level of the HY. The presence and extent of development of the buccal grooves cannot be ascertained because of wear. The lingual face is markedly convex MD and OC, bulging at the level of the ME. The mesial face is featureless, except for the tiny ICF. Only a few millimetres of the root system are present. The sharp edges of the root remnants and the scooping of its internal surface indicate that the roots have been naturally resorbed, causing the tooth to be shed. Shedding of $dm_1$ in modern humans occurs when the first permanent premolar emerges in the mouth, an event that averages around 10.5-11.5 years of age (AlQahtani *et al.*, 2010), although with a wide range of variability.

*2931CA 15 HUM. TO 2 (Rdi$_1$)*

The specimen has an intact crown and remnants of the partially resorbed root (Fig. 2b). Preservation is very good, with only minor post mortem cracks across the surface, not affecting the overall morphology. The incisal wear is marked, with the flat wear plane tilted slightly distally. The exposed dentine measures 1.3 mm BL at its largest point. Its profile tapers distally, truncated by a marked, distal ICF (BL 0.8 IC 1.5). The mesial ICF is faint. The labial face has a square shape (*sensu* Grine, 1984), in that the mesial and distal edges are almost parallel and the almost straight cervical enamel line does not extend much cervically. The face is slightly convex IC, and more so MD. The MD convexity is slightly skewed distally. Numerous microscratches cross it, with different orientations, visible under a microscope. On the lingual face the cervical eminence is well developed and symmetrically placed. From it a faint median ridge moves toward the incisal edge. Both the mesial and the distal MR are thick, but low. The preserved root is subtriangular in cross section, tapering lingually. Some 4.1 mm of it are still present on the labial side and 1.1 mm on the lingual side.

The root has sharp edges and its internal surface is scooped, suggesting that the root might has been naturally resorbed, possibly having caused the shedding of the tooth. Shedding of $di_1$ in modern humans occurs when the first permanent incisor emerges in the mouth, that is on average around 5.5-6.5 years of age (AlQahtani *et al.,* 2010).

**Comparative dental crown metrics**

*2931CA 15 HUM. TO 1 (Ldm1)*

The estimated MD diameter of the $Ldm_1$ is 8.9 mm (8.7 mm as measured) and the BL diameter is 7.2 mm. These values fall into the size range of the other specimens of the South African MSA from Die Kelders (AP6246 and AP6291) and Diepkloof Rock Shelter (DRS 3). Together with the South African specimens, other lower dm1 are available in the Late Pleistocene human fossil record. Table 1 shows the mean values of MD and BL diameters for specimens belonging to different populations, plus four samples of modern human populations (American Whites, Australian Aboriginals, South Africans and San). Inspection of the data indicates some dental size differences between groups in regard to the mean MD diameter (Fig. 3): Middle Paleolithic (MP) samples (Qafzeh and Skhul) display the highest value, while South African MSA, early Upper Paleolithic Aurignacian (EUPA) and early Upper Paleolithic Gravettian (EUPG) show similar values; late Upper Paleolithic (LUP, i.e. Epigravettian and Magdalendian) have the lowest values, and are not dissimilar from extant populations; Iberomaurusian (IBM) specimens have intermediate values between the latter two. No comparable differences seem to exist in the BL mean values. A scatterplot of the two variables (MD and BL) (Fig. 4a) emphasizes the results.

The differences observed between populations have been tested with a MANOVA, which suggests significant differences both for the interaction of MD and BL ($p<0.01$) and for MD alone ($p<0.001$). The MP sample is the one that diverges most from the other samples and this could affect the analysis. Thus, we repeated the MANOVA excluding the MP samples to test whether the significance persists; the results give significance ($p<0.05$) only for the interaction of the two variables analysed. This means that, even if the differences observed are largely linked to the high MD values of the MP specimens, crown diameters nevertheless reveal some differences between the populations.

*2931CA 15 HUM. TO 2 (Rdi1)*

The corrected MD diameter of the $Rdi_1$ is 4.9 mm (4.7 mm as measured) and the BL is 4.3 mm. Compared to the other specimen of the MSA (AP6290 from Die Kelders) the Sibudu specimen is smaller in both diameters (Tab. 2). The specimens used for comparison are plotted in Figure 4b. Different populations seem to cluster together: MSA in the right portion of the plot, with higher MD diameter; IBM, EUP and LUP occupy the central part, with intermediate MD values; MP and EHS have low MD and are positioned on the left portion of the plot. The BL diameter does not seem to distinguish the different groups. The MANOVA confirms these observations giving significant p-values only in the case of MD ($p<0.01$).

The relative enamel thickness (RET) index of $Rdi_1$ and the comparative samples are presented in Table 3. The Z-score computed for the $Rdi_1$ places the tooth close to EHS at wear stage 4; however, if we also consider Late Pleistocene *H. sapiens* and

Neandertals the range of RET values among these species overlaps and the Sibudu specimen falls within the range of variability of both species.

## Discussion and conclusions

The South African MSA human fossil record includes remains from 15 sites (Grine, 2016; Grine et al., 2017), among these, Sibudu Cave, from where a few, undescribed specimens have been reported (Plug, 2004). Thus any addition to this record, for example the two deciduous teeth described here, is important, since it allows us to understand better the anatomical features of early populations of *Homo sapiens* and their variability. Of the two deciduous teeth from Sibudu Cave, the $Ldm_1$ comes from the layer BS5 that is dated at around 77.2±2.2 ka and it is associated with pre-Still Bay lithic assemblages; it is thus the oldest of the four deciduous first molars from the South African MSA described so far in the literature (see above). The $Rdi_1$ comes from the PGS layers, which are dated at 64.7±2.3 and it is associated with a Howiesons Poort assemblage (Wadley 2015). Hence, the two specimens come not only from different individuals, but also from different populations that occupied the site in different times. The two specimens, deriving from juvenile individuals, add to the MSA deciduous dental sample from other South African sites, and confirm the observation by Grine et al. (2016) that juvenile individuals (largely represented by deciduous teeth) are relatively more abundant than adult specimens at other MSA South African sites (Die Kelders Cave 1, Blombos and Klipdrift Shelter), with the notable exception of remains from Klasies Main Site.

The comparative metrical analysis has provided interesting results. Both teeth cluster with the other MSA specimens from South Africa, especially for MD diameters. In particular, in the metrical study of $dm_1$ a few points are relevant since they derive from the analysis of deciduous teeth, which are recognized as more conservative in their morphology than permanent teeth (Brabant, 1967; von Koenigswald, 1967; Margetts & Brown, 1978; Smith, 1978; Aiello & Dean, 1990; Hemphill, 2015; Bailey et al., 2016). As such, deciduous teeth are more informative than permanent ones when addressing taxonomic and evolutionary issues.

First, the MSA populations show similar mean MD values to EUP European populations, both Aurignacian and Gravettian, the latter two having almost identical mean values. Secondly, the MSA/EUP $dm_1$ is smaller than the mean value for MP populations. The similarities in size with Upper Paleolithic specimens, and the differences with the MP sample have also been noted by Verna et al. (2013) in their description of the Diepkloof Rock Shelter (DRS 3) specimen. Thirdly, MSA/EUP samples differ from both LUP and IBM populations, both having smaller mean values than the earlier groups. Of broader significance, it is interesting to note the similarities between the MD values of the Aurignacian and Gravettian (EUP) samples and the smaller mean values of the Epigravettian and Magdalenian samples (LUP). This points to a pattern of reduction taking place between EUP and LUP already noted by Frayer (1978) for dentition and aspects of cranial and postcranial dimensions (see Holt & Formicola, 2008 for a review). A similar pattern seems to exist when comparing MSA and IBM. Lastly, the mean value for the four EHS samples is even smaller, and is notably distinct from all earlier samples. At the same time the BL mean values do not show a similar pattern. In the $di_1$, the MSA and the other samples are too limited to carry out any analysis, although differences between the fossil samples and the EHS are apparent, with the latter being smaller than the former.

In conclusion, the two deciduous teeth described here, a $dm_1$ and a $di_1$, expand the still limited sample of fossil human skeletal remains from the African Late Pleistocene. The analysis has shown that they are comparable in size with the other MSA specimens described in the literature. In the case of the $dm_1$ metrical differences among samples of fossil and extant populations have been highlighted.


***Acknowledgments***

*We would like to thank Shara Bailey and Vincenzo Formicola for sharing with us the raw data of the deciduous dentition from Le Figuier (S.B.) and Arene Candide (V.F.). We are grateful to Lucinda Backwell for help in many stages of the project and to Jamie Clark who first recognised that the teeth might be human when she was making a preliminary sort of the faunal remains.*


**Author Contribution**

A.R. and J.M.C. designed research; D.P. and P.A.S. performed microCT analysis; G.O., S.B., A.R., J.M.C. performed digital and metrical data analysis; L.W. provided archeological and stratigraphical information; all authors wrote the paper.

**References**


Aiello L. & Dean C. 1990. *An introduction to human evolutionary anatomy*. Academic Press, Cambridge MA.

AlQahtani S.J., Hector M.P. & Liversidge H.M. 2010. The London atlas of human tooth development and eruption. *Am. J. Phys. Antrhopol.,* 142: 481-490.

Backwell L.R., d'Errico F. & Wadley L. 2008. Middle Stone Age bone tools from the Howiesons Poort layers, Sibudu Cave, South Africa. *J. Archaeol. Sci.,* 35: 1566-1580.

Bailey S.E., Benazzi S., Buti L. & Hublin J.J. 2016. Allometry, Merism and tooth shape of the lower second deciduous molar and first permanent molar. *Am. J. Phys. Anthropol.,* 159: 93-105.

Bayle P. 2008. *Analyses quantitatives par imagerie à haute résolution des séquences de maturation dentaire et des proportions des tissus des dents déciduales chez les Néanderthaliens et les Hommes modernes.* Ph.D. Dissertation, University of Toulouse III.

Bayle P., Braga J., Mazurier A. & Macchiarelli, R. 2009. Brief communication: High resolution assessment of the dental developmental pattern and characterization of tooth tissue proportions in the late Upper Paleolithic child from La Madeleine, France. *Am. J. Phys. Anthropol.,* 138: 493-498.

Benazzi S., Panetta D., Fornai C., Toussaint M., Gruppioni G. & Hublin J.J. 2014. Technical note: guidelines for the digital computation of 2D and 3D enamel thickness in hominoid teeth. *Am. J. Phys. Anthropol.,* 153: 305-313.

Black T.K. III 1978. Sexual dimorphism in the tooth-crown diameters of the deciduous teeth. *Am. J. Phys. Anthropol.,* 48: 77-82.

Brabant H. 1967. Comparison of the characteristic and anomalies of the deciduous and the permanent dentition. *J. Dent. Res.,* 46: 897-902.

Chase B.M. 2010. South African palaeoenvironments during marine ocygen isotope stage 4: a context for the Howiesons Poort and Still Bay industries. *J. Archaeol. Sci.,* 37: 1359-1366.

d'Errico F., Vanhaeren M. & Wadley L. 2008. Possible shell beads from the Middle Stone Age layers of Sibudu Cave, South Africa. *J. Archaeol. Sci.,* 35: 2675-2685.

Fabbri P.F., Panetta D., Sarti L., Martini F., Salvadori P.A., Caramella D., Fedi M. & Benazzi S. 2016. Middle paleolithic human deciduous incisor from Grotta del Cavallo, Italy. *Am. J. Phys. Anthropol.,* 161: 506-512.

Favati-Vanni V. 1964. Studio antropologico dello scheletro d'un bambino del Paleolitico superiore, rinvenuto nella Grotta Maritza presso Avezzano. *Atti. Soc. Toscana Sc Nat. Ser B,* 71: 475-487.

Feldkamp I.A., Davis L.C. & Kress J.W. 1984. Practical cone-beam algorithm. *J. Opt. Soc. Am. A,* 1: 612-619.

Formicola V. 1986. Anthropologie dentaire des restes de l'Epigravettien final retrouvés dans la grotte des Arene Candide (Ligurie). *Bull. Mem. Soc. Anthrop. Paris,* 3: 37-46.

Frayer D.W. 1978. *The Evolution of Dentition in Upper Paleolithic and Mesolithic Europe.* University of Kansas Publications in Anthropology, No. 10.

Grine F.E. 1984. *The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene hominids.* Ph.D. Dissertation, University of the Witwatersrand.

Grine F.E. 2000. Middle Stone Age human fossils from Die Kelders Cave 1, Western Cape Province, South Africa. *J. Hum. Evol.,* 28: 129-145.

Grine F.E. 2016. The Late Quaternary Hominins of Africa: The Skeletal Evidence from MIS 6-2. In S.C Jones & B.A. Stewart (eds.): *Africa from MIS 6-2. Population Dynamics and Paleoenvironments*, pp. 323-381. Springer, Netherlands.

Grine F.E., Wurz S. & Marean C.W. 2017. The Middle Stone Age human fossil record from Klasies River Main Site. *J. Hum. Evol.,* 103: 53-78.

Hemphill B.E. 2015. Measurement of Tooth Size (Odontometrics). In J.D. Irish & G.R. Scott (eds.): *A Companion to Dental Anthropology,* pp.287-310. Wiley-Blackwell.

Hand D.J. & Taylor C.C. 1987. *Multivariate Analysis of Variance and Repeated Measures: a practical approach for behavioural scientists.* Chapman and Hall, London.

Henry-Gambier D. 2001. *Les enfants de Grimaldi (grotte des Enfants, site des Baoussé-Roussé, Italie), Anthropologie et palethnologie funéraire.* CTHS/RMN, Paris.

Henry-Gambier D., Maureille B. & White R., 2004. Vestiges humains des niveaux de l'Aurignacien ancien du site de Brassempouy (Landes). *B. Mem. Soc. Anthro. Par.,* 16: 49-87.

Hillson S.W., Trinkaus E. 2002. Comparative Dental Crown Metrics. In J. Zilhão & E. Trinkaus (eds.): *Portrait of the Artist as a Child,* pp. 356-364. Instituto Português de Arqueologia, Lisboa.

Hodgskiss T. 2012. Attribute analysis of the Sibudu Middle Stone Age ochre assemblage. *S. Afr. Humanit.,* 24: 99-120.

Hodgskiss T. 2013. Ochre use in the Middle Stone Age at Sibudu, South Africa: grinding, rubbing, scoring and engraving. *J. Afr. Archaeol.,* 11: 75-95.

Holt B.M., Formicola V. 2008. Hunters of the Ice Age: The Biology of Upper Paleolithic People. *Yearb. Phys. Anthropol.,* 51: 70-99.

Jacobs Z., Roberts R.G., Galbraith R.F., Deacon H.J., Grün R., Mackay A., Mitchell P. & Wadley L. 2008a. Ages for the Middle Stone Age of southern Africa: implications for human behaviour and dispersal. *Science,* 322: 733-735.

Jacobs Z., Wintle A.G., Duller G.A.T., Roberts R.G. & Wadley L. 2008b. New ages for the post-Howiesons Poort, late and final Middle Stone Age at Sibudu Cave, South Africa. *J. Archaeol. Sci.,* 35: 1790-1807.

Jacobs Z. & Roberts R.G. 2017. Single-grain OSL chronologies for the Still Bay and Howieson's Poort industries and the transition between them: Further analyses and statistical modelling. *J. Hum. Evol.,* 107: 1-13.

von Koenigswald G.H.R. 1967. Evolutionary trends in the deciduous molars of the hominidea. *J. Dent. Res.,* 46: 779-786.

Lombard M. 2007. The gripping nature of ochre: the association of ochre with Howiesons Poort adhesive and Later Stone Age mastics from South Africa. *J. Hum. Evol.,* 53: 406-419.

Lombard M. 2011. Quartz-tipped arrows older than 60 ka: further use-trace evidence from Sibudu, KwaZulu-Natal, South Africa. *J. Archaeol. Sci.,* 38: 1918-1930.

Lombard M. & Phillipson L. 2010. Indications of bow and stone-tipped arrow use 64,000 years ago in KwaZulu-Natal, South Africa. *Antiquity,* 84: 635-648.

Margetts B. & Brown T. 1978. Crown diameters of the deciduous teeth in Australian Aboriginals. *Am. J. Phys. Anthropol.,* 48: 493-502.

Molnar S. 1971. Human Tooth Wear, Tooth Function and Cultural Variability. *Am. J. Phys. Anthropol.,* 34: 175-190.

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

Panetta D., Belcari N., Del Guerra A., Moehrs S. 2008. An optimization-based method for geometrical calibration in cone-beam CT without dedicated phantoms. *Phys. Med. Biol.,* 53: 3841-61.

Plug I. 2004. Resource exploitation: animal use during the Middle Stone Age at Sibudu Cave, KwaZulu-Natal. *S. Afr. J. Sci.,* 100: 151-158.

R Core Team 2017. *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna.

Rots V., Lentfer C., Schmid V.C., Porraz G., Conard N.J. 2017. Pressure flaking to serrate bifacial points for hunt during the MIS5 at Sibudu Cave (South Africa). PLoS ONE, 12: e0175151.

Smith P. 1978. Evolutionary changes in the deciduous dentition of near eastern populations. *J. Hum. Evol.,* 7: 401-408.

Soriano S., Villa P. & Wadley L. 2009. Ochre for the toolmaker: Shaping the Still Bay points at Sibudu (KwaZulu-Natal, South Africa). *J. Afr. Archaeol.,* 7: 41-54.

Teschler-Nicola M.E., Antl-Weiser W. & Prossinger H. 2004. Two Gravettian human deciduous teeth from Grub/Kranawetberg, Lower Austria. *Homo,* 54: 229-239.

Tillier A.M. 1999. *Les enfants moustériens de Qafzeh. Interprétation phylogénétique et paléoauxologique.* CNRS Éditions, Paris.

Trinkaus E., Bailey S.E., Davis S.J.M. & Zilhão J. 2011. The Magdalenian Human Remains from the Galeria da Cisterna (Almonda karstic system, Torres Novas, Portugal) and their Archaeological Context. *Arqueol. Port.,* 1: 395-413.

Trinkaus E., Buzhilova A.P., Mednikova M.B. & Dorbrovolskaya M.V. 2014. *The People of Sunghir. Burials, Bodies and Behavior in the Earlier Upper Paleolithic.* Oxford University Press, New York.

Verna C., Texier P.J., Rigaud J.P., Poggenpoel C. & Parkington J. 2013. The Middle Stone Age human remains from Diepkloof Rock Shelter (Western Cape, South Africa). *J. Archaeol. Sci.,* 40: 3532-3541.

Wadley L. 2012. Two ‘moments in time’ during Middle Stone Age occupations of Sibudu, South Africa. *S. Afr. Humanit.,* 24: 79-97.

Wadley L. 2015. Those marvellous millennia: the Middle Stone Age of Southern Africa. *Azania,* 50: 155-226.

Wadley L. & Jacobs Z. 2004. Sibudu Cave, KwaZulu-Natal: background to the excavations of Middl Stone Age and Iron Age occupations. *S. Afr. J. Sci.,* 100: 145-151.

Wadley L. & Langejans G. 2014. Preliminary study of scrapers around combustion features in layer SS, Sibudu, 58,000 years ago. *S. Afr. Archaeol. Bull.* 69: 19-33.

Wadley L., Sievers C., Bamford M., Goldberg P., Berna F. & Miller C. 2011. Middle Stone Age bedding construction and settlement patterns at Sibudu, South Africa. *Science*, 334: 1388-1391.

Wilczyński J., Szczepanek A., Wojtal P., Diakowski M., Wojenka M. & Sobieraj D. 2014. A Mid Upper Palaeolithic Child Burial from Borsuka Cave (Southern Poland). *Int. J. Osteoarchaeol.,* 26: 151-162.

**Info on the web**

Voisin J.L., Condemi S., Wolpoff M.H. & Frayer D.W. Human fossil teeth. Online database, http://anthropologicaldata.free.fr. Last access 23 October 2017.

## Tables

Table 1. Mean mesiodistal (MD) and buccolingual (BL) diameters (in mm) of deciduous first mandibular molars in Late Pleistocene *Homo sapiens* fossil specimens and extant samples. The left $dm_1$ from Sibudu (2931CA 15 HUM. TO 1, MD=8.9, BL=7.2) is included in the MSA sample. See Appendix for the list of the fossil specimens with individual values and references.

| **Sample** | **MD** | **n** | **sd** | **BL** | **n** | **sd** |
|---|---|---|---|---|---|---|
| **Middle Stone Age (MSA)** | 8.75 | 4 | 0.44 | 7.17 | 4 | 0.52 |
| **Middle Paleolithic (MP)** | 9.23 | 7 | 0.27 | 7.50 | 7 | 0.58 |
| **Iberomaurusian (IBM)** | 8.38 | 4 | 0.53 | 7.72 | 4 | 0.41 |
| **Early Upper Paleolithic (EUP)** | 8.77 | 10 | 0.37 | 7.11 | 11 | 0.43 |
| **Late Upper Paleolithic (LUP)** | 8.20 | 5 | 0.58 | 7.10 | 5 | 0.35 |
| **American Whites** | 7.80 | 133 | 0.42 | 7.34 | 133 | 0.46 |
| **Australian Aboriginals** | 8.19 | 179 | 0.53 | 7.71 | 185 | 0.51 |
| **South Africans** | 8.22 | 35 | 0.50 | 7.13 | 38 | 0.39 |
| **San** | 8.13 | 90 | 0.48 | 6.89 | 97 | 0.34 |

Table 2. Mesiodistal and buccolingual diameters (in mm) of 2931CA 15 HUM. TO 2 ($Rdi_1$) and of deciduous first mandibular incisors in Pleistocene *Homo sapiens* fossil specimens and extant samples.

**Fossil specimens**

| | Site | specimen | side | MD | BL | Reference |
|---|---|---|---|---|---|---|
| **Middle Stone Age (MSA)** | Sibudu cave | 2931CA 15 HUM. TO 2 | R | 4.9 | 4.3 | This paper |
| | Die Kelders | AP 6290 | L | 5.1 | 4.8 | Grine, 2000 |
| **Middle Paleolithic (MP)** | Qafzeh | Qafzeh 10 | R | 4.2 | 4.4 | Tillier, 1999 |
| **Iberomaurusian (IBM)** | Afalou-bou-Rhummel | Afalou 4 | L | 4.6 | 4.0 | Voisin et al. 2017 |
| | Afalou-bou-Rhummel | Afalou 16 | L | 4.6 | 4.6 | Voisin et al. 2017 |
| **Early Upper Paleolithic (EUP) Gravettian** | Lagar Velho | Lagar Velho 1 | L | 4.7 | 4.3 | Hillson and Trinkaus, 2002 |
| **Late Upper Paleolithic (LUP) Magdalenian** | Le Figuier | Le Figuier 1 | R | 4.2 | 4.3 | Bailey, pers. comm. |
| **Late Upper Paleolithic (LUP) Epigravettian** | Grotte des enfants | GE 2 | R | 4.5 | 3.8 | Henry-Gambier, 2001 |
| | Arene Candide | AC 6 | R | 4.6 | 4.2 | Formicola, pers. comm. |
| | Arene Candide | AC 8 | L | 4.3 | 4.3 | Formicola, pers. comm. |

**Extant populations**

| | side | MD | n | sd | BL | n | sd | References |
|---|---|---|---|---|---|---|---|---|
| **American Whites** | R | 4.07 | 133 | 0.32 | 3.85 | 133 | 0.37 | Black, 1978 |
| **Australian Aboriginals** | R | 4.43 | 36 | 0.39 | 4.26 | 26 | 0.34 | Margetts and Brown, 1978 |
| **South Africans** | R | 4.22 | 23 | 0.35 | 3.82 | 23 | 0.35 | Grine, 1984 |
| **San** | R | 3.97 | 37 | 0.38 | 3.91 | 35 | 0.36 | Grine, 1984 |

Table 3. Values of the components of three-dimensional (3D) enamel thickness of Sibudu ($Ri_1$), Neandertals, Upper Paleolithic *Homo sapiens* (UPHS) and recent *Homo sapiens* (RHS) $di_1$s. For the comparative samples (N): mean±SD (range).

| | Wear stage[a] | Enamel volume ($mm^3$) | Coronal dentine + pulp volume ($mm^3$) | EDJ surface ($mm^2$) | 3D AET (mm) | 3D RET (scale-free) | Z-score for RET index |
|---|---|---|---|---|---|---|---|
| **2931CA 15 HUM. TO 2** | 4 | 11.52 | 35.34 | 45.67 | 0.25 | 7.69 | |
| **Neandertals[b](3)** | 1-3 | 12.89 ± 3.07 (9.91-16.05) | 40.05 ± 0.76 (39.18-40.53) | 57.40 ± 5.85 (50.65-61.06) | 0.22 ± 0.04 (0.20-0.26) | 6.52 ± 1.08 (5.70-7.74) | 1.08 |
| **Neandertal(1)[c]** | 5 | 10.86 | 42.62 | 53.57 | 0.2 | 5.8 | |
| **La Madeleine 4 LUP [d]** | 3-4 | 10.16 | 18.94 | 31.66 | 0.32 | 12.04 | |
| **RHS(5)[c]** | 2-3 | 11.21±1.92 (9.45-14.45) | 22.52±1.79 (20.07-24.96) | 41.21±2.12 (38.39-43.30) | 0.27±0.03 (0.24-0.33) | 9.62±1.32 (8.52-11.83) | -1.46 |
| **RHS(4)[c]** | 4 | 8.53 ± 2.59 (5.55-10.81) | 21.95 ± 3.40 (18.22-25.60) | 37.49 ± 4.55 (33.15-43.37) | 0.22 ± 0.04 (0.17-0.27) | 7.98 ± 1.33 (6.36-9.51) | -0.21 |
| **RHS(9)[e]** | 5 | 4.78 ± 1.13 (3.12-6.19) | 16.35 ± 2.63 (12.21-19.93) | 22.98 ± 3.31 (16.89-27.43) | 0.21 ± 0.03 (0.15-0.26) | 8.15 ± 1.12 (6.11-10.28) | 0.41 |

[a]Based on Molnar (1971).

[b]ForAbriSuard S14 and Spy VI see Bayle (2008); for Roc de Marsal see Bayle et al. (2009).

[c]Fabbri et al. (2016).

[d]Bayle (2008).

[e]Digital removal of tooth crown up to wear stage 5 (Fabbri et al., 2016).

Appendix. Mesiodistal and buccolingual diameters (in mm) of 2931CA 15 HUM. TO 1 ($Ldm_1$) and of deciduous first mandibular molars in Late Pleistocene *Homo sapiens* fossil specimens and extant samples.

| Fossil specimens | Site | specimen | side | MD | BL | Reference |
|---|---|---|---|---|---|---|
| **Middle Stone Age (MSA)** | Sibudu cave | 2931CA 15 HUM. TO 1 | L | 8.9 | 7.2 | This paper |
| | Die Kelders | AP 6246 | L | 8.1 | 6.8 | Grine 2000 |
| | | AP 6291 | L | 9.1 | 7.9 | Grine 2000 |
| | Diepkloof Rock Shelter | DRS 3 | L | 8.9 | 6.8 | Verna et al. 2013 |
| **Middle Paleolithic (MP)** | Qafzeh | Qafzeh 10 | R | 9.2 | 7.8 | Tillier 1999 |
| | | Qafzeh 14 | L | 9.1 | 6.8 | Tillier 1999 |
| | | Qafzeh 21 | L | 9.3 | 7.1 | Tillier 1999 |
| | | Qafzeh 12 | R | 9.3 | 7.1 | Tillier 1999 |
| | | Qafzeh 4 | R | 8.8 | 7.8 | Tillier 1999 |
| | | Qafzeh 15 | R | 9.2 | 8.5 | Tillier 1999 |
| | Skhul | Skhul 1 | R | 9.7 | 7.4 | Tillier 1999 |
| **Iberomaurusian (IBM)** | Afalou-bou-Rhummel | Afalou 4 | L | 8.1 | 7.2 | Voisin et al 2017 |
| | | Afalou 16 | L | 9.1 | 7.8 | Voisin et al 2017 |
| | | Afalou 19 | R | 8.4 | 8.2 | Voisin et al 2017 |
| | | Afalou 41 | R | 7.9 | 7.7 | Voisin et al 2017 |
| **Early Upper Paleolithic (EUP) Aurignacian** | Brassempouy | Brassempouy 112 | L | 8.4 | 7.8 | Henry-Gambier 2004 |
| | Isturitz 2000 | Isturitz 1 | R | 8.1 | 7.1 | Henry-Gambier 2004 |
| | Cueva del Castillo | CDC 2 | R | 9.0 | 7.0 | Henry-Gambier 2004 |
| | La Quina | La Quina 761 | R | 9.0 | 7.2 | Henry-Gambier 2004 |
| | Bacho Kiro | BK 1124 | L | 8.8 | 7.5 | Henry-Gambier 2004 |
| **Early Upper Paleolithic (EUP) Gravettian** | Lagar Velho | Lagar Velho I | R | 8.4 | 7.3 | Hillson and Trinkaus 2002 |
| | Grub/Kranawetberg | G/K1 | R | 8.5 | 6.6 | Teschler-Nicola et al. 2004 |
| | Borsuka Cave | C7/682 | L | 8.9 | 6.3 | Wilczyński et al. 2014 |
| | Kostenki | Kostenki 3 | - | 8.9 | 6.75 | Wilczyński et al. 2014 |
| | Kostenki | Kostenki 4 | - | 8.7 | 7.35 | Wilczyński et al. 2014 |
| | Sunghir | Sunghir 3 | R | - | 7.3 | Trinkaus et al. 2014 |
| **Late Upper Paleolithic (LUP) Epigravettian** | Grotte des Enfants | GE2 | R | 8.4 | 6.9 | Henry-Gambier 2001 |
| | Grotta Maritza | GM | L+R | 8.0 | 7.0 | Favati-Vanni 1964 |
| | Arene Candide | AC 6 | R | 7.4 | 6.8 | Formicola pers.comm.; Formicola 1986 |
| | | AC 8 | R | 8.2 | 7.1 | Formicola. pers. comm.; Formicola 1986 |
| **Late Upper Paleolithic (LUP) Magdalenian** | Galeria da Cisterna | L12-220 | R | 9.0 | 7.7 | Trinkaus et al. 2011 |

## Figures

Figure 1. Stratigraphy of the MSA site Sibudu Cave (KwaZulu-Natal, South Africa).

PGS and BS5 layers are in colour.

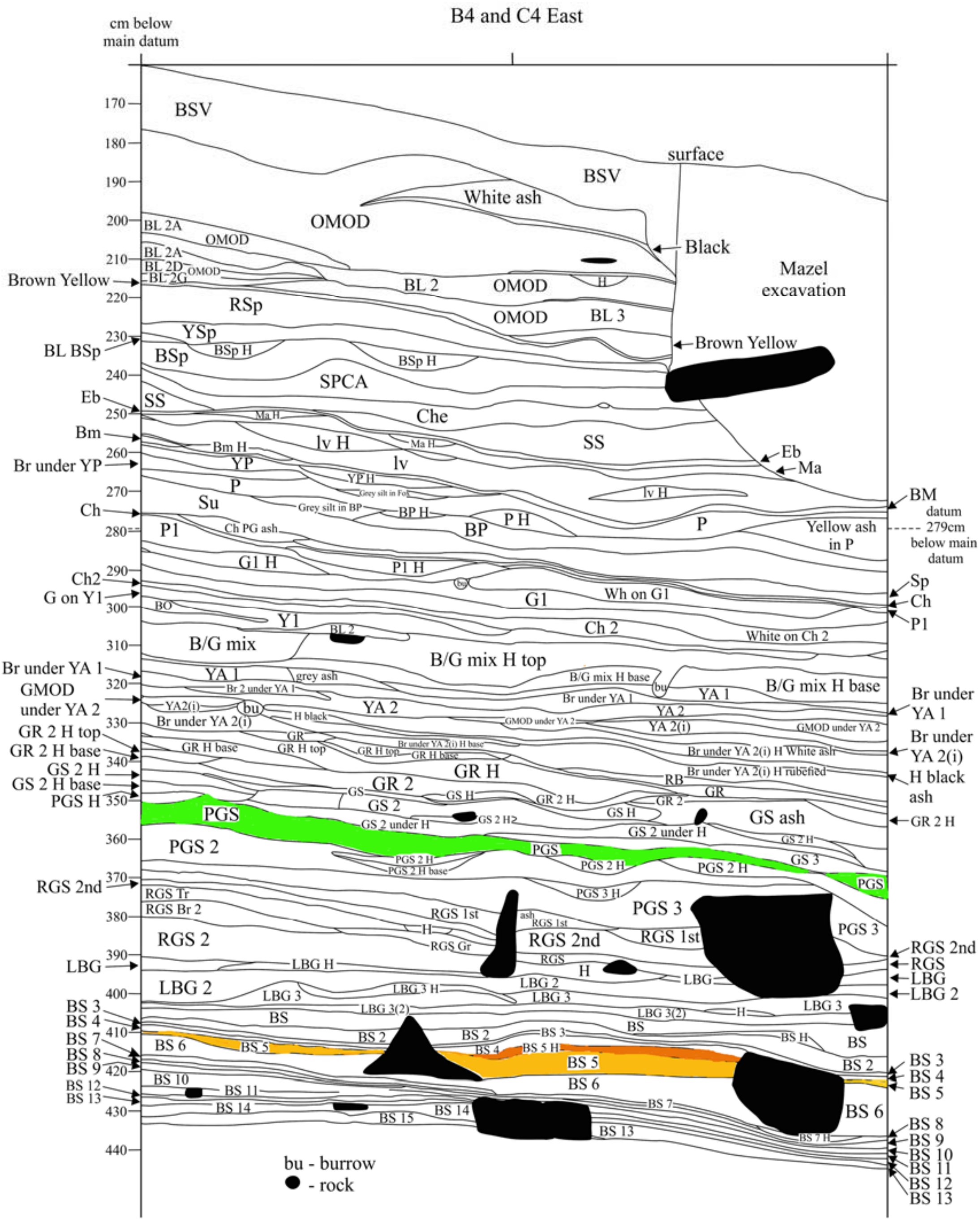

Figure 2. Three dimensional digital models of: a) 2931CA 15 HUM. TO 1 (lower left first deciduous molar, $Ldm_1$); b) 2931CA 15 HUM. TO 2 (lower right central deciduous incisor, $Rdi_1$). The black bar is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal.

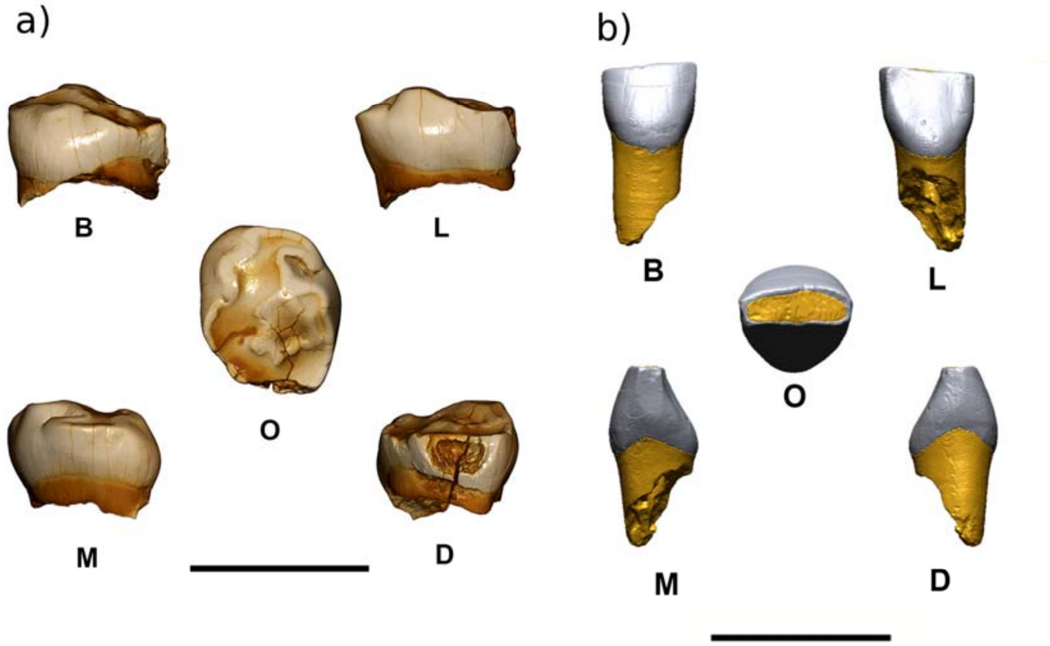

Figure 3. Boxplot of the variability in $dm_1$ MD diameters for each group considered. MP: Middle Paleolithic; MSA: Middle Stone Age; EUPA: Early Upper Paleolithic Aurignacian; EUPG: Early Upper Paleolithic Gravettian; LUP: Late Upper Paleolithic (Epigravettian and Magdalenian); IBM: Iberomaurusian; EHS: Extant *Homo sapiens*.

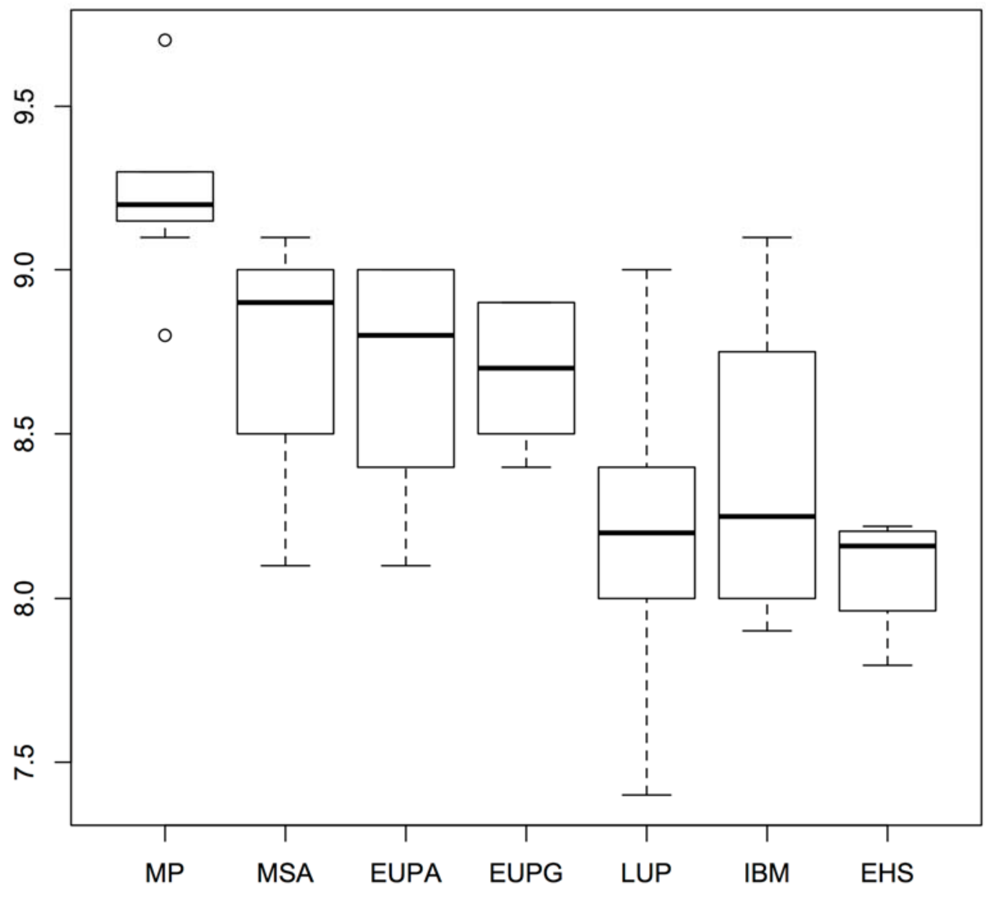

Figure 4. Bivariate plots comparing the dental dimensions (MD and BL diameters) of (a) 2931CA 15 HUM. TO 1 (Ldm$_1$) and (b) 2931CA 15 HUM. TO 2 (Rdi$_1$) to those of Late Pleistocene fossil specimens and extant samples. Specimens included and references are listed in Tables 1, Table 2 and Appendix. The polygons encompass the variability of each group. The dashed line represents the standard deviation of the total sample of EHS. The EUP group includes both Aurignacian and Gravettian samples.