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

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Summary - *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. 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.*

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.*, 2008a; 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.*, 2008a,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.

Fig. 1 - Stratigraphy of the MSA site Sibudu Cave (KwaZulu-Natal, South Africa). PGS and BS5 layers are in colour. The colour version of this figure is available at the JASs website.

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 μm^3.

Measurements

Mesio-Distal (MD) and Bucco-Lingual (BL) crown diameters of both teeth were measured using a digital caliper.

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 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). 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 (Ldm₁)

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 dm₁ 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.

Tab. 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 dm1 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

2931CA 15 HUM. TO 2 (Rdi1)

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

Tab. 2 - Mesiodistal and buccolingual diameters (in mm) of 2931CA 15 HUM. TO 2 (Rdi1) and of decid-
uous 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 &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 & 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

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
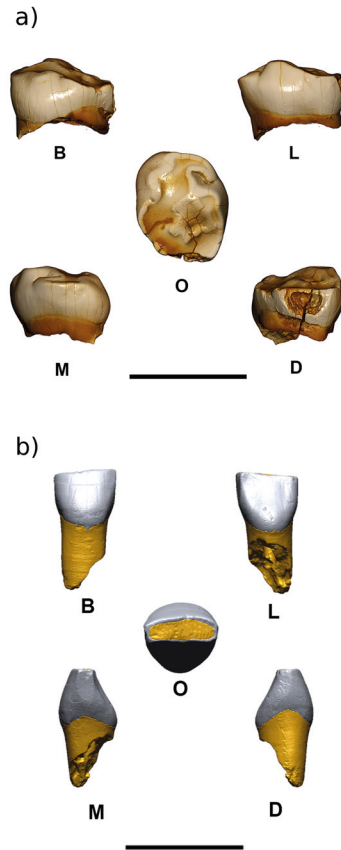

Fig. 2 - Three dimensional digital models of: a) 2931CA 15 HUM. TO 1 (lower left first deciduous molar, Ldm1); b) 2931CA 15 HUM. TO 2 (lower right central deciduous incisor, Rdi1). The black bar is equivalent to 1 cm. B, buccal; D, distal; L, lingual; M, mesial; O, occlusal. The colour version of this figure is available at the JASs website.

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 ($p<0.01$).
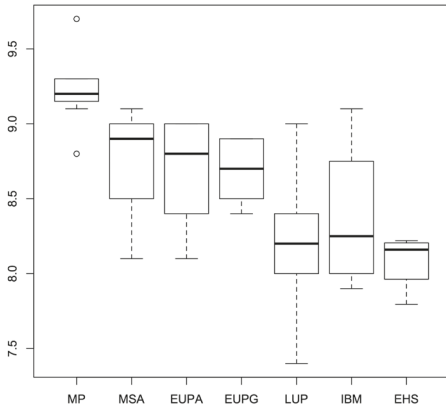
Fig. 3 - Boxplot of the variability in dm1 MD diameters for each group considered. MP: Middle Paleolithic; MSA: Middle Stone Age; EUPA: Early Upper Paleolithic Aurignacian; EUPG: Early Upper Paleolithic Gravettian; LUP: Late Upper Paleolithic (Epigravettian and Magdalenian); IBM: Iberomaurusian; EHS: Extant Homo sapiens.

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
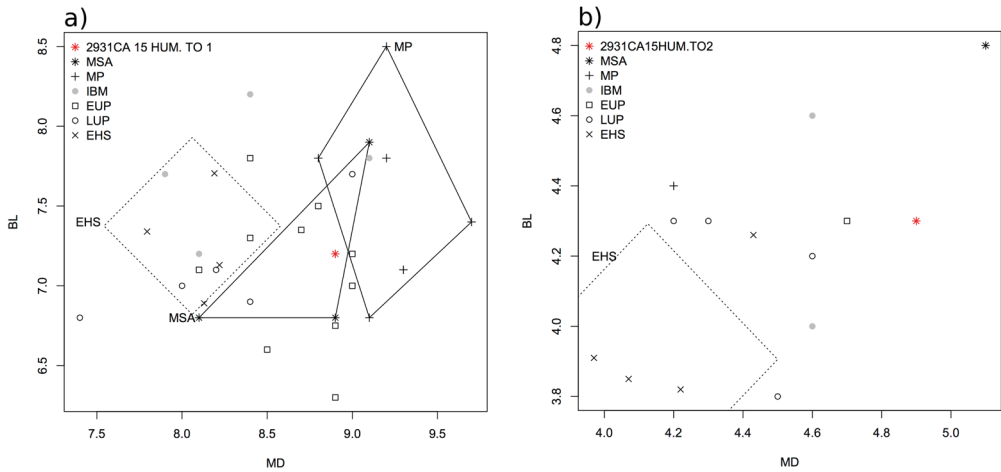
Fig. 4 - Bivariate plots comparing the dental dimensions (MD and BL diameters) of (a) 2931CA 15 HUM. TO 1 (Ldm1) and (b) 2931CA 15 HUM. TO 2 (Rdi1) to those of Late Pleistocene fossil specimens and extant samples. Specimens included and references are listed in Tables 1, Table 2 and Appendix. The polygons 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. The colour version of this figure is available at the JASs website.

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.

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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.

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Appendix - Mesiodistal and buccolingual diameters (in mm) of 2931CA 15 HUM. TO 1 (Ldm1) 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

Appendix - Continued.

FOSSIL SPECIMENS	SITE	SPECIMEN	SIDE	MD	BL	REFERENCE
Early Upper Paleolithic (EUP)						
Gravettian	Lagar Velho	Lagar Velho I	R	8.4	7.3	Hillson &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