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Human teeth from securely stratified Middle Stone Age contexts at Sibudu, South Africa

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Abstract

The fossil record of early *Homo sapiens* in the African Pleistocene remains sparse. In contrast to its prominent position regarding the cultural evolution of our species, southern Africa plays a secondary role in narratives regarding human biological origins. Reasons for this are a limited and fragmentary fossil record from the Middle Stone Age (MSA), further complicated by a number of human remains coming from contexts lacking chronostratigraphic information. Similar to the southern African MSA overall, the rich archeological deposits of Sibudu stand in opposition to its scarce record of hominin fossils. Here, we report on three human teeth (SIB-1, 2, 3) from securely stratified MSA deposits at Sibudu dating between > 77 and 64 ka. The teeth include two lower deciduous molars (Ldm_2) with heavy occlusal wear and one fragment. We focus on describing the find and archeological context, followed by an initial assessment of the fossils and their contextualization within the African record. The juvenile teeth derive from rich and well-stratified archeological deposits, associated with a Howiesons Poort industry at ~ 64 ka from PGS3 (SIB-3) and pre-Still Bay occupations in strata Casper and Danny at > 77 ka (SIB-1, 2). The latter constitute the oldest human fossils from Sibudu. Metric and morphological analyses of the Ldm_2s (SIB-2, 3) find a combination of archaic traits (e.g., mid-trigonid crest) and crown dimensions that overlap with ranges of both Pleistocene and recent *Homo sapiens*. These results match with a population of *Homo sapiens* that lies chronologically between the earliest members of the species and recent humans.

Keywords Hominin dental remains · Modern human origins · Anatomically modern humans · Pleistocene

Introduction

Skeletal remains interpreted as the earliest members of our species from north of the Sahara at Jebel Irhoud have recently been dated to ~ 300 ka (Hublin et al. 2017; Richter et al. 2017). In addition, genomic studies on a larger number of modern and aDNA have provided a more scattered picture for the geographical origin of *Homo sapiens* (Schlebusch et al. 2017; Skoglund et al. 2017; van de Loosdrecht et al. 2018). New models for the origins of our species thus see a "pan-African" (Hublin et al. 2017) or "African multiregionalism" (Stringer 2016) pattern with a strong signal of ancient population substructure and anatomical diversity persisting until the final Pleistocene (Gunz et al. 2009; Harvati et al. 2011; Crevecoeur et al. 2016; Lahr 2016). Yet, southern Africa continues to play a relatively minor role in narratives regarding the biological origins of our species (Klein 2001; Grine et al. 2007; Henn et al. 2011), standing in marked contrast to the subcontinent's part in discussions on the cultural evolution of *Homo sapiens* within the Middle Stone Age (MSA; Henshilwood and Marean 2003; Conard 2014; Wadley 2015).

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The southern tip of the continent has yielded comparatively few human fossils from a small number of sites, with frequently fragmented remains and a high abundance of teeth (Table 1; Dusseldorp et al. 2013; Harvati et al. 2015; Grine 2016), mostly from the Late Pleistocene. Studies on these fossils show a mix of archaic and derived traits (see for more details Rightmire and Deacon 1991; Grine 2000; Grine and Henshilwood 2002; Marean et al. 2004; Rightmire et al. 2006; Verna et al. 2013; Grine 2016), potentially echoing findings from other regions regarding complex ancient population structure in early *Homo sapiens* (Gunz et al. 2009; Harvati et al. 2011; Crevecoeur et al. 2016; Lahr 2016; Stringer 2016). The record is further complicated by a number of human fossils coming from the surface or contexts lacking chronostratigraphic information (Table 1; see Millard 2008).

Here, we report on newly discovered and securely stratified human fossils from Sibudu Cave in KwaZulu-Natal, South Africa. Sibudu is a key locality for studying the cultural evolution of modern humans in Africa, with numerous important findings over the past years (Wadley and Jacobs 2006; Wadley 2008; Wadley et al. 2009, 2011; d'Errico et al. 2012; Rots et al. 2017). In contrast, the anthropological record from Sibudu is scarce. Previously, Plug (2004) reported on the discovery of a toe bone, a lateral malleolus of a fibula, a distal manual phalanx, and a sternum fragment from the uppermost MSA layers dated to ~48 ka. These finds, however, were described as fresh and likely an intrusion from overlying Iron Age pits (Plug 2004; Wadley 2006; but see Grine 2016). More recently, Riga et al. (in press) have reported on the recovery of two deciduous teeth (Ldm_1, Rdi_1) coming from layers dated to ~65 and ~77 ka. Still, the number of fossils with secure stratigraphy from Sibudu remains low, particularly in comparison to its rich archeological record and long sequence. In 2016 and 2017, excavations from the University of Tübingen led by N. Conard recovered and identified three human teeth (SIB-1, 2, 3) during sorting of sieved material as part of the processing of finds during field season. These finds add to the scarce fossil record of the southern Africa MSA and extend the time depth and morphological variability of human remains at Sibudu. We put a particular focus on providing a detailed description of the find context of the human teeth—which has at times been lacking in anthropological studies (e.g., Millard 2008)—followed by an initial assessment of the fossils and their contextualization within the African record.

Materials and methods

The site of Sibudu: overview and stratigraphy

The large rockshelter of Sibudu lies about 40 km north of Durban and 15 km from the Indian Ocean. The site features Iron Age occupations directly overlying MSA deposits without an intermediate Later Stone Age (LSA). Sibudu preserves a long and complex stratigraphy that comprises over 50 distinct MSA find horizons. From 1998 to 2011, a team led by Lyn Wadley excavated the MSA deposits over an area of 21 m^2 until a depth of up to 3 m. This sequence, dating between < 77 and 38 ka, includes Wadley's pre-Still Bay (SB), SB, Howiesons Poort (HP), post-HP, late MSA, and final MSA strata (Wadley 2006; Wadley and Jacobs 2006; Jacobs et al. 2008; Wadley 2013). In the uppermost part of the sequence ("final" and "late" MSA), several large pits dug by Iron Age people into the MSA deposits created some mixture of sediments (Wadley 2006). Below these levels, the depositional sequence of the "post-HP" or Sibudan is devoid of these intrusions and includes a succession of well-stratified centimeter thin, distinct layers, and lenses, almost entirely of anthropogenic origin (Fig. 1; Wadley and Jacobs 2006; Goldberg et al. 2009; Wadley et al. 2011; Miller 2015). The deposits of the HP and below remain mostly anthropogenic and exhibit little indication of vertical mixing. They differ from the upper deposits in appearing relatively homogenous in color and texture, although isolated features such as ash lenses occur and define surfaces, allowing for stratigraphic distinctions between excavated units (Goldberg et al. 2009; Miller 2015). Stone artifacts, faunal remains, and other find categories are very abundant throughout the entire MSA sequence.

Excavation methods

On Lyn Wadley's invitation, current work at Sibudu has been carried out by a team of the University of Tübingen under N. Conard's direction since 2011. Presently, the Tübingen team has excavated over 30 archeological find horizons within the MSA deposits, removing a total sediment volume of ~9 m^3. Excavations since 2011 follow Wadley's naming system for stratigraphic layers to facilitate comparisons between both phases of excavation (Wadley and Jacobs 2006: Table 2). Find horizons are usually designated with an abbreviated label (e.g., "PGS") which carries descriptive information about the excavated sediment (PGS = pinkish gray sand). To achieve more clarity within the complex stratigraphy, newly excavated horizons below where Wadley's work stopped were given descriptive field names, but also names of people in alphabetical order modified from systems used by Parkington and colleagues on the Western Cape at sites such as Elands Bay Cave and Diepkloof (Parkington et al. 2013; Porraz et al. 2013). For example, layer Gray-Brown Patchy (GBP) is also designated as Bea.

We divided the excavation area into two zones which are dug on different vertical levels (Fig. 1). The "Eastern Excavation" comprises 6 m^2 and has been excavated in ca. 1.8 m thickness from the top of the Sibudan (post-HP) until the Still Bay (LBG). The "Deep Sounding" is located just west of this zone. Here, the Tübingen excavations began at the bottom

Table 1 Overview of previously published human fossils in South Africa associated with MSA material (data combined from Dusseldorp et al. 2013: Supplementary Table 1 and Grine 2016). In bold face are direct comparative samples to the human teeth from Sibudu reported here

Site	*n*	Element[a]	Species	Associated archeology	Age estimate
Florisbad	2	Partial cranium, M^3	*H. heidelbergensis*/*Homo helmei*; archaic *H. sapiens*	Possible early MSA	259 ± 35
Blombos	9	RP^3, RP^4, M fragmentary, Ldi^1, Rdi^1, Ldm^1, RdM^1, Ldm^2	*H. sapiens*	"Pre-Still Bay"; Still Bay	~ 100–94 ka (pre-SB); ~ 72 ka (SB)
Border Cave	8	Partial cranium (?); Mandible (2; 1?); Partial infant skeleton (?); Humerus; Ulna; Metarsus IV; Metatarsus V	*H. sapiens*	Early MSA; informal MSA; Howiesons Poort (?)	~ 171–152 ka; 91–71 ka; 72–61 ka
Die Kelders	27	Mandible, Rdm^2 (3), Rdi^2, Ldi_1, Ldi_2, LP^4, LP_4, RP_4, RM_1, Ldm_1 (2), Ld_c, Rdi^1 (2), Rdi_2, Rd^c (2), LI^1, LM_1, RC, RP_4, RP^4, RM_2, Phalanx (2)	*H. sapiens*	Undefined MSA; possibly Mossel Bay/MSA 2	~ 70–60 ka
Diepkloof	3	Ldm_1, Middle pedal phalanx; Distal pedal phalanx	*H. sapiens*	Howiesons Poort; post-HP	61–58 ka (HP); 55–48 ka (post-HP)
Equus Cave	10	9 Isolated teeth (?); partial mandible (?)	*H. sapiens*	Hyena den with some MSA and Robberg artifacts	75–27 ka; 12–10 ka (?)
Klipdrift Shelter	1	$\mathbf{Ldm_2}$	*H. sapiens*	Howiesons Poort	65–60 ka
Klasies River	40	Maxilla fragment (2), Cranial fragment (3), Parietal fragment/bone (7), Frontal, Zygomatic, Mandible fragment (4), Mandible with 3 M, Mandible, Rdm_2, I^2, LM_1 (2), LM_2, LM_3, LM^2, LM^3, LP_1, Ulna, Radius, Mt. I, Mt. II, Mt. V, Rdm^1, $\mathbf{Rdm_2}$, Ld^1, RP_4, Clavicle, Pelvis fragment, Lumbar vertebra	*H. sapiens*	Klasies River (MSA 1); Mossel Bay (MSA 2); Howiesons Poort; post-HP	~ 110 ka (Klasies River); ~ 100 ka (Mossel Bay); 65–60 ka (Howiesons Poort); ~ 60–40 ka (post-HP)
Sibudu	4	Ldm_1, Rdi_2, fibula fragment (?), 3rd manual phalanx (?), toe bone (?), sternum fragment (?)	*H. sapiens*	Final MSA or Iron Age	77–64 ka; ~ 48 ka/recent
Pinnacle Point 13B	2	Parietal fragment (?), Central Incisor	*H. sapiens*	Mossel Bay (MSA 2)	~ 100–90 ka
Plovers Lake	5	Ulna fragment (?), Tibia fragment (?); RP_4 (?), RM_1 (?), RM_2 (?)	*H. sapiens*	Informal MSA	88.7–62.9 ka
Witkrans	3	LM_1 (?), RM_1 (?), RM_2 (?)	*H. sapiens*	Mossel Bay (MSA 2)	103–86 ka
Ysterfontein 1	3	Three teeth (unpublished)	*H. sapiens*	Informal MSA	105–71 ka

[a] ? = Uncertain stratigraphic context or attribution to the MSA

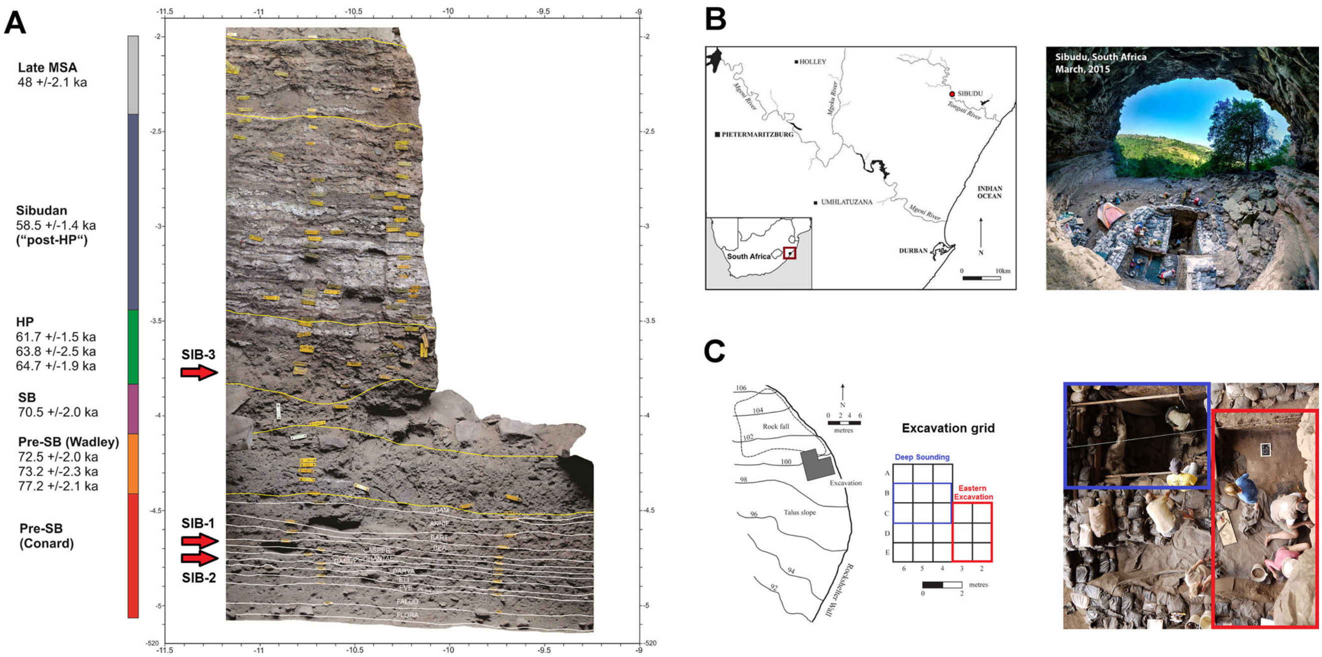

Fig. 1 Stratigraphy and overview on the excavation area of Sibudu. **a** Composite stratigraphy of Sibudu with indication of chronometric ages, cultural attributions, and the stratigraphic position of the three human teeth (red arrows). **b** Geographical map of Sibudu and panoramic view within the rockshelter. **c** Horizontal plan of the rockshelter floor and excavation grid. The red box indicates the Eastern Excavation with the blue box denoting the Deep Sounding, both shown during excavations in different vertical levels (Figure by V.C. Schmid, M. Zeidi, M. Haaland and M. Will)

of Wadley's "pre-SB" layer BS15 where she stopped in 2011 (Wadley 2013). So far, we have excavated a trench of 4 m^2 in these deepest sediments at the site which encompass 12 find horizons over a thickness of ~ 50–60 cm. From top to bottom, they include Adam, Annie, Bart, Bea, Casper, Chantal, Danny, Darya, Eli, Eve, Falco, and Flora (Fig. 1).

Table 2 Buccolingual (BL) and mesiodistal diameters (MD) in mm of the Sibudu teeth compared to those of lower second deciduous molars of various populations. Data for the comparative groups is taken from Harvati et al. (2015) for Klipdrift; Grine (2012) for Klasies River, Toussaint et al. (2010) for H. heidelbergensis, early *H. sapiens*, Upper Paleolithic *H. sapiens*, Neanderthals, and recent Europeans, Hershkovitz et al. (2011) for *H. heidelbergensis*, Benazzi et al. (2011) for Upper Paleolithic *H. sapiens*, Moss and Chase (1966) for Recent African, Grine (1986) for the Recent South African and Grine (1984) for African San groups

Specimen/population	MD				BL			
	n	Mean	SD	Range	*n*	Mean	SD	Range
SIB-2	1	–			1	9.57		
SIB-3	1	10.42			1	9.16		
Klipdrift	1	10.30			1	8.50		
Klasies River	1	–			1	8.30		
H. heidelbergensis (Europe, Near East)	3	10.83	0.45	10.40–11.30	3	9.50	0.10	9.40–9.60
Neanderthals	40	10.34	0.59	9.20–11.50	40	9.29	0.47	8.00–10.20
Early *H. sapiens* (Near East, North Africa)	10	10.92	0.54	9.90–11.40	10	9.71	0.73	8.60–10.70
Upper Paleolithic *H. sapiens*	10	10.57	0.54	9.90–11.50	10	9.33	0.41	8.50–10.0
Recent Europeans	50	10.07	0.48	9.10–11.10	50	8.87	0.45	8.20–9.70
Recent African (Liberian)	20	10.09	0.5.1	8.30–10.00	20	8.86	0.45	8.20–10.0
Recent South African Bantu-speaking (Males)	18	10.39	0.44	9.50–11.20	18	9.03	0.37	8.20–9.70
Recent South African Bantu-speaking (Females)	17	10.13	0.57	8.90–10.90	17	8.76	0.39	8.00–9.30
Recent San (Males)	54	10.06	0.49	8.90–11.20	56	8.68	0.41	7.80–9.70
Recent San (Females)	41	9.88	0.45	9.00–10.90	45	8.48	0.39	7.60–9.50

Throughout the MSA deposits, the team excavates in 1–25 mm thick "Abträge" (singular "Abtrag"; a technical term from German excavation methodology). These excavation units follow the contours of the stratigraphic sequence without crosscutting geological strata to establish reliable and high-resolution cultural chronological units. These *Abträge* constitute the smallest stratigraphic units we discern at Sibudu during excavations and sometimes equal defined archeological strata in case the latter do not exceed a maximum thickness of 25 mm. We usually group several *Abträge* in larger units that we call find horizons (i.e., archeological layers) which form our main analytical units (Fig. 1; for naming conventions see Wadley and Jacobs 2006). We carefully piece-plot archeological material > 30 mm using a Leica total station and the EDM program developed by Dibble and McPherron (1996). Smaller material is collected by screening buckets of sediment, which are subsequently sorted (see below). As the buckets are also plotted, the provenience of finds from the screens can be located to within a quarter meter and a thickness of 1–25 mm.

Due to the very high density of archeological materials at Sibudu—often several tens of thousands of artifacts and > 20 kg of faunal remains per cubic meter—much methodical emphasis at the site has been put on the recovering and studying of smaller finds (< 30 mm) which are not piece-plotted. In the field, excavated buckets of sediment containing these finds are sieved on-site by crew members using a coarse screen with a mesh of 5 mm and a fine screen with a mesh of 1 mm. The coarse fraction is then bagged with a find tag indicating the find number, square, layer, and z-value and transported to the dig house. Experienced archeologists sort these sediments and identify different classes of finds, which are then bagged separately for further analyses. During this processing of finds during and after field season, the three human teeth reported here were recovered and identified. In 2016, we discovered a small fragment preserving only the lateral part of the crown (SIB-1; ID: B5-1170.10; layer Casper) plus a heavily worn tooth with a slightly broken crown, mostly without roots (SIB-2; ID: A5-888.1; layer Danny). During our field and analytical season in 2017, we discovered an additional human tooth (SIB-3; ID: C3-4004.1; layer PGS 3), preserving a more complete worn crown with broken roots. The buckets containing the teeth had a volume of 1–4 l and included abundant lithic artifacts and other faunal remains < 30 mm. Rigorous sorting of sediments from adjacent squares and *Abträge* has not resulted in the retrieval of further human remains.

Methods of morphological and metric analyses

The dental material includes three human specimens (SIB-1, 2, 3; Figs. 2 and 3), permanently stored at the KwaZulu-Natal Museum in Pietermaritzburg. The analyses of the anthropological remains include a general anatomical description and metric characteristics (2D measurements) taken with digital calipers. The morphological descriptions of the Sibudu dental material follow standard terminology (e.g., Scott and Turner II 1997). Regarding metric analyses, we recorded mesiodistal (MD) and buccolingual (BL) diameters of the crowns following Tobias (1967) and compared those with measurements collected from the literature for deciduous second molars from fossil and recent *Homo* specimens. The comparative sample focuses on Pleistocene *Homo sapiens* from Africa and South Africa in particular, but also includes *Homo heidelbergensis*, *Homo neanderthalensis*, early *Homo sapiens* from the Near East and North Africa, Upper Paleolithic (UP) European specimens, and recent human samples from African and Europe (Table 2; Moss and Chase 1966; Grine 1984, 1986; Toussaint et al. 2010; Benazzi et al. 2011; Hershkovitz et al. 2011). High-resolution micro-computed tomographic (CT) images for visualization and data management purposes were acquired with a GE Phoenix v|tome|x micro-CT at the University of Tübingen (voxel size 0.015 × 0.15 × 0.15 mm). More in-depth analyses (crown outline, enamel-dentine junction, lateral crown tissue proportions) and publication of the virtual models are planned as part of a larger-scale comparative study.

Fig. 2 Photographs of the potential human tooth fragment SIB-1 from six views

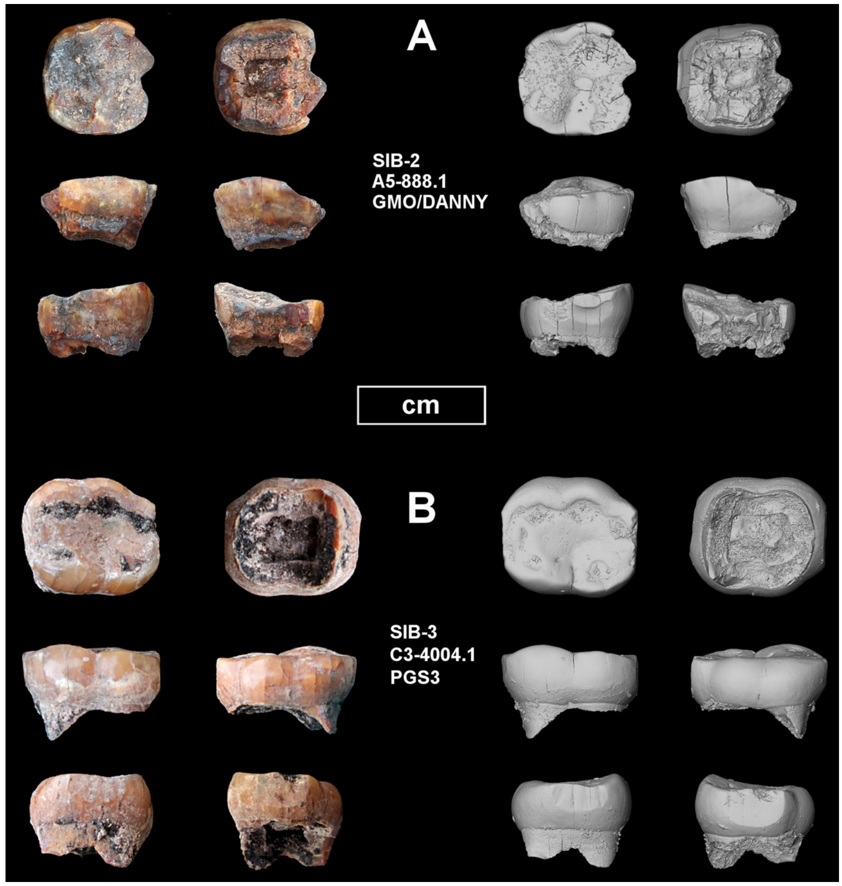

Fig. 3 Photographs and images of the virtual models derived from micro-CT scans of the two more complete human teeth (both dm_2) associated with MSA archeology at Sibudu. Six views each from top left to bottom right: occlusal (buccal left, lingual right, distal top, mesial bottom), apical, lingual, buccal, mesial, distal. **a** SIB-2 (A5-888.1; Layer GMO/Danny). **b** SIB-3 (C3–4004.1; Layer PGS3). (Figure by C. Röding, M. Will and S. El-Zaatari)

Results

Context and stratigraphic situation of the human teeth

SIB-3 (ID: C3-4004.1) was found in the uppermost *Abtrag* of PGS3 in the Eastern Excavation (Fig. 1) and can be firmly attributed to the HP industry with an associated age of this stratum by OSL to 64.7 ± 2.3 ka (Wadley and Jacobs 2006; Jacobs et al. 2008). Other than occasional roots and rootlets, no intrusions or obvious disturbances were observed during excavations. The two other human teeth (SIB-1, ID: B5-1170.10, layer Casper; SIB-2, ID: A5-888.1, layer Danny) are located in the Deep Sounding (Figs. 1 and 2), 30–40 cm below the bottom of layer BS dated by OSL to 77.2 ± 2.1 ka (Jacobs et al. 2008; Wadley 2013), providing a *terminus ante quem* for the age of the teeth. No burrows or other indications of large-scale vertical displacement of finds were noted during and after excavation. Modern intrusion of the three teeth from non-MSA contexts can be rejected based on the outstating stratigraphic and taphonomic integrity of Sibudu (Wadley 2006; Miller 2015). Furthermore, the teeth are exclusively associated with MSA artifacts.

The location and measurements of excavated buckets provide the spatial context of the teeth, showing that they were embedded well within discrete stratigraphic layers (Fig. 4). The two teeth from the Deep Sounding were deposited within an area of 0.75 m^2. The z-values of the buckets containing the teeth are − 4.55 and − 4.63 m, respectively, indicating a vertical distance of ~ 8 cm. The tooth from Danny was found in *Abtrag* 2 from a total of five *Abträge*, in the middle of this stratum. The tooth fragment from Casper derives from the lowermost *Abtrag* 6, lying right on top of layer Chantal (~ 5 cm thick) which separates the two tooth-bearing strata (Figs. 2 and 3). SIB-1 was found ~ 80 cm above the teeth from the Deep Sounding in the Eastern Excavation.

In sum, all three human teeth were embedded within three different stratigraphic layers without evidence for post-depositional disturbance. SIB-3 is associated with a HP lithic industry dated to ~ 64 ka, with SIB-1 and SIB-2 coming from deeper layers that pre-date 77 ka. No other human remains were found in adjacent squares though detailed sorting of surrounding sediments was undertaken. For two of the three teeth, the stratigraphic context, lack of burial or related structure, and juvenile age (see below) suggest the loss during life. The three teeth could not have

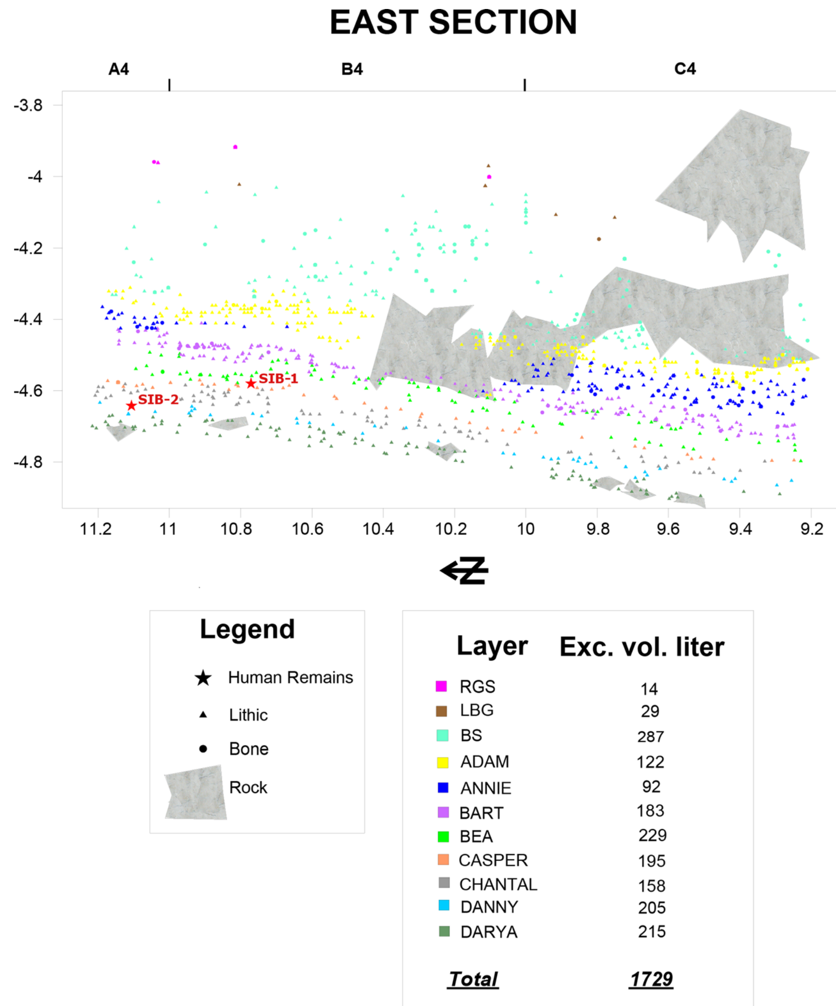

Fig. 4 Two-dimensional vertical plot of SIB-1 and SIB-2 in the East Section in relation to other measured archeological finds in the Deep Sounding at Sibudu. Note that both teeth lie well below lowermost BS (dated to ~77 ka)

been deposited in the same event by a single individual as they are separated by at least one stratigraphic unit, and because SIB-2 and SIB-3 come from the same anatomical position. The teeth thus represent the remains of separate non-adult individuals (see also below).

In terms of archeological material, the human teeth are associated with high numbers ($n > 10{,}000$) of lithic artifacts and faunal remains in layers that are rich in finds. The lithic artifacts recovered from PGS3 by our team demonstrate an association of SIB-3 with the HP, being a blade and bladelet industry with typical “HP cores” (Villa et al. 2010: 643) and dominated by various types of backed pieces (see also Wadley 2008; Peña et al. 2013). The manufacture of bone tools in the HP layers is attested by our own finds and previous studies (d’Errico et al. 2012). The teeth from the lower part of the sequence are associated with assemblages featuring abundant bifacial technology—including serrated pieces that were manufactured by pressure flaking (Rots et al. 2017)—and blade manufacture. While these assemblages pre-date the SB at Sibudu and were informally designated as pre-SB by Wadley (Wadley and Jacobs 2006; Wadley 2013), they share some techno-typological characteristics with the SB. Assemblages Casper and Danny are currently under study and have not been formally named.

Morphological description

SIB-1 (layer CASPER, Abtrag 6, square B5, $z = -4.548$)

This is a very small fragment of a tooth crown measuring 6.5 mm buccolingually and 3.8 mm mesiodistally (Fig. 2). The fragment preserves an interproximal facet. The fragmentary nature of this piece renders its identification problematic and precludes further analyses.

SIB-2 (layer DANNY, Abtrag 2, square A5, $z = -4.631$)

This is a right dm_2 (Fig. 3). The root is almost completely resorbed with only around 1 mm in height still present. The crown is extremely worn (wear stage 7 of Skinner 1997), with all occlusal enamel worn away and only a very thin enamel ring preserved. This enamel ring is broken off on the distal side. The mesial side of the crown shows an interproximal contact facet with two beveled surfaces, one superior and one inferior, suggesting that the dm_1 had already been shed and the P_3 had already erupted into functional occlusion while this dm_2 was still in occlusion. Thus, in comparison with modern human dental development rate (Ubelaker 1989), this individual was at least 10 years old when this tooth was shed. The crown's minimum buccolingual diameter measures 9.6 mm. Its mesiodistal diameter cannot be accurately measured due to the lack of complete preservation of the crown surface on the distal side. The extreme enamel wear of this tooth impedes further morphological description.

SIB-3 (layer PGS3, Abtrag 1, square C3, *z* = − 3.751)

This is the best preserved and most complete among the three teeth described here. It is also a right dm_2, and therefore a separate individual from SIB-2 (Fig. 3). The root is mostly resorbed and in some parts broken. It is best preserved on the mesial side where it measures 2.9 mm in maximum preserved height. The crown is completely preserved. It measures 9.2 mm in buccolingual diameter and 10.4 mm in mesiodistal diameter. It exhibits two interproximal facets, one mesial (measuring 2.2 mm in height and 5.0 mm in width) and one distal (measuring 2.9 mm in height and 4.6 mm in width). The presence of interproximal facets on both the mesial and distal surfaces of the crown indicates that both the RM_1 and the Rdm_1 were present and in full occlusion when this individual died or when this tooth was shed. Thus, based on modern human dental development rate (Ubelaker 1989), this tooth belonged to an individual older than 7 years.

The crown is moderately worn (between stages 5 and 6 of Skinner 1997), with the presence of dentine islands on all five cusps of this molar and with some degree of coalescence of these islands on the buccal cusps. This level of wear has left the crown nearly flat, obliterating most of the occlusal morphology. The tooth possesses five well-developed main cusps with their tips all internally compressed as far as can be concerned with regard to the occlusal wear. There seems to be no tuberculum sextum (C6). There might have been a small postmetaconulid, but even if present, which cannot be confirmed due to the surface flattening by occlusal wear, it does not seem to have formed a separate cuspulid for it to form a tuberculum intermedium (C7). An anterior fovea is clearly visible, bordered distally by the central crests of the protoconid and metaconid which appear to have joined to form a continuous mid-trigonid crest. Yet the level of occlusal wear of this tooth precludes certain assessment of this feature.

Metric analysis

The buccolingual diameter of SIB-2 is large but falls within the range of variation of all comparative groups except the recent South African Bantu-speaking and San females, which show lower values (Table 2). Its value is closest to the means of the Paleolithic groups (*Homo heidelbergensis*, Neanderthals, and *Homo sapiens*), early *Homo sapiens* from the Near East and Africa, and falls within one standard deviation of the means of these groups (Fig. 5; Table 2). SIB-3 buccolingual and mesiodistal diameters fall within the ranges of variation for all groups with one exception: its buccolingual diameter is smaller and outside the range of *Homo heidelbergensis*. When considering the mean values of both diameters, SIB-3 falls within the one standard deviation of ranges of Neanderthals, Upper Paleolithic *Homo sapiens*, and recent South African Bantu-speaking males (Fig. 5; Table 2).

Discussion and conclusions

The human dental fossils from Sibudu add to the growing record of MSA human remains from South Africa, being only the second site recorded from the east of the country, the other being Border Cave (Cooke et al. 1945). The teeth are associated with the HP (PGS 3; ~65 ka) and pre-SB (Danny; > 77 ka) industries, providing important chronological and archeological context to the finds. The comparative analyses and identification of the remains are limited by their isolated nature (one fragment, two deciduous second molars), the strong wear obliterating most of the crown structure (particularly on SIB-2), and the nearly complete lack of dental comparative material from South African MSA contexts. Direct

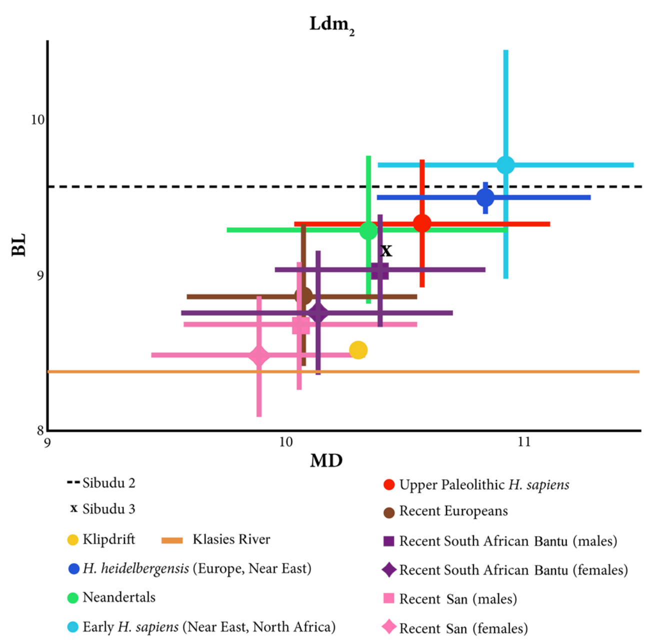

Fig. 5 Bivariate plot of buccolingual and mesiodistal diameters of the Sibudu teeth in comparison to the means and one standard deviation ranges of the means of the comparative groups. Since only the buccolingual diameter is available for SIB-2, this value is represented by a dotted line

comparisons with human remains from relevant South African sites are only possible for a nearly complete Ldm_2 from Klipdrift Shelter, deriving from the HP and dated to ~66–60 ka (KDS PBE; Harvati et al. 2015), and a broken Rdm_2 (SAM-AP 6378) from Klasies River Member SAS-U (MSA II, ~90–70 ka; Grine 2012; Grine et al. 2017).

The crown dimensions of the two teeth from Sibudu lie within the modern human range of variation—particularly SIB-3—but are larger compared to KDS PBE and SAM-AP 6378 (Fig. 5; see Harvati et al. 2015). The metric dimensions overlap with ranges of both archaic and recent humans, but are closest to Neanderthal and UP European *Homo sapiens* remains, and generally larger than those of extant humans. In terms of morphology, the less-worn crown of SIB-3 possesses several features similar to KDS PBE (e.g., 5 main cusps) some of them archaic (possible mid-trigonid crest, anterior fovea); SAM-AP 6378 is too fragmentary to assess these features. The preserved morphology on SIB-3 is compatible with either archaic or modern humans, though the expression of some traits (e.g., mid-trigonid crest) is low in recent and contemporary populations (see Online Source 1). In sum, the Sibudu teeth dated to > 77–64 ka fit within the pattern of variation described for South African MSA humans—featuring populations with variable expressions of archaic and derived morphological traits and metric dimensions (see Grine 2000, 2016; Grine and Henshilwood 2002; Marean et al. 2004; Rightmire et al. 2006; Verna et al. 2013; Harvati et al. 2015)—and more generally match with a population of *Homo sapiens* that lies chronologically between the earliest members of the species and recent humans.

Our finds also enlarge the scarce record of MSA human remains from Sibudu, one of the key sites for studying the cultural evolution of early *Homo sapiens* (Wadley and Jacobs 2006; Wadley 2008; Wadley et al. 2009, 2011; d'Errico et al. 2012; Rots et al. 2017). In contrast to its rich and diverse archeological record, Sibudu has yielded few fossils attributable to the MSA. Recently, Riga et al. (in press) have reported on two deciduous teeth from MSA layers excavated by Wadley's team, consisting of an Ldm_1 (HUM. TO 1) and a Rdi_1 (HUM. TO 2). HUM. TO 1 derives from layer BS 5 dated to 77.3 ± 2.7 ka whereas HUM. TO 2 comes from stratum PGS with an age of 64.7 ± 2.3 ka. The new teeth reported here from Conard's excavation expand on the morphological variability (here Ldm_2s) and extend the time depth of human remains known from the site, with SIB-2 located approximately 50 cm below layer BS 5 and dating to > 77 ka (Fig. 4). Comparing the findings between the studies of the Sibudu deciduous teeth, HUM. TO 1 and TO 2 were found to fall well within the metric variability of MSA and early UP remains, but with both being larger compared to extant *Homo sapiens* (Riga et al. in press). These results are broadly similar to the comparisons of crown dimensions of the Ldm_2s reported here, which are similar to UP European *Homo sapiens* and other MSA remains but larger compared to our recent sample. The only difference is a much closer value of crown sizes for SIB-2 and SIB-3 to Neanderthals compared to the Ldm_1 from Wadley's excavations (Riga et al. in press). Unfortunately, further morphological comparisons were not performed on the deciduous teeth recovered by Wadley's team. Whether the Rdi_2 from PGS by Wadley's team and the Ldm_2 from PGS3 reported here (found in the adjacent square meters C3 and C4 of the excavation; see Fig. 1) derived from the same individual remains a possibility that cannot be ascertained at this point.

So far, only the remains of juvenile individuals have been found securely attributed to the MSA of Sibudu (see also Riga et al. in press), concurrent with the fossil evidence from many other southern African sites during this time frame (Grine 2016). The lack of discernible burial structures at Sibudu likewise fits the record of sheltered MSA sites in the same region (e.g., Grine 2000; Grine et al. 2000; Verna et al. 2013; Harvati et al. 2015; Wadley 2015; Grine 2016), supporting the notion that most juvenile remains (i.e., deciduous teeth) resulted from loss during life in the course of site occupations. For early modern humans during the MSA, burials might either not have been part of the behavioral repertoire or performed outside the mostly sheltered residential sites from which the majority of archeological and anthropological information in southern Africa derive, thus rendering such practices archeologically invisible (e.g., Wadley 2015).

Our report on the Sibudu dental remains emphasizes the importance of documenting well-stratified contexts for the rare human fossil material in detail, including information on excavation and processing strategies. The fossils add to the growing record of human remains from southern Africa from well-defined archeological deposits at other sites such as Klipdrift (Harvati et al. 2015), Klasies River (Grine 2012; Grine et al. 2017), Blombos (Grine et al. 2000; Grine and Henshilwood 2002), Diepkloof (Verna et al. 2013), and Die Kelders (Grine et al. 1991, 1996; Grine 2000). At Sibudu, the human fossils are associated with three-dimensional stratigraphic data and detailed diachronic information on material culture. This context might help to inform patterns of biocultural evolution in our species and allows for the anatomical characterization of Late Pleistocene human populations associated with early behavioral innovations such as the manufacture of plant bedding (Wadley et al. 2011), formal bone tools (d'Errico et al. 2012), compound adhesives used in hafting technologies (Wadley et al. 2009) and serrated bifacial pieces by pressure flaking (Rots et al. 2017).

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