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Middle Stone Age human fossils from Die Kelders Cave 1, Western Cape Province, South Africa

Die Kelders Cave 1 (DK1) preserves a thick series of Middle Stone Age (MSA) horizons that date to a fairly short temporal interval sometime between about 60 and 80 ka ago. Twenty-seven human fossils, comprising 24 isolated teeth, a mandibular fragment, and two manual middle phalanges derive from seven of the 12 layers. The vast majority are children, and all may have come from sub-adult individuals. The entire assemblage may represent a minimum of ten individuals. As might be expected for teeth of such antiquity, most of the DK1 crowns tend to be large in comparison to recent African homologues. They tend to be smaller than, albeit more similar in size to, the teeth of penecontemporaneous archaic populations from Eurasia. The majority of morphological variants displayed by the DK1 crowns characterize the teeth of recent sub-Saharan Africans, and the DK1 crowns resemble those of recent Africans in a number of traits that have been used to define a sub-Saharan African regional complex. The morphological similarities between the DK1 MSA and recent African teeth, however, do not necessarily signify a close evolutionary relationship between them, because these crowns variants appear to be plesiomorphic.

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Introduction

The site of Die Kelders (34°32'S, 19°22'E) comprises a pair of contiguous caves, Die Kelders 1 (DK1) and Die Kelders 2 (DK2), located at sea level on the southern coast of the Western Cape Province about 1 km from the town of De Kelders. Excavation by F. R. Schweitzer between 1969 and 1973 revealed a thick series of Middle Stone Age (MSA) deposits in DK1 (Tankard & Schweitzer, 1974, 1976; Tankard, 1976; Schweitzer, 1979). These were recognized as comprising 12 layers (numbered 4–15) of alternating MSA occupation and non-occupation horizons. The even numbered occupation horizons were observed to be generally rich in archaeological debris, being typically highly compacted and heavily organic. The odd numbered non-

occupation layers contained abundant microfauna, but less artefactual and organic material (Tankard & Schweitzer, 1974, 1976; Tankard, 1976). As noted by Marean *et al.* (1999), however, these so-called “sterile” layers have variable abundances of lithic artefacts and large mammal bones.

Schweitzer's work resulted in the recovery of 13 human teeth. Nine of these specimens were described by Grine *et al.* (1991); the other four were described in Avery *et al.* (1997). Two 8-week excavation seasons in 1992 and 1993 under the joint leadership of a team from the State University of New York at Stony Brook, Stanford University and the South African Museum resulted in the recovery of an additional two human fossils. These specimens were also described in Avery *et al.* (1997). A third 8-week field season in 1995 resulted in the recovery of a

further 12 human specimens. These have been described by Grine (1998).

Sedimentological and faunal evidence obtained by Tankard and Schweitzer (Tankard & Schweitzer, 1974, 1976; Tankard, 1976) placed the DK1 MSA sequence in a cold interval, perhaps equivalent to oxygen-isotope stage 4, between approximately 74 and 59 ka (Grine *et al.*, 1991). Electron spin resonance (ESR) data obtained from the 1992 and 1993 field seasons suggested that the top of the MSA sequence dates to either ca. 60 ka (assuming an Early Uptake Model) or ca. 80 ka (assuming a Linear Uptake Model), although it was intimated by Avery *et al.* (1997) that the younger age was perhaps more likely because of an earlier suggestion that the Howieson's Poort might be represented in the DK1 sequence (Grine *et al.*, 1991). However, the 1995 excavation season provided a large number of additional artefacts, and analysis of the whole lithic assemblage has led to the conclusion that the Howieson's Poort is not represented at DK1 (Thackeray, 2000). This observation weakens the circumstantial archaeological rationale for preference of the younger of the two possible ESR ages recorded in Avery *et al.* (1997).

The 1995 field season also provided Thermoluminescence (TL) and additional ESR samples. The former have yielded a date of ca. 60–70 ka (Feathers & Bush, 2000), and the ESR data have been interpreted to be consistent with that date (Schwarcz & Rink, 2000). However, because both techniques are dependent upon the same environmental factors—most notably the level of water saturation of the sediments—the employment of a date obtained from one (TL) to determine the other (ESR) is circular. TL and ESR do not provide independent verification of the age of the site. Nevertheless, these techniques yield dates that are consistent with the original sedimentological interpretation,

which placed the MSA sequence in DK1 between approximately 74 and 59 ka (Grine *et al.*, 1991).

Perhaps most importantly, the ESR data indicate that the entire MSA sequence at this site accumulated over a very short temporal interval (Schwarcz & Rink, 2000). This means that the human fossil assemblage from DK1 may be treated as a temporally rather uniform sample.

As noted above, the human fossils from the MSA layers of DK1 have been described in detail and illustrated elsewhere. This paper provides a summary of the salient morphological details and metrical parameters of these specimens. The location of each human fossil within the stratigraphic and coordinate systems adopted by us (Marean *et al.*, 2000) is documented, and possible individual associations among the isolated elements are discussed.

Human remains from the MSA

Twenty-seven separate human remains have been recovered from the MSA sediments of DK1 (Table 1). Most of the specimens comprise isolated teeth; one is a small fragment of mandible, and two are manual phalanges. The majority (18 specimens, or 2/3 of the sample) derive from Layer 6, although human fossils are known also from Layers 4/5, 8, 10, 11, 14 and 15 (Table 1). The vast majority of the specimens represent children, and all may derive from sub-adult individuals. Thus, 15 are deciduous teeth, one is a mandibular fragment with an unerupted LI₁, and two are immature permanent tooth germs. The seven permanent teeth display only minimal to moderate wear, suggesting that they come from adolescents or very young adults. The two manual middle phalanges do not preserve the proximal base; thus, their epiphyseal status cannot be determined.

The human fossil assemblage is considered here to represent a minimum of ten

Table 1 Human remains from the MSA horizons of Die Kelders Cave 1

Specimen	Element	Layer	Grid	
			co-ordinate	Excavation
AP 6245	Rdi ²	4	F-5*	Schweitzer
AP 6244	Rdm ²	4	F-5*	Schweitzer
AP 6264	LP ⁴	4/5	E-9	1993
AP 6242	RM ₁	6	G-4*	Schweitzer
AP 6243	Rdm ²	6	G-4*	Schweitzer
AP 6246	Ldm ₁	6	G-4*	Schweitzer
AP 6247	Ld _c	6	G-4*	Schweitzer
AP 6248	Rdi ₂	6	D-5*	Schweitzer
AP 6255	Rd ^c	6	C-6†	Schweitzer
AP 6256	Ld _c	6	C-6†	Schweitzer
AP 6257	Rdm ²	6	F-5†	Schweitzer
AP 6267	phalanx	6	E-8	1993
AP 6275	LI ¹	6	E-8	1995
AP 6276	mandible	6	F-12	1995
AP 6277	LM ₁	6	H-12	1995
AP 6280	RC	6	G-10	1995
AP 6281	RP ⁴	6	E-11	1995
AP 6282	RM ₂	6	E-11	1995
AP 6288	Ldi ₂	6	G-8	1995
AP 6289	phalanx	6	G-11	1995
AP 6290	Ldi ₁	6	E-11	1995
AP 6291	Ldm ₁	8	E-2	1995
AP 6278	Rdi ¹	10	F-11	1995
AP 6258	LP ⁴	11	D-4†	Schweitzer
AP 6250	Rd ^c	14	D-5*	Schweitzer
AP 6279	RP ₄	14	E-6	1995
AP 6249	Rdi ¹	15	H-4*	Schweitzer

*Specimens listed in Grine *et al.* (1991; Table 4), and †specimens listed in Avery *et al.* (1997; Table 5) employed Schweitzer's grid reference. That reference is one letter designation (i.e., 1 m) to the north of the co-ordinates established in 1992. The grid co-ordinates used in the present table correspond to the latter.

juvenile individuals. One pair of specimens from Layer 4/5, four pairs from Layer 6, and one pair from Layers 4/5 and 6 are considered to be very strong candidates for association (i.e., to come from one individual). Possible individual association among specimens are discussed after each descriptive summary.

The following provides a brief discussion of the human remains according to the stratigraphic layer from which they were excavated. The descriptive terminology employed here follows that used elsewhere (Grine *et al.*, 1991; Avery *et al.*, 1997; Grine,

Table 2 Crown diameters of human deciduous teeth from the MSA horizons of Die Kelders Cave 1

Element	Specimen	MD meas.	MD est.	BL
Maxillary				
di ¹	AP 6249	7.2	(7.5)	5.3
	AP 6278	8.2	—	6.4
di ²	AP 6245	5.8	5.8	5.2
d ^c	AP 6250	7.5	7.7	6.0
	AP 6255	7.7	7.9	7.2
dm ²	AP 6243	9.4	9.4	10.5
	AP 6244	8.5	(8.8)	9.6
	AP 6257	9.0	9.5	10.3
Mandibular				
di ₁	AP 6290	4.8	(5.1)	4.8
di ₂	AP 6248	5.6	5.7	4.5
	AP 6288	5.0	—	5.0
d _c	AP 6247	6.9	7.1	6.3
	AP 6256	6.5	6.6	5.7
dm ₁	AP 6246	9.0	9.1	7.9
	AP 6291	8.0	8.1	6.8

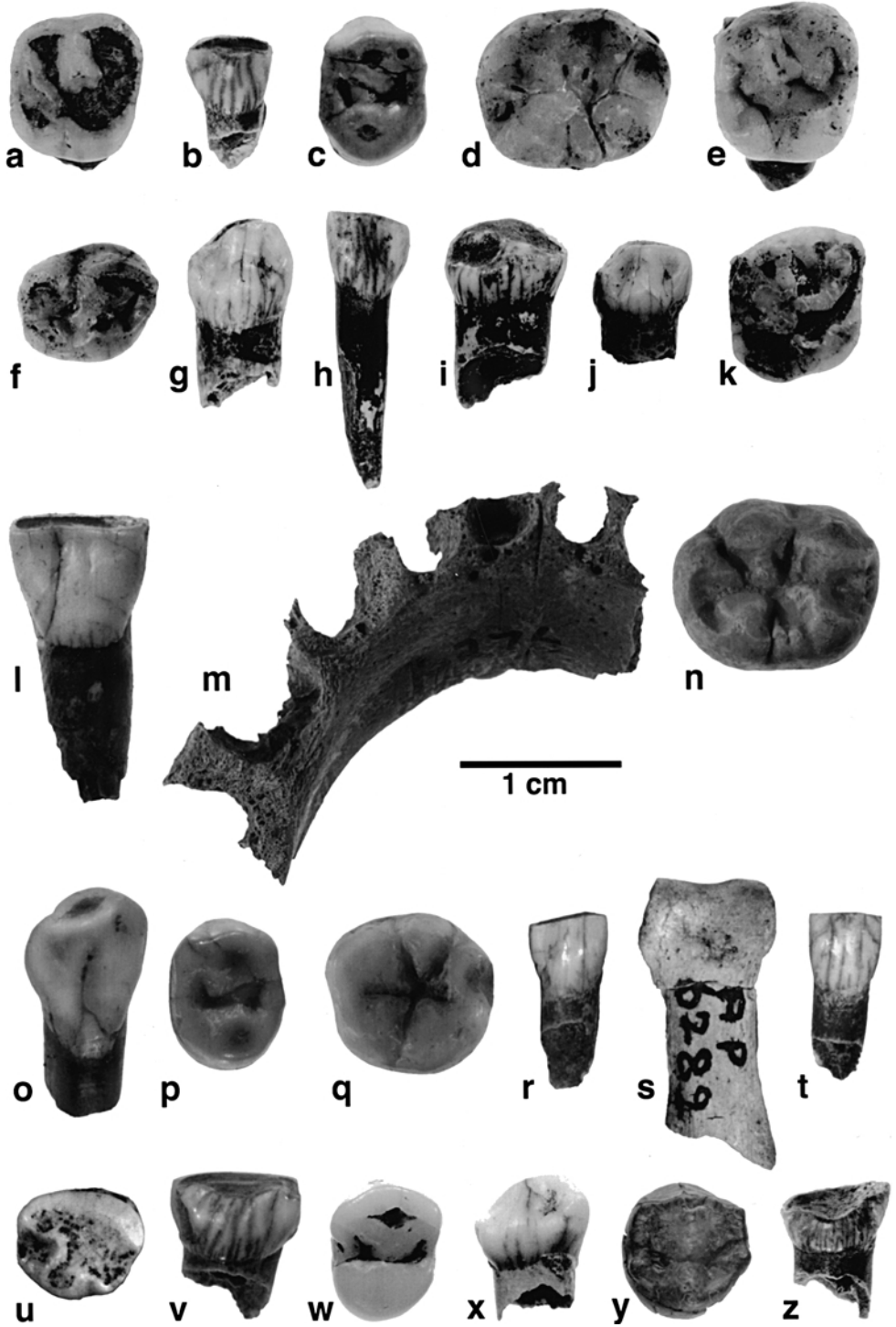
Table 3 Crown diameters of human permanent teeth from the MSA horizons of Die Kelders Cave 1

Element	Specimen	MD meas.	MD est.	BL
Maxillary				
I ¹	AP 6275	9.1	9.3	6.6
C	AP 6280	8.1	8.2	8.8
P ⁴	AP 6258	7.5	7.7	9.4
	AP 6264	7.3	7.6	10.1
	AP 6281	7.2	7.5	9.8
Mandibular				
P ₄	AP 6279	8.2	8.3	—
M ₁	AP 6242	12.2	12.2	10.0
	AP 6277	13.3	13.3	11.2
M ₂	AP 6282	10.7	10.8	10.3

1998). The mesiodistal (MD) and buccolingual (BL) diameters of the tooth crowns are recorded in Tables 2 and 3. The specimens are depicted in Figure 1.

Layer 4/5 specimens

Three teeth derive from this stratigraphic layer. Two (SAM-AP 6244 and 6245) were excavated by Schweitzer from the eastern



side; one (SAM-AP 6264) was recovered later from a more westerly location where, as noted by Marean *et al.* (2000), the rather atypical eastern division of Layers 4 and 5 is not apparent. Marean *et al.* (2000) have observed that Layers 4 and 5 in the more extensive western exposures are not readily separable; rather “Layer 4” in this larger area consists of a number of “occupation” lenses within a sedimentologically rather uniform horizon. Thus, while SAM-AP 6244 and SAM-AP 6245 were described as deriving from Layer 4 (Grine *et al.*, 1991), and SAM-AP 6264 was identified as being from Layer 4/5 (Avery *et al.*, 1997), all three are considered to come from a single stratigraphic unit.

SAM-AP 6244 [Figure 1(a)] is a heavily worn Rdm² with a short segment of the root neck. The crown has a square outline, and it is apparent that all four principal cusps were well-developed. A qualitative assessment suggests that the pulp chamber was likely to have been, at most, only marginally “hypotaurodont”.

SAM-AP 6245 [Figure 1(b)] is a heavily worn Rdi² with a short root segment. The moderate lingual cervical eminence is distally skewed. There is no lingual shoveling; instead, this surface is dominated by a moderate median eminence.

SAM-AP 6264 [Figure 1(c)] is a moderately worn LP⁴ with a complete root. The protocone and paracone are of nearly equivalent size, and situated on the same transverse axis. They are connected by a

low transverse ridge that separates a small mesial from a larger distal fovea.

Associations. Two of the three specimens (SAM-AP 6244 and 6245) almost certainly come from the same individual. Their degree of wear is compatible, they are identically preserved, and they derive from the same grid square. SAM-AP 6264 represents a second, ontogenetically older individual. This specimen is probably associated with SAM-AP 6281, a RP⁴ from subjacent Layer 6. These premolars are considered to be antimeres because the crowns are very similar in size (Table 3), they have the same degree of wear, and they possess nearly identical crown morphology, including the relatively unusual transverse ridge. Both crowns also display the same pattern of enamel hypoplasia, which consists of one or more large, separate pits on the buccal face and a horizontal band of small pits along the lingual surface. Moreover, the hypoplastic mottling occurs at the same level (i.e., the same distance from the cervical margin) on both specimens, which suggests a developmental “insult” at approximately seven to eight years of age. Finally, SAM-AP 6264 and 6281 are from reasonably proximate horizontal coordinates (i.e., grid squares E-9 and E-11 respectively).

Layer 6 specimens

Fifteen isolated teeth, a small mandibular fragment, and two manual phalanges derive from this layer. Eight of these specimens were excavated by Schweitzer, one was

Figure 1. Middle Stone Age human remains from the Die Kelders Cave 1. (a) occlusal view of SAM-AP 6244 Rdm², (b) lingual view of SAM-AP 6245 Rdi², (c) occlusal view of SAM-AP 6264 LP⁴, (d) occlusal view of SAM-AP 6242 RM₁, (e) occlusal view of SAM-AP 6243 Rdm², (f) occlusal view of SAM-AP 6246 Ldm₁, (g) lingual view of SAM-AP 6247 Ld₃, (h) lingual view of SAM-AP 6248 Rdi₂, (i) lingual view of SAM-AP 6255 Rd^c, (j) lingual view of SAM-AP 6256 Ld₃, (k) occlusal view of SAM-AP 6257 Rdm², (l) lingual view of SAM-AP 6275 LI¹, (m) superior view of SAM-AP 6276 mandible, (n) occlusal view of SAM-AP 6277 LM₁, (o) lingual view of SAM-AP 6280 RC, (p) occlusal view of SAM-AP 6281 RP⁴, (q) occlusal view of SAM-AP 6282 RM₂, (r) lingual view of SAM-AP 6288 Ldi₂, (s) palmar view of SAM-AP 6289 manual middle phalanx, (t) lingual view of SAM-AP 6290 Ldi₁, (u) occlusal view of SAM-AP 6291 Ldm₁, (v) lingual view of SAM-AP 6278 Rdi¹, (w) occlusal view of SAM-AP 6258 LP⁴, (x) lingual view of SAM-AP 6250 Rd^c, (y) occlusal view of SAM-AP 6279 RP₄, (z) lingual view of SAM-AP 6249 Rdi¹.

recovered in 1993, and the others were found during the 1995 field season.

SAM-AP 6242 [Figure 1(d)] is a very lightly worn RM_1 with nearly complete roots. The apices of the roots had not yet completed closure at time of death, suggesting an age of about 6 years on the basis of modern human standards (Smith, 1991). All principal cusps are well-developed; there is no tuberculum sextum (C6), but a very large tuberculum intermedium (C7) is present. The distal trigonid crest is incised; the Y occlusal pattern results from the presence of a distinct metaconid deflecting wrinkle. The shallow mesiobuccal groove terminates in a small pit, and there is no protostylid development. The pulp chamber is marginally hypotaurodont according to the quantitative categories defined by Keene (1966) and Shifman & Chanannel (1978).

SAM-AP 6243 [Figure 1(e)] is a very slightly worn Rdm^2 with much of the mesiobuccal root and short segments of the lingual and distobuccal roots. All four principal cusps are well-developed, and the mesial and distal marginal ridges are moderately thick. A distinct, V-shaped Carabelli pit does not interrupt the curve of the lingual surface. There is no paramolar tubercle. A qualitative assessment suggests that the pulp chamber is, at most, only marginally "hypotaurodont."

SAM-AP 6246 [Figure 1(f)] is a moderately worn Ldm_1 . The crown has a trapezoid occlusal outline, being BL broader across the trigonid. Four principal cusps are present, and there is a moderately convex tuberculum molare.

SAM-AP 6247 [Figure 1(g)] is a moderately worn Ld_c . The moderate lingual cervical prominence is skewed distally; there is no lingual tubercle. Lingual shoveling is absent; there is a broad median lingual ridge.

SAM-AP 6248 [Figure 1(h)] is a moderately worn Rdi_2 with a nearly complete root. The lingual cervical prominence is slight, and there is no tubercle. Shoveling is absent.

SAM-AP 6255 [Figure 1(i)] is a heavily worn Rd_c with a moderate, distally skewed lingual cervical prominence.

SAM-AP 6256 [Figure 1(j)] is a slightly worn Ld_c . The slight to moderate lingual cervical eminence supports a moderate median ridge. There is no lingual tubercle, and shoveling is absent.

SAM-AP 6257 [Figure 1(k)] is a moderately worn Rdm^2 crown. It has a slightly trapezoidal occlusal outline; all four principal cusps are well-developed. The buccal groove terminates gradually, and there is no paramolar tubercle.

SAM-AP 6267 (no illustration) is the distal portion of a manual middle phalanx. Because the proximal base is missing, it is not possible to determine the state of epiphyseal fusion. If this represents an adult element, the ML diameter of 7.9 mm across the distal epicondyles places it within the fiducial limits of modern human sample means for ray V (Susman, 1976).

SAM-AP 6275 [Figure 1(l)] is the moderately worn LI^1 with a short segment of root. The slight lingual cervical enamel prominence rises to a faint median ridge; there is no lingual tubercle, and no lingual shoveling.

SAM-AP 6276 [Figure 1(m)] is part of the alveolar margin of a juvenile mandible containing the developing LI_1 crown in its crypt. The degree of crown formation corresponds to an age at death of between 4 and 5 years on the basis of recent human standards. The fragment is preserved from the Ldm_{1-2} alveolar septum to the Rdi_{1-2} alveolar septum. The presence or absence of a chain cannot be ascertained because the mental region below the incisive alveoli is missing.

SAM-AP 6277 [Figure 1(n)] is an incompletely formed LM_1 crown. Its degree of development conforms to an age at death of about 5 years on the basis of recent human standards. The five principal cusps are well-developed, exhibiting a Y pattern.

There is a bifid C7, but no C6. The fovea anterior is enclosed distally by a low ridge. There is no metaconid deflecting wrinkle, and no accessory distal trigonid crest. The mesiobuccal and distobuccal grooves end in vertical rows of small pits, and there is no protostylid development.

SAM-AP 6280 [Figure 1(o)] is a moderately worn RC with a short segment of root. The crown is somewhat asymmetric, with a higher mesial and a lower, but more prominent distal shoulder. The lingual cervical prominence is moderately elevated, rising to a broad median ridge; there is no tubercle, and no shoveling. Although the crown is worn, there is no indication of an accessory mesial ridge [the "Bushman" canine variant (Morris, 1975)], and there is no distal accessory ridge.

SAM-AP 6281 [Figure 1(p)] is a moderately worn RP⁴ with a short root segment. The protocone and paracone are nearly equal in size and bisected by the midcrown BL axis. A moderate transverse ridge runs between their apices; this appears to represent the morphogenetic equivalent of an occlusal "odontome".

SAM-AP 6282 [Figure 1(q)] is a slightly worn RM₂ with a short segment of root. The crown has an asymmetrical outline. All five cusps are present, and the hypoconulid is reduced. There is a large C6, but no C7. The cusps and occlusal fissures form a + pattern. There is no metaconid deflecting wrinkle, and no accessory distal trigonid ridge. The mesiobuccal and distobuccal grooves are very shallow. The buccal protoconid face is pitted in the region of the protostylid cingulum.

SAM-AP 6288 [Figure 1(r)] is a moderately worn Ldi₂ with a short segment of root that appears to be resorptive, conforming to an age at death of some 5 years on the basis of recent human standards. The slight lingual cervical prominence is skewed strongly distally, and there is no shoveling.

SAM-AP 6289 [Figure 1(s)] is an incomplete manual middle phalanx, preserving the distal end and much of the body. Because the proximal base is missing, it is not possible to determine the state of epiphyseal fusion. If this represents an adult element, the ML diameter of 8.5 mm across the distal epicondyles places it within the fiducial limits (i.e., two standard deviations of the mean) of modern human sample means for rays II through V (Susman, 1976). Its gray discoloration, surface fragmentation and calcined appearance, however, indicate that it was burnt, and its size may have been affected by the shrinkage that commonly accompanies burning. This may reduce a bone's size by some 12–15% (Warren, 1995).

SAM-AP 6290 [Figure 1(t)] is a moderately worn Ldi₁ with a short segment of root that appears to be resorptive, conforming to an age at death of approximately 5 years on the basis of recent human standards. The lingual cervical enamel prominence is slight; there is no tubercle, and there is no shoveling.

Associations. A minimum of four individuals is represented by this assemblage. As noted above, the SAM-AP 6281 RP⁴ quite probably represents the antimere of SAM-AP 6264 from Layer 4/5. SAM-AP 6281 may also be associated with SAM-AP 6275 (LI¹), 6280 (RC) and 6282 (M₂), inasmuch as the degree of wear displayed by the four is compatible with their having derived from a single adolescent individual.

SAM-AP 6246 (Ldm₁) and 6247 (Ld_c) almost certainly come from one individual. They are comparably worn, and their opposing interproximal contact facets (ICFs) fit together well. These two teeth also may be associated with the virtually unworn SAM-AP 6242 M₁ and the slightly worn SAM-AP 6243 dm².

SAM-AP 6255 (Rd^c) and 6257 (Rdm²) are very likely to be associated with one another. They display wear that is

compatible with their having derived from a single individual, and they are identically preserved.

SAM-AP 6248 (Rdi₂) and 6290 (Ldi₁) are considered very likely to be associated with one another. They display wear that is consistent with their having derived from the same individual, and they are preserved identically. These two deciduous incisors are compatible in terms of wear with either the individual represented by SAM-AP 6246/6247 or the one represented by SAM-AP 6255/6257. The former association is considered to be perhaps more reasonable. Elsewhere (Grine, 1998), it was noted that the opposing ICFs of SAM-AP 6290 and 6288 closely matched one another, and it was suggested that these two specimens probably derive from a single individual. Upon further examination of the entire sample, however, this putative association is considered to be less likely. As noted below, SAM-AP 6288 is regarded as being more reasonably associated with SAM-AP 6256.

SAM-AP 6256 (Ld_c) and 6288 (Ldi₂) are considered to probably represent a single, very young child. They display wear that is compatible with their having derived from a single individual, and they are preserved identically. These two teeth are possibly associated with the SAM-AP 6276 mandibular fragment inasmuch as their root stumps are compatible in size with the preserved alveoli of the latter (the roots of the other d_c and the other di₂, on the other hand, do not fit into the respective alveoli). Finally, the SAM-AP 6277 developing M₁ crown is probably associated with SAM-AP 6276 inasmuch as its degree of development is the same as that of the I₁ preserved in its mandibular crypt. The developmental status of both crowns indicate derivation from a child of approximately 5 years on the basis of modern human standards.

Thus, the ontogenetically youngest individual from Layer 6 is represented by the

SAM-AP 6256/6276/6277/6288 composite. The next youngest child is represented by the SAM-AP 6242/6243/6246/6247/6248/6290 composite. The oldest of the three children is represented by the SAM-AP 6248/6255/6257/6290 composite. The fourth individual, which is also the oldest (probably being adolescent) is represented by the SAM-AP 6275/6280/6281/6282 composite.

The two manual phalanges (SAM-AP 6267 and 6289) may derive from one or two individuals. This individual may have been the adolescent and/or the oldest of the three children. Alternatively, of course, they may come from an individual (or individuals) not represented by dental remains.

Layer 8 specimens

One tooth is known from this layer. It was recovered during the 1995 field season.

SAM-AP 6291 [Figure 1(u)] is a heavily worn Ldm₁ with a short segment of root neck that appears to be resorptive. This would conform to an age of 9 or 10 years by modern standards. The crown is asymmetric, with a trapezoidal outline. Only three cusps (with a dominant protoconid) are evident. The tuberculum molare is slight.

Associations. SAM-AP 6291 displays a degree of occlusal wear that is comparable to that shown by the oldest child (i.e., the SAM-AP 6255 composite) from Layer 6, but there is no indication of association between the specimens from these two layers.

Layer 10 specimens

One tooth is known from this layer. It was recovered during the 1995 field season.

SAM-AP 6278 [Figure 1(v)] is a heavily worn Rdi¹ with a very short segment of root. The lingual cervical enamel prominence is moderate; there is no tubercle. The base of a broad, weak median ridge is preserved. The degree of shoveling cannot be ascertained.

Associations. SAM-AP 6278 displays a degree of wear that is comparable to that evinced by the oldest child (i.e., the SAM-AP 6255 composite) from Layer 6, and is thus compatible in its degree of wear with SAM-AP 6291 from Layer 8, but there is no indication of association between the specimens from these different layers.

Layer 11 specimens

One tooth is known from this layer. It was recovered during Schweitzer's excavations.

SAM-AP 6258 [Figure 1(w)] is a slightly worn LP⁴ with a complete root. The protocone is somewhat larger than the paracone. Their apices are bisected by the BL crown axis, and separated by a deep longitudinal fissure.

Associations. There is no indication that SAM-AP 6258 is associated with any other specimens from the MSA sequence.

Layer 14 specimens

Two teeth are known from this layer. One was recovered during Schweitzer's excavations; the other was discovered during the 1995 field season.

SAM-AP 6250 [Figure 1(x)] is a moderately worn Rd^c with a short segment of root. The crown has an asymmetric outline; the higher mesial shoulder is more prominent. The moderate lingual cervical enamel prominence is skewed distally; there is no tubercle. The crown is not shoveled.

SAM-AP 6279 [Figure 1(y)] is an unworn, incomplete RP₄ crown. The protoconid is larger than the metaconid. They occupy the same BL axis, and are joined by a low transverse ridge. The mesial marginal ridge supports a single, small accessory cuspid; the distal presents two small accessory cuspidals.

Associations. A minimum of one juvenile individual is represented by these two teeth. However, there are no morphological grounds for their association beyond the

presumed degree of P₄ crown development being compatible with it and the d^c having derived from a single child.

Layer 15 specimens

One tooth is known from this layer. It was recovered during Schweitzer's excavations.

SAM-AP 6249 [Figure 1(z)] is a heavily worn Rdi¹ with a short segment of root. The moderate lingual cervical enamel prominence is skewed distally. The degree of shoveling cannot be determined.

Associations. There is no indication that SAM-AP 6249 is associated with any other specimen from the MSA sequence.

Crown size comparisons

The dimensions of the DK1 MSA tooth crowns are recorded in Tables 2 and 3. Elsewhere (Grine *et al.*, 1981; Avery *et al.*, 1997; Grine, 1998) these values have been compared individually with those recorded for penecontemporaneous archaic Eurasian (i.e., Neandertal) and modern African samples. To summarize those analyses, the DK1 crown diameters generally fall within, but commonly close to the upper termini of the fiducial limits of the modern African sample means. The most notable exceptions, which fall above those limits, are the MD and BL values for one of the upper and one of the lower deciduous canines. In all but two cases (the BL diameters of the I¹ and one of the di¹s), the DK1 values fall within the fiducial limits of the Neandertal sample means. The DK1 diameters tend to be larger than the recent African sample means, and in most instances they more closely approximate the larger Neandertal sample averages. Exceptions are the MD and BL diameters of the M₂, the MD diameter of one of the P⁴s, the MD and BL diameters of one of the dm₁s, and the BL diameter of the I¹.

Crown morphology comparisons

With regard to the permanent teeth from DK1, the sole I^1 lacks a lingual tubercle and is not shoveled. [Jacobson \(1982\)](#) has recorded that approximately 90% of recent southern African blacks also lack an I^1 tubercle, and that about 15% display any degree of lingual shoveling. [Scott and Turner \(1997\)](#) have also recorded low frequencies of I^1 shoveling in South African blacks (ca. 9%) and San (ca. 13%), and [Irish](#) has noted a low incidence of this trait among sub-Saharan Africans in general, although quite different frequencies (28.1% vs. 5.3%) are recorded by him for this population ([Irish, 1997](#); cf. Tables 3 and 4).

The sole C for DK1 appears to lack a mesial canine ridge. This feature occurs in close to 40% of recent San canines ([Irish, 1997](#); [Scott & Turner, 1997](#)), but in lower frequencies among South Africans (13%) ([Jacobson, 1982](#)) and sub-Saharan Africans in general (18.1%) ([Irish, 1997](#)). The DK1 crown lacks a distal accessory ridge, which occurs among 70% of sub-Saharan Africans ([Irish, 1997](#)).

With regard to the P^4 , two (probable antimeres) have a distinct transverse occlusal ridge. This rare feature is probably the morphogenetic equivalent of the occlusal tubercle (odontome) that [Scott & Turner \(1997\)](#) have recorded in 0% of San and 0.5% of South Africans. The third DK1 P^4 lacks this variant.

The sole P_4 crown is morphologically unremarkable insofar as it is preserved. It is two-cusped, in which it resembles the majority of recent human homologues.

The two M_1 s are five-cusped with a Y-pattern, which are common features in almost all recent human populations, including South Africans and San ([Grine, 1981](#)). Both DK1 crowns lack a C6, in which they resemble the majority (ca. 70%) of modern sub-Saharan Africans ([Irish, 1997](#)), and about 94% of recent South

Africans and 84% of San ([Grine, 1981](#)). Both have a C7, which has been identified by [Irish \(1997\)](#) as part of the dental suite that differentiates sub-Saharan Africans from other populations. He cited an overall sub-Saharan incidence of about 39%; some 15% to 25% of southern Africans evince it ([Grine, 1981](#); [Scott & Turner, 1997](#)). One of the two crowns lacks a deflecting wrinkle, while the other possesses it. This variant is absent from the vast majority (ca. 70% to 85%) of recent sub-Saharan African homologues ([Grine, 1981](#); [Scott & Turner, 1997](#); [Irish, 1997](#)). Both DK1 M_1 s lack an accessory distal trigonid crest, which is a worldwide rarity. Both lack a protostylid, which conforms to the condition of about 95% of South African homologues ([Jacobson, 1982](#)).

The sole M_2 is five-cusped, a variant that is present with somewhat greater frequency among recent Africans (ca. 48% to 70% of South Africans; ca. 78% to 90% of San) than among other populations ([Grine, 1981](#); [Scott & Turner, 1997](#)). Its + pattern is possessed by 67% of South African and 47% of San homologues ([Grine, 1981](#)), and its lack of a C7 corresponds with the vast majority of South African (98%) and San (100%) M_2 s ([Grine, 1981](#)). On the other hand the DK1 crown has a C6. South African and San M_2 s display among the lowest frequencies (4% and 13% respectively) of this variant among worldwide populations ([Grine, 1981](#)). The DK1 crown lacks a metaconid deflecting wrinkle, which accords with over 95% of South African and San homologues ([Grine, 1981](#)), and its lack of a protostylid accords with nearly 100% of recent South African M_2 s ([Jacobson, 1982](#)).

With regard to the DK1 deciduous incisors, the two di^1 s lack a lingual tubercle, a feature that is very infrequent among recent black South African (0%) and San (9%) homologues ([Grine, 1986, 1990](#)), and infrequent also among other worldwide populations. Both DK1 crowns have a moderate

lingual cervical enamel prominence that is skewed distally, whereas the cingulum on the majority of modern South African black and San homologues is weaker (90% and 100% respectively) and symmetrical (72% and 86% respectively) (Grine, 1986, 1990). The sole DK1 di^2 also lacks a lingual tubercle, which accords with the vast majority of recent southern African homologues, but it has a moderate, distally skewed lingual cingulum. In this it differs from the majority of South African and San di^2 s, which display a weaker (100% and 98% respectively) and symmetrically disposed (85% and 66% respectively) cingulum (Grine, 1986, 1990). Neither the sole di_1 , nor the pair of di_2 s exhibits lingual tubercle development, which is in accord with the majority of modern human homologues. None of the deciduous incisors that preserve the lingual face (i.e., the di^2 , and both di_2 s) is shoveled, a rare variant among recent southern African homologues as well (Grine, 1986, 1990).

With reference to the DK1 deciduous canines, both d^c s and both d_c s possess a moderate, distally skewed lingual cingulum. In this regard they differ from the great majority of recent South African and San homologues, in which this character is weaker and symmetrically disposed (Grine, 1986, 1990). However, none of the DK1 crowns possesses a lingual tubercle. The upper canine crown that preserves the lingual surface, and both mandibular crowns lack shoveling. In these features they resemble the vast majority of modern South African and San homologues (Grine, 1986, 1990).

The two DK1 dm_1 s have a trapezoidal occlusal outline, which is manifest also by the majority of South African (95%) and San (80%) homologues. The fovea anterior of one is closed by a complete mesial marginal ridge, while in the other this ridge is incised mesial to the protoconid. Only some 4% of San and 8% of South African dm_1 s

share the former configuration; the majority have the latter morphology. One of the DK1 crowns has four cusps, in which it is like the molars of the vast majority of recent sub-Saharan African and other populations. The other DK1 dm_1 is unusual in possessing only three cusps. This variant is present in very few recent South African (0%) and San (9%) teeth (Grine, 1986, 1990). It appears to be uncommon also among other recent human populations, with a maximum frequency of 18% having been recorded for a Tristanite sample of European heritage (Thomsen, 1955).

The three dm_2 s from DK1 are like the majority (ca. 90%) of recent Southern African homologues in that they have four well-developed principal cusps, and they resemble the majority (ca. 70%) of these recent crowns in that the buccal groove is shallow and terminates gradually. The one crown that preserves the mesiolingual face of the protocone possesses a Carabelli pit, a configuration that characterizes the majority of modern southern African dm_2 s (Grine, 1986, 1990). The two DK1 molars that preserve any occlusal detail present moderate mesial and distal marginal ridges, in which they differ from the majority of recent South African black and San homologues, where these crests are thinner (Grine, 1986, 1990).

Discussion

The question of whether modern humans (i.e., *Homo sapiens*) arose from a common source population in Africa and then spread through migration and replacement (Stringer, 1984, 1989; Bräuer, 1984, 1989; Stringer & Andrews, 1988), or whether we arose polycentrically through multiregional evolution (Thorne & Wolpoff, 1981; Wolpoff *et al.*, 1984, 1994; Wolpoff, 1989, 1992, 1999; Frayer *et al.*, 1993) continues to be debated by palaeoanthropologists. In

particular, the meager palaeontological evidence has been viewed by a number of workers as suggesting that modern human ancestry can be traced back to an African population that is in the order of 100 ka old (Bräuer, 1984; Stringer & Andrews, 1988; Waddle, 1994; Lahr, 1996). Genetic data from both nuclear and mitochondrial DNA and the Y chromosome are generally viewed as being concordant with that scenario (Vigilant *et al.*, 1991; Ruvulo *et al.*, 1993; Hammer, 1995; Pääbo, 1995; Donnelly *et al.*, 1996; Tishkoff *et al.*, 1996; Weiss & von Haeseler, 1996; Hammer *et al.*, 1997; Mountain, 1998), although there have been suggestions that the pattern may have been somewhat more complex (e.g. Templeton, 1993; Relethford, 1995; Harpending *et al.*, 1997).

However, the degree to which the Late Pleistocene inhabitants of sub-Saharan Africa exhibited modern human morphology has been truly a matter of contention. The African fossil evidence from this period comprises two crania from Jebel Irhoud and two crania and a mandible from Dar es Soltan, Morocco (Stringer, 1984; Debénath *et al.*, 1986), two crania and a partial skeleton from the Kibish Formation, Ethiopia (Day & Stringer, 1982; Rightmire, 1984; Day *et al.*, 1991), and a few molars from Mumba Rock Shelter, Tanzania (Bräuer & Mehlman, 1988). In addition, a number of mostly fragmentary specimens are known from South Africa. Among these are a handful of isolated teeth and a fragmentary mandibular corpus from Equus Cave (Grine & Klein, 1985), a few molars from Witkrans Cave (McCrossin, 1992), an incomplete cranium, two mandibles and a few postcranial fragments from Border Cave (de Villiers, 1973, 1976; Rightmire, 1979, 1984, 1986; de Villiers & Fatti, 1982; Bräuer, 1984; Smith, 1985; Morris, 1992; Pfeiffer & Zehr, 1996; Pearson & Grine, 1996), and several cranial, mandibular and postcranial pieces from Klasies River Mouth

(Singer & Wymer, 1982; Rightmire & Deacon, 1991; Grine *et al.*, 1998).

Much of the debate has centered on the South African fossils from Border Cave and Klasies River Mouth. The modern morphology of the cranial and mandibular specimens from Border Cave has been demonstrated by a number of investigators (de Villiers, 1973, 1976; Rightmire, 1979, 1984, 1986; de Villiers & Fatti, 1982; Bräuer, 1984; Smith, 1985). Although multivariate morphometric analyses have questioned the recent African affinities of the BC-1 cranium (van Vark *et al.*, 1989; Corruccini, 1990), their conclusions are rather suspect. Thus, van Vark *et al.* (1989) suggested that while BC-1 may appear modern, it is "quite different from recent *Homo sapiens*." However, this study also indicated that BC-1 is perhaps "only slightly more distinct from Asiatic *Homo erectus* than it is from recent *Homo sapiens*" (van Verk *et al.*, 1989:54). In the same vein, Corruccini (1990) reported that BC-1 falls "far outside the 'morphometric' envelope of all modern African populations," and that "the fossil in no way can be equated with living *H. sapiens*." Such (sometimes patently bizarre) conclusions are difficult to accept in view of the manifestly modern appearance of this large cranium. Indeed, although Beaumont and colleagues (Beaumont *et al.*, 1978; Butzer *et al.*, 1978; Beaumont, 1980) have defended the purported MSA provenience of the BC specimens, Klein (1983) has cited several factors relating to their mode of discovery and state of preservation which indicate that they may not derive from an MSA context. A study of bone mineral crystallinity by Sillen & Morris (1996) has suggested that the postcranial fragments are perhaps the only specimens from Border Cave that are from the MSA with an age in excess of 40 ka. These pieces—particularly the ulna and humerus—display some archaic attributes (Pearson & Grine, 1996; Pfeiffer & Zehr, 1996).

The Klasies River Mouth fossils are probably the most securely dated South African specimens referred to above (Deacon *et al.*, 1986; Deacon & Geleijnse, 1988; Deacon, 1989; Grün *et al.*, 1990). Many of these bones have been interpreted as being indistinguishable from recent human homologues (Stringer & Andrews, 1988; Smith *et al.*, 1989; Rightmire & Deacon, 1991; Bräuer, 1992; Smith, 1993; Stringer & Bräuer, 1994; Bräuer & Singer, 1996; Lam *et al.*, 1996; Pearson & Grine, 1997; Grine *et al.*, 1998). Others, especially the postcranial elements, have been argued to display archaic morphology (Caspari & Wolpoff, 1990; Wolpoff & Caspari, 1990; Wolpoff, 1992; Frayer *et al.*, 1993; Churchill *et al.*, 1996; Pearson & Grine, 1997). Overall, there appears to be a mosaic of archaic and modern morphologies in the Klasies River Mouth assemblage (Smith, 1993; Lam *et al.*, 1996; Pearson & Grine, 1997).

The specimens from the MSA horizons of DK1 add to the meager and all too fragmentary human fossil sample from the Late Pleistocene of South Africa and, as such, may provide additional evidence pertaining to the morphological affinities of these people.

Most of the DK1 MSA teeth tend to be larger than the majority of recent African homologues. Overall they tend to be smaller than, albeit more similar to, the sizes of the teeth of penecontemporaneous archaic populations from Eurasia (i.e., Neandertals). In this regard, they are similar to some of the other later Pleistocene specimens from southern African sites, such as Klasies River Mouth, Equus Cave, and Witkrans (Singer & Wymer, 1982; Grine & Klein, 1985; Rightmire & Deacon, 1991; McCrossin, 1992). However, as with these other samples, the DK1 crown dimensions alone obviously do not signify a closer relationship to Neandertals than to modern Africans. Not only is large tooth size plesio-

morphic, but crown reduction has been shown to have occurred from even more recent archaeological samples to living populations (Frayer, 1977; Brace & Vizthum, 1984; Brace, 1995). Indeed, it is hardly surprising that teeth from a Late Pleistocene South African population should be larger than those of the majority of living southern Africans. Differences of similar (or even greater) magnitude have been recorded elsewhere (e.g., Europe and Asia) between Upper Paleolithic, Mesolithic, Neolithic, and modern-day samples.

Most of the morphological variants possessed by the DK1 teeth characterize the majority, or at least a substantial proportion of the recent indigenous inhabitants of southern Africa. Thus, of more than 40 discrete traits discussed above, in only about ten instances are the DK1 crown variants rare among recent sub-Saharan Africans, and in several of these cases (e.g., P⁴ occlusal “odontome”) the DK1 variants are equally rare among all recent human populations. Irish (1993, 1997) and Scott & Turner (1997) have identified a number of dental variants that serve to define a sub-Saharan regional complex, although there appears to be some disagreement over the frequencies of these variants among these populations. Among the features that have been identified as serving to define the sub-Saharan complex are low incidences of I¹ shoveling, high to moderate frequencies of the \underline{C} mesial ridge, high frequencies of the Carabelli trait on the M¹, high incidences of the M₁ C7, high incidences of five-cusped M₂s, and high incidences of M₂s with a +occlusal pattern. The DK1 crowns are in concert with the majority of recent Africans in most of these characters. Thus, the I¹ (as well as the deciduous incisors, deciduous canines and permanent canine) from DK1 lacks lingual shoveling, the dm² has a Carabelli pit (by extension, it is likely that the M¹ would also display this), both M₁s

possess a C7, and the M₂ has five cusps. In only two instances (the absence of an accessory mesial ridge on the C, and the absence of a Y-pattern on the M₂) do the DK1 crowns differ from the majority of Africans in features that define the sub-Saharan regional complex (Irish, 1993, 1997; Scott & Turner, 1997). Thus, in the majority of cases, the resemblances between the DK1 and modern African teeth serve to differentiate the latter from other geographic populations (Scott & Turner, 1997; Irish, 1997).

Irish (1993) argued that at least one of the variant frequencies that define the sub-Saharan African regional complex (high incidence of M¹ Carabelli trait) is plesiomorphic, but that the high incidences of C mesial ridge and M₁ C7 African populations are derived. Stringer *et al.* (1997), on the basis of a cladistic analysis that included the Krapina Neandertal sample as an outgroup, concurred with Irish (1993) with regard to the M¹ Carabelli trait, but identified all of the other variant frequencies that define the sub-Saharan African regional complex as primitive for modern humans. In most instances, Stringer *et al.* (1997) observed that the frequencies for most crown variants in the Krapina sample to be similar to those for modern sub-Saharan African population samples. Thus, for example, they noted that more than 50% of the Krapina Cs have a mesial ridge, the M₁s show a high incidence of the C7, and 100% of the M₂s are five-cusped. Smith (1976), however, recorded that only 54% of the Krapina M²s have five cusps. On the other hand, Stringer *et al.* (1997) noted that all of the Krapina I¹s are shoveled, which stands in contradistinction to the sub-Saharan African frequencies.

Thus, the morphological similarities between the DK1 teeth and those of recent sub-Saharan Africans do not necessarily indicate modernity for this MSA sample. Similarly, the resemblances do not necessarily signify a close evolutionary relationship between the MSA and recent

inhabitants of southern Africa. This is because the features that serve to characterize recent sub-Saharan Africans appear to be plesiomorphic (Irish, 1997; Stringer *et al.*, 1997). These same dental variants may have characterized earlier populations from which the South African MSA people derived. Unfortunately, dental remains from earlier MSA (or Early Stone Age) populations in sub-Saharan Africa are inadequate to determine crown variant frequencies.

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