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Additional human fossils from Klasies River Mouth, South Africa

A fragmentary temporal bone and partial atlas from the Middle Stone Age (MSA) at Klasies River Mouth (KRM) are described and analyzed. The atlas (SAM-AP 6268) is comparable to Levantine ''Early Modern'', Neandertal and recent human vertebrae. The temporal (SAM-AP 6269) is similar to recent African homologues except that the posteromedial wall of the glenoid fossa is composed entirely of the squamous temporal, a situation that appears to be infrequent among other Pleistocene fossils. The KRM glenoid fossa is also mediolateraly broad and anteroposteriorly short in comparison with many, but not all recent specimens. Nevertheless, the KRM temporal is decidedly modern, both morphologically and metrically, by comparison with other Pleistocene specimens. The limited evidence provided by this bone is consistent with that of other MSA cranial remains from this site in suggesting an overall, if somewhat ambiguous pattern of morphological modernity.

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Introduction

Two human bones, a fragmentary right temporal and a partial atlas, have been identified recently among the faunal remains that were excavated in 1967–1968 by Singer & Wymer (1982) from the Middle Stone Age (MSA) deposits at Klasies River Mouth (KRM). The temporal (SAM-AP 6269) derives from level 16, and the atlas (SAM-AP 6268) from level 14 of Main Cutting A of Cave 1, according to the field nomenclature employed by Singer & Wymer (1982). They therefore come from the Shell and Sand (SAS) Member of Deacon & Geleijnse (1988) and, in common with the majority of the human specimens recovered by Singer & Wymer from layers 14 through 17, they derive from the lower part of that Member (Deacon & Shuurman, 1992). In particular, the temporal is from layer SAS U of Deacon & Geleijnse (1988), and was found in the

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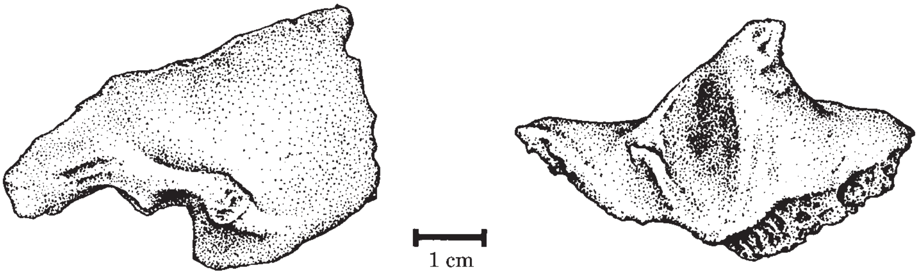

Figure 1. The SAM-AP 6269 right temporal fragment from the Shell and Sand Member of Klasies River Mouth Cave 1 in lateral and inferior views (anterior is to right).

same area as the frontal fragment (KRM 16425). It is possible that both pieces represent a single individual. Evidence from a variety of sources would place the SAS Member remains between about 90 and 60 kyr BP, and probably closer to the former (Deacon & Shuurman, 1992).

Although SAM-AP 6268 and 6269 are incomplete, they are of some significance because of the role that the other (generally equally fragmentary) human fossils from the MSA deposits at KRM have assumed in current debates over the evolution of modern human morphology (Singer & Wymer, 1982; Smith *et al.*, 1989; Caspari & Wolpoff, 1990; Wolpoff & Caspari, 1990; Rightmire & Deacon, 1991; Smith, 1992; Bräuer *et al.*, 1992; Deacon & Shuurman, 1992; Frayer *et al.*, 1993, 1994; Stringer & Bräuer, 1994; Bräuer & Singer, 1996; Deacon, 1995; Churchill *et al.*, 1996; Lam *et al.*, 1996). The temporal and atlas are also important because morphological information pertaining to these elements has yet to be documented from the MSA inhabitants of KRM, or any other South African site of this age.

Descriptions

Temporal (SAM-AP 6269) (Figure 1)

This fragment of a right temporal preserves the glenoid fossa, the root of the zygomatic arch, a small bit of the tympanic plate, part of the anterolateral surface of the mastoid process, and a triangular wedge of the squamous plate. The anteromedial suture with the sphenoid is intact, as is part of the sphenotypanic fissure.

The glenoid fossa is moderately deep (5·9 mm measured from its roof to a line tangent to the tips of the articular eminence and postglenoid process), and strongly concave superiorly. It measures 9·6 mm anteroposteriorly (AP) from the small postglenoid process, and 20·6 mm mediolaterally (ML) from the sphenotypanic fissure. The articular eminence is gently convex, measuring 9·0 mm AP and 19·4 mm ML. The entoglenoid process is composed largely by the temporal; the contribution from the spinous process of the sphenoid would have been slight. The posteromedial wall of the glenoid fossa is formed entirely by the squamous temporal without contribution from the tympanic. The suprameatal triangle houses a deep, 5·6 mm long furrow. The posterior root of the zygoma is very thin (3·1 mm supero-inferiorly (SI) at the margin of the glenoid fossa). The squamous plate is 5·6 mm thick at the level of the squamous suture, and 3·4 mm thick at the broken margin immediately above the root of the zygomatic arch.

Atlas (SAM-AP 6268) (Figure 2)

This preserves an 11 mm segment of the left side of the anterior arch, much of the right lateral mass, and a bit of the anterior root of the ring around the foramen transversarium.

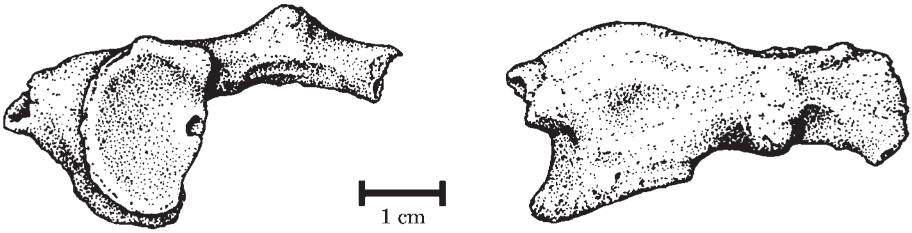

Figure 2. The SAM-AP 6268 atlas vertebra from the Shell and Sand Member of Klasies River Mouth Cave 1 in inferior and anterior views.

The anterior arch measures 10·9 mm SI and 7·2 mm AP. It has sharp inferior and broader superior margins, and supports a moderate anterior midline tubercle. There is a 13·2 mm broad by 8·2 mm high articular facet for the dens of the axis. A small part of the anterior aspect of the superior articular surface is preserved, and while most of this facet is missing, the original height of the lateral mass has been reduced only minimally. This measures 19·0 mm in height. There is a small tubercle just above the inferior articular facet on the medial surface of the lateral mass. The anterior root of the transverse process measures about 8·3 mm SI and 6·5 mm AP. The oval articular surface for the axis measures 21·2 mm long and 14·7 mm broad, and is slightly concave ML. It slopes inferiorly at approximately 27° to the horizontal. The maximum transverse diameter between the lateral margins of the inferior articular facets is estimated to have been 46·4 mm.

Comparisons

Temporal (SAM-AP 6269)

Non-metrical features. Because the KRM fragment does not preserve the sphenoid, it is difficult to ascertain the degree to which this bone may have contributed to the formation of the entoglenoid process. However, the articular surface appears to ride over the sphenotemporal suture, which suggests that the sphenoid provided at least some contribution to the formation of the entoglenoid process. Several workers (Gorjanovic-Kramberger, 1906; Smith, 1976; Sothman, 1994) have noted that the majority (83%) of Krapina Neandertal temporals are unusual in that they lack any contribution from the sphenoid spine to the medial wall of mandibular fossa. Sothman (1994) has also observed that the medial margin of the articular surface on these temporals is located lateral to the sphenotemporal suture.

Sothman (1994: 47) noted that the Krapina mandibular fossae are generally ‘‘shallow with little anterior relief’’, and that this is related to the ‘‘virtually non-existent articular eminence’’ in these specimens. This observation is in keeping with those on other Neandertals, where the glenoid fossa is characteristically shallow with a poorly developed articular process (Vandermeersch, 1978), although some (e.g., Shanidar 5) have a deep glenoid that ‘‘approximates more closely the morphology typical of recent humans’’ (Stringer & Trinkaus, 1981: 146). In contrast to the condition described as characteristic of Neandertals, the KRM glenoid fossa is moderately deep and strongly concave, with a distinct articular eminence. Among African Pleistocene crania, Ndutu, Eliye Springs, Omo II, Singa, Ngaloba (LH 18) and Jebel Irhoud 1 and 2 have capacious, moderately deeply excavated fossae that are bordered by a distinct articular eminence. On the other hand, the Kabwe and Bodo fossae are

Table 1 **Non-metrical variation in temporal bone morphology exhibited by modern African samples (values = %)**

		n	Absent	Small	Moderate	Large
Size of postglenoid process						
Zulu	Male	23	0·0	26·1	47·8	26·1
	Female	27	3·7	33·3	59·3	3·7
	Pooled	50	2·0	30·0	54·0	14·0
Khoisan	Male	28	3·6	28·6	46·4	21·4
	Female	22	0·0	27·3	54·5	18·2
	Pooled	50	2·0	28·0	50·0	20·0
		n	Temporal	Tympanic	Both	
Posteromedial wall of glenoid fossa						
Zulu	Male	23	17·4	73·9	8·7	
	Female	27	11·1	51·9	37·0	
	Pooled	50	14·0	62·0	24·0	
Khoisan	Male	28	10·7	78·6	10·7	
	Female	22	4·6	86·4	9·1	
	Pooled	50	8·0	82·0	10·0	

somewhat shallower, with a rather weakly developed articular eminence. Neandertal and African Pleistocene glenoid fossae appear to be characteristically archaic.

A small postglenoid process, as on the KRM temporal, is exhibited by about 30% of the recent African (Zulu and Khoisan) crania, being more fully developed in the majority (Table 1). This process tends to be well-developed on Neandertal crania. With reference to the Krapina sample, Sothman (1994: Table 11) has recorded that the postglenoid process projects below porion an average 11·6 mm ($n = 12$; S.D. = 1·6 mm; observed range = 9·0 mm–13·7 mm), which is significantly ($P < 0{\cdot}05$) greater than the average of 9·9 mm she reported for a Bosnian Bronze Age sample ($n = 64$; S.D. = 1·5 mm; observed range = 6·0 mm–14·1 mm). Although it is not possible to accurately measure the projection of the postglenoid process below porion in the KRM fragment, this may be estimated at about 6·4 mm, which places the specimen well below the Krapina sample, and at the lower end of Sothman's (1994) recent European range. The postglenoid process is variably developed among African Pleistocene crania. It is large on Bodo, Kabwe, Ndutu, and Jebel Irhoud 1; it is broad but does not project far inferiorly on Omo II; it is moderate on Eliye Springs and Ngaloba, and it is virtually absent on Singa.

The formation of the posteromedial wall of the glenoid fossa by only the squamous temporal, as in the KRM specimen, is unusual among modern Africans, with only about 14% of Zulu and 8% of Khoisan crania exhibiting this condition (Table 1). In the majority, the tympanic forms the medial wall of the mandibular fossa because the squamous temporal does not project downward to any appreciable extent between the entoglenoid and postglenoid process. The majority of European Neandertals also exhibit this configuration (F. H. Smith & P. Sothman, pers. comms) as do the Ndutu, Eliye Springs, Omo II and Singa crania. The squamous temporal and tympanic both contribute to the formation of the medial wall of the glenoid fossa in Bodo and Kabwe.

Table 2 **Measurements of the KRM temporal bone (SAM-AP 6269) compared to recent African sample values**

		n	X	S.D.	Observed range
Depth of glenoid fossa					
	SAM-AP 6269		5·9		
Zulu	Male	23	6·2	1·2	4·1–8·4
	Female	27	5·6	0·9	4·0–7·0
Khoisan	Male	27	5·3	0·9	3·7–6·7
	Female	22	5·1	1·0	3·5–6·6
ML diameter of glenoid fossa					
	SAM-AP 6269		20·6		
Zulu	Male	23	20·4	1·9	17·0–24·0
	Female	27	19·2	1·2	22·5–27·0
Khoisan	Male	27	19·9	1·8	16·0–22·9
	Female	22	19·2	2·1	15·5–22·2
AP diameter of glenoid fossa					
	SAM-AP 6269		9·6		
Zulu	Male	23	11·0	1·3	8·2–12·8
	Female	27	10·7	0·8	9·1–12·3
Khoisan	Male	27	11·0	1·2	9·2–13·5
	Female	22	10·7	1·2	8·5–12·6
Shape of glenoid fossa (AP diam./ML diam. × 100)					
	SAM-AP 6269		46·6		
Zulu	Male	23	54·0	7·0	40·7–68·7
	Female	27	56·1	5·5	46·2–65·4
Khoisan	Male	27	55·7	6·6	43·0–72·6
	Female	22	56·7	10·2	45·8–81·3
ML diameter of articular eminence					
	SAM-AP 6269		19·4		
Zulu	Male	23	21·2	1·9	17·5–25·0
	Female	27	20·3	1·5	17·3–21·7
Khoisan	Male	27	19·5	2·0	15·8–23·8
	Female	22	19·2	2·4	14·4–23·0
AP diameter of articular eminence					
	SAM-AP 6269		9·0		
Zulu	Male	23	8·8	1·2	6·8–11·5
	Female	27	8·5	1·1	6·3–10·7
Khoisan	Male	27	8·6	1·0	7·0–10·5
	Female	22	8·4	1·2	6·4–12·1
Thickness of posterior root of Zygoma					
	SAM-AP 6269		3·1		
Zulu	Male	23	4·7	1·1	2·5–6·9
	Female	27	4·5	1·0	3·2–6·5
Khoisan	Male	27	4·3	1·1	2·0–6·3
	Female	22	4·3	0·9	3·0–6·1

In common with the KRM specimen, the temporal forms a distinct cup in Jebel Irhoud 1 and Tabun C1.

Metrical features. The depth of the KRM glenoid fossa falls comfortably within one standard deviation (S.D.) of the recent South African sample means (Table 2). Sothman (1994: Table 14) recorded an average of 5·8 mm for a Bronze Age European sample (*n* = 61; S.D. = 1·3; observed range = 2·1–8·2), and a mean of 6·9 mm for the Krapina Neandertal sample (*n* = 12; S.D. = 2·0; observed range = 4·4–11·9).

Table 3 **Measurements of the glenoid fossa recorded by Macchiarelli *et al.* (1991) and Sothman (1994)**

	n	X	S.D.	Obs. range
Glenoid fossa breadth				
Krapina Neandertals[1]	8	25·2	2·4	21·2–28·0
‘‘Riss-Würm’’ European Neandertals	3	26·7		25·8–28·0
‘‘Würm’’ European Neandertals	6	23·7		21·8–26·3
Levantine Neandertals	2	24·9		23·3–26·5
Skhul-Qafzeh	2	23·8		23·5–24·0
European Upper Paleolithic	5	26·1		22·5–30·6
Bronze Age European*	55	24·0	3·2	17·0–29·2
SAM-AP 6269		25·6		
Glenoid fossa length				
Krapina Neandertals*	11	11·1	1·7	7·5–13·2
Bronze Age European*	55	14·2	2·1	9·9–18·0
SAM-AP 6269		12·5		

*Data from Sothman (1994); other comparative data from Macchiarelli *et al.* (1991).

While the ML diameter of the KRM glenoid fossa exceeds the recent South African sample averages, its AP diameter is noticeably smaller than the corresponding means, falling more than 1 S.D. below all but that for the Khoisan female sample (Table 2). The relatively AP short nature of the KRM fossa is revealed by its shape index value (46·6%), which falls about 1 S.D. below the recent African sample means (Table 2).

The ML diameter of the glenoid fossa in various Neandertals and in a sample of Upper Paleolithic Europeans (Macchiarelli *et al.*, 1991; Sothman, 1994) tends to be noticeably larger than in the KRM specimen and in recent African crania. However, this difference is possibly exacerbated by differences in the measuring techniques used. We measured the ML diameter of the glenoid fossa from the midpoint of its lateral margin to a point on the sphenotemporal suture along a line that bisects the ML long axis of the fossa. Macchiarelli *et al.* (1991) and Sothman (1994) used Demirjian’s (1967) definition, which employs the distance from ‘‘the tip of the medial glenoid tubercle [=entoglenoid process]’’ to a point ‘‘midway between the postglenoid process and the tubercle of the root of the zygoma [=articular tubercle]’’. This dimension will exceed the ML diameter of the fossa itself because it also expresses the height of the entoglenoid process. By this method, the KRM glenoid measures 25·6 mm ML, which falls within 1 S.D. of the means for the Krapina Neandertal and recent European samples (Table 3).

Sothman (1994: Table 12) measured the AP diameter of the glenoid fossa for Krapina Neandertal and recent European crania, employing Demirjian’s (1967) definition as the distance from the ‘‘tip of the postglenoid process to the apex of the convexity on the articular eminence’’. She aptly noted that the latter landmark may be difficult to define. Her Neandertal values are comparable to those of recent Africans (Tables 2 & 3), but her recent European values are noticeably higher.

The ML diameter of the KRM articular eminence falls between the Khoisan and Zulu sample averages (Table 2). Its AP diameter falls above, but within 1 S.D. of the means for the recent African samples (Table 2).

The posterior root of the KRM zygomatic arch is quite thin by comparison with recent South African crania (Table 2). The KRM

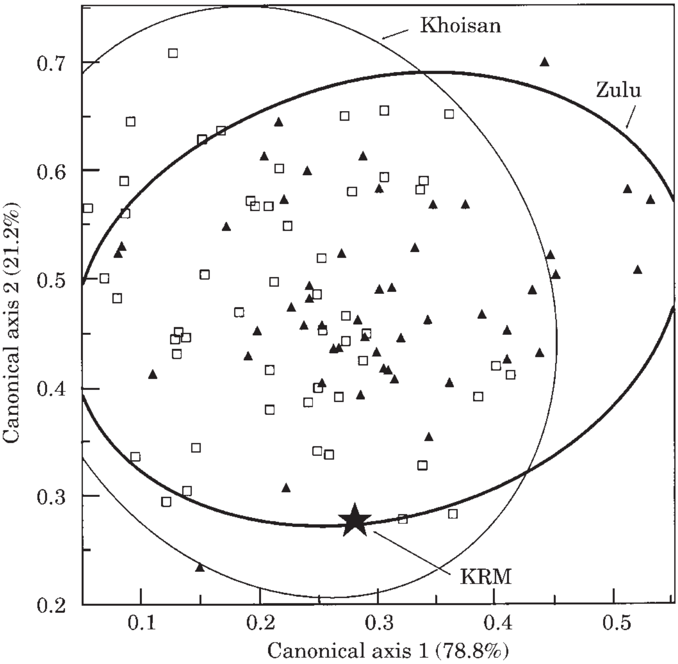

Figure 3. Canonical Variates Analysis scores for the SAM-AP 6269 temporal (KRM) and two recent African samples. The 95% confidence ellipses are drawn for the combined-sex Zulu (▲) and Khoisan (□) samples. Eigenvector values are: fossa depth 0·1008; ML fossa − 0·0065; AP articular eminence 0·0075; AP fossa − 0·0399; SI zygomatic root − 0·04433.

value falls within the lower part of the recent African sample ranges, and more than 1 S.D. below their means. By contrast, the posterior root of the zygomatic arch is noticeably thicker in most Neandertals, where it may attain a depth in excess of 9·0 mm. It is noteworthy that the zygomatic root also tends to be thicker in Middle Pleistocene European crania (e.g., Steinheim, Petralona, and Arago, where it exceeds 6·0 mm) than in the Middle Pleistocene African specimens (e.g., Bodo and Kabwe, where it is thinner than 7·0 mm).

The foregoing non-metrical and metrical comparisons point to the overall morphological modernity of the KRM temporal. In some features (e.g., the composition of the posteromedial wall of the glenoid fossa, the AP diameter of the glenoid, and the thickness of the posterior root of the zygomatic arch), however, the KRM specimen differs from the majority of recent African homologues.

A Canonical Variates Analysis that employs five measurements was used to assess the relationship of the KRM temporal to recent Khoisan and Zulu samples (Table 2). The variables chosen were (1) depth of the glenoid fossa, (2) ML diameter of the fossa, (3) AP diameter of the fossa, (4) AP diameter of the articular eminence, and (5) SI thickness of the posterior root of the zygomatic arch. The ML diameter of the articular eminence was excluded. Not only is this likely to be closely related to the ML diameter of the fossa that it borders, but because the articular tubercle on SAM-AP 6269 is damaged, this measurement is rendered imprecise. The results (Figure 3) illustrate the anatomical modernity of the KRM temporal. It falls

Table 4 **Measurements of the temporal bone recorded for four samples of Pleistocene hominid samples. (Data are from casts)**

	n	X	S.D.	Observed range
Neandertals				
Fossa depth	11	5·7	1·7	3·9–8·3
Fossa ML	11	21·3	3·4	15·5–25·8
Fossa AP	11	11·0	1·2	9·2–12·8
Art. emin. AP	11	7·7	0·8	6·1–9·2
Post. root SI	11	7·9	1·5	5·8–11·1
European Middle Pleistocene				
Fossa depth	3	5·6	0·9	4·8–6·6
Fossa ML	3	23·0	2·6	20·2–25·3
Fossa AP	3	10·7	1·9	9·0–12·7
Art. emin. AP	3	7·9	1·6	6·3–9·5
Post. root SI	3	8·2	2·0	6·3–10·2
African Middle Pleistocene				
Fossa depth	3	5·6	1·8	4·0–7·5
Fossa ML	3	24·3	3·2	20·9–27·1
Fossa AP	3	8·7	2·1	6·7–10·9
Art. emin. AP	3	10·3	1·3	9·0–11·6
Post. root SI	3	5·8	0·9	5·3–6·9
Pleistocene ‘‘Early Modern’’				
Fossa depth	7	6·2	1·0	4·8–7·8
Fossa ML	7	22·7	1·5	20·7–24·6
Fossa AP	7	10·7	1·8	8·3–14·0
Art. emin. AP	7	10·0	2·2	6·0–13·3
Post. root SI	7	6·4	0·7	5·5–7·5

The specimens comprising these four samples are: Neandertal: Shanidar 1, Amud 1, Tabun C1, Le Moustier 1, Krapina C, Krapina 39·1, Forbes’ Quarry, Guattari 1, Saccopastore 1, Ehringsdorf 9, Reilingen 1; European Middle Pleistocene: Steinheim 1, Petralona 1, Arago; African Middle Pleistocene: Salé, Ndutu 1, Kabwe (Broken Hill) 1; Pleistocene ‘‘Early Modern’’: Ngaloba (LH 18), Jebel Irhoud 1, Jebel Irhoud 2, Singa 1, Omo II, Skhul IV, Skhul V.

within the 95% confidence ellipse of the Khoisan sample, and on the margin of the Zulu ellipse.

Unfortunately, homologous data have not been published for other fossil specimens. Nevertheless, in an attempt to gauge the relative phenetic affinities of the KRM specimen vis-à-vis recent and more archaic humans, these five measurements were recorded by one of us (FEG) from casts of Neandertal, European Middle Pleistocene, African Middle Pleistocene, and ‘‘Early Modern’’ Pleistocene crania (Table 4). The Pleistocene ‘‘Early Modern’’ sample groups Ngaloba and other late Middle–early Late Pleistocene African crania with specimens from Skhul, and while all of these fossils exhibit aspects of morphology that recall more archaic remains, they constitute better ancestors for recent humans than do other fossils because they also variably exhibit modern features. A CVA employing these fossil and recent human groups (Figure 4) establishes the comparative modernity of the KRM temporal, which falls within the 95% confidence ellipses of the recent African samples, but outside the corresponding Neandertal and Pleistocene ‘‘Early Modern’’ sample ellipses. The raw Canonical coefficients indicate that along Axis 1, which serves to differentiate the KRM specimen most readily from other Pleistocene specimens (Figure 4), the thickness of the zygomatic root and the ML breadth of

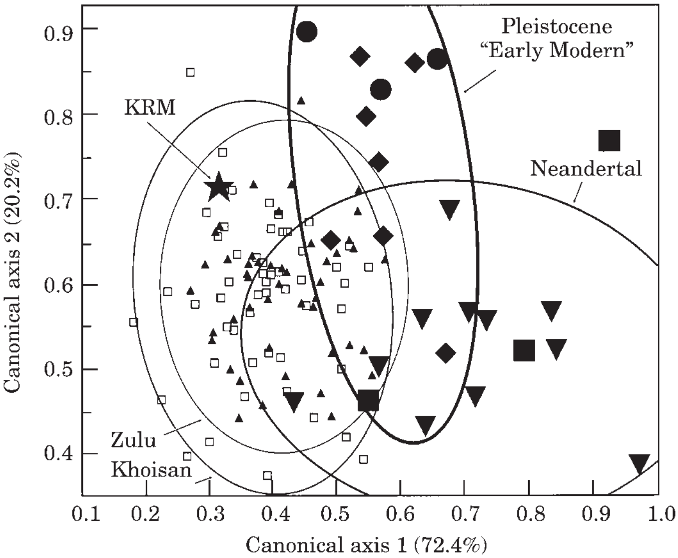

Figure 4. Canonical Variates Analysis scores for the SAM-AP 6269 temporal (KRM), two recent African samples, and four Pleistocene hominid samples. The 95% density ellipses are drawn for the combined-sex Zulu (▲) and Khoisan (□) samples, and for the Neandertal (▼), and Pleistocene ‘‘Early Modern’’ (◆) samples. The three African Middle Pleistocene specimens (●) fall within the 95% confidence ellipse of the Pleistocene ‘‘Early Modern’’ sample; two of the three European Middle Pleistocene specimens (■) fall within the 95% density ellipse for the Neandertal sample. Eigenvector values are: fossa depth 0·0054; ML fossa 0·0134; AP articular eminence −0·0185; AP fossa −0·0074; SI zygomatic root 0·0784.

the glenoid fossa drive specimens towards the ‘‘archaic’’ side, whereas a large AP diameter of the articular eminence drives specimens towards the ‘‘modern’’ side. It is perhaps noteworthy that the three African Middle Pleistocene specimens form a cluster that falls within the 95% confidence ellipse of the Pleistocene ‘‘Early Modern’’ sample, but outside the Neandertal ellipse. The three African Middle Pleistocene temporals are also quite distinct from European Middle Pleistocene homologues, two of which overlap the 95% confidence ellipse of the Neandertal sample.

Atlas (SAM-AP 6268)

The KRM atlas is indistinguishable from those of recent humans. This is perhaps not unexpected. Studies of the few Neandertal atlases that are known have concluded that they too are essentially fully comparable to recent human homologues (Gorjanovic-Kramberger, 1906; McCown & Keith, 1939; Patte, 1955; Trinkaus, 1983; Arensburg, 1991).

The estimated maximum transverse diameter between the lateral margins of the inferior articular facets of the KRM bone (46·4 mm) is only marginally smaller than the corresponding values recorded by Arensburg (1991) for penecontemporaneous specimens such as Kebara KMH2 (47·5 mm) and Skhul V (47·0 mm), although the diameter of 58·4 mm estimated by Trinkaus (1983) for Shanidar 2 is larger. Similarly, the odontoid facet of the KRM atlas is only slightly shorter (9·2 mm) and slightly broader (13·2 mm) than those recorded by Arensburg (1991) for Kebara 2 (9·5 mm by 12·5 mm) and Skhul V (10·0 mm by 11·0 mm).

The height of the KRM lateral mass falls among the means for recent African samples (Table 5). It is slightly shorter than the

Table 5 **Measurements of the KRM atlas vertebra (SAM-AP 6268) compared to recent African sample values**

		n	X	S.D.	Observed range
Height of lateral mass					
SAM-AP 6268			19·0		
Zulu	Male	25	21·8	1·8	19·0–24·7
	Female	24	19·6	1·5	15·9–22·5
Khoisan	Male	21	18·7	1·6	16·7–22·4
	Female	13	19·0	1·2	17·3–21·2
Height of anterior arch					
SAM-AP 6268			10·9		
Zulu	Male	25	11·4	1·2	8·2–13·1
	Female	24	10·2	1·1	8·2–12·2
Khoisan	Male	21	10·1	2·3	7·2–16·8
	Female	13	9·3	1·2	7·7–11·5
Length of inferior articular facet					
SAM-AP 6268			21·2		
Zulu	Male	25	18·7	1·4	17·2–22·3
	Female	24	18·0	1·4	15·9–21·8
Khoisan	Male	21	18·0	1·2	15·7–21·0
	Female	13	18·0	1·0	16·0–19·7
Breadth of inferior articular facet					
SAM-AP 6268			14·7		
Zulu	Male	25	15·7	1·5	13·0–18·4
	Female	24	14·3	0·6	13·3–15·3
Khoisan	Male	21	14·4	1·0	12·8–16·5
	Female	13	13·5	0·7	12·0–14·5

majority of Zulu and slightly taller than the majority of Khoisan atlases. Corresponding measurements for atlases from Krapina, Skhul, and La Chapelle are slightly lower at 17·0 mm, 17·6 mm, and 18·3 mm respectively.

The height of the anterior arch of the KRM atlas also falls among recent African sample means (Table 5), and among the values recorded by Gorjanovic-Kramberger (1906) and McCown & Keith (1939) for La Chapelle (9·0 mm), Tabun C1 (9·2 mm), Skhul V (10·5 mm) and Krapina (12·5 mm).

The length of the KRM inferior articular facet (21·2 mm) exceeds the Khoisan and Zulu sample averages. While the KRM value is within the observed limits of the Zulu sample, it exceeds the largest Khoisan value, falling more than 1 S.D. above the Zulu male mean and 2 S.D.s above those of the other three samples (Table 5). The corresponding diameters recorded by McCown & Keith (1939) for La Chapelle (18·0 mm) and Skhul V (20·5 mm), by Arensburg (1991) for Kebara 2 (17·4 mm), and by Trinkaus (1983) for Shanidar 2 (18–19 mm) are also slightly smaller than the KRM value. The width of the KRM inferior articular facet (14·7 mm), however, falls among the recent African sample means (Table 5). It is only slightly larger than the width recorded by McCown & Keith (1939) for Skhul V (14·0 mm), and it is slightly smaller than the values obtained by McCown & Keith (1939) for La Chapelle (16·8 mm), by Arensburg (1991) for Kebara 2 (15·0 mm), and by Trinkaus (1983) for Shanidar 2 (15–17 mm).

Thus, the KRM atlas is, with one possible exception, unremarkable both morphologically and metrically among either recent Africans or penecontemporaneous fossils from Europe and the Levant. By comparison with these samples, the KRM atlas has a rather long inferior articular facet.

Summary and conclusions

The temporal and atlas described here add to the small, fragmentary sample of MSA human remains from KRM and elsewhere in sub-Saharan Africa. They are, therefore, of some relevance to the debate concerning the evolution of modern morphology.

The atlas is morphologically and metrically comparable to recent African homologues, and to Pleistocene specimens (both Neandertals and ''Early Modern'' humans) from Europe and the Levant. The only possible exception is that the inferior articular facet of KRM is somewhat longer than on most recent African and Neandertal atlases. This similarity is not unexpected, since Neandertal atlases are essentially like those of recent humans (Gorjanovic-Kramberger, 1906; McCown & Keith, 1939; Patte, 1955; Trinkaus, 1983; Arensburg, 1991).

The temporal, like some other fossils from the SAS Member at KRM, is suggestive of a comparatively small individual. This fragment is morphologically and metrically similar to recent African homologues with two possible exceptions. In the first instance, the posteromedial wall of the glenoid fossa is formed by the squamous temporal alone, a condition exhibited by fewer than 15% of recent Africans. In this regard, the KRM fossil also appears to be distinct from the majority of archaic specimens, in which the squamous temporal and tympanic both contribute to the posteromedial wall of the fossa. In the second instance, the KRM glenoid fossa is ML broad and AP short in comparison to recent African fossae, although some of its dimensions are by no means unknown among modern humans. By contrast, the glenoid fossa of the KRM temporal tends to be somewhat smaller, especially ML, than those of other Pleistocene crania. In contrast to the Neandertals, the KRM specimen has a comparatively deep fossa with a distinct articular eminence; in this respect it is more similar to both recent humans and Pleistocene crania from Africa. Finally, the KRM postglenoid process is smaller than those on Neandertal and archaic African specimens; it is comparable to those of recent Europeans and Africans, although only about 30% of the latter possess a similarly small process.

A Canonical Variates Analysis based on five measurements reveals that the overall similarity of the KRM and recent African (especially Khoisan) temporals, and the distinctiveness of the KRM bone from other Pleistocene specimens. The KRM temporal is decidedly modern in comparison to Neandertal homologues, and a tentative multivariate assessment (based on measurements of casts) suggests that it has more modern lineaments than those of African Middle Pleistocene crania (e.g., Kabwe and Bodo) or some ''Early Modern'' crania from Africa and the Levant.

While the evidence provided by the KRM temporal is rather limited, it is consistent with some other MSA cranial remains from this site suggesting an overall, but not unambiguous, pattern of modern morphology. In particular, the supraorbital morphology of the KRM 16425 frontal fragment is undeniably modern (arguments about its possible juvenile status notwithstanding). As noted above, the proximity of the temporal and the frontal in the KRM deposit, as well as their size and preservation suggest that they might have been derived from a single individual. While the chin of the KRM 13400 mandible is not particularly well-developed, and that of KRM 14695 is perhaps even weaker, the KRM 21776 and especially the 41815 mandibles, on the other hand, bear distinct chins that resemble those of recent humans (Rightmire & Deacon, 1991; Lam *et al.*, 1996).

The KRM postcrania, particularly the ulna and radius (which are the only bones to have been subjected to detailed comparative analysis), possess a mixture of archaic and modern features (Churchill *et al.*, 1996; Pearson & Grine, 1997).

Thus, some of the KRM specimens evince arguably archaic traits, such as the ratio of ulnar coronoid to olecranon heights, the cortical thickness of at least some (radial and ulnar) diaphyses, the absence or weak development of a chin in some mandibles, and an elevated level of presumed sexual size dimorphism (as revealed by the mandibles). Nevertheless, as aptly observed by Smith *et al.* (1989, p. 42; Smith, 1992, p. 148), not only is the total morphological pattern of this sample commensurate with its ''designation as modern human'', but the ''somewhat primitive aspects of certain features in some specimens'' are to be expected in an otherwise morphologically modern population of this geological antiquity. Such primitive traits are simply symplesiomorphies that have been retained from an earlier, more archaic ancestor.

The limited evidence provided by the KRM temporal is consistent with other MSA cranial remains from this site in suggesting a pattern of overall, albeit incomplete morphological modernity. The cranial and especially the postcranial bones from KRM present a mixture of primitive and modern features. This sort of mosaic should be expected in later Pleistocene members of the evolutionary lineage leading to recent people.

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