

VARIABILITY IN SHAPE OF THE DENTAL ARCADE OF *HOMO SAPIENS* IN LATE PLEISTOCENE AND MODERN SAMPLES FROM SOUTHERN AFRICA

by

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ABSTRACT

Mandibles are among the most common skeletal elements of Late Pleistocene specimens of *Homo sapiens* from southern African sites (notably Klasies River Mouth and Border Cave). For this reason mandibles have been selected for study to compare with samples drawn from modern populations (including South African negroes, Khoisanoid "Bushmen" and caucasoids). An analysis of shape of the dental arcade, based on the spatial distribution of molars, premolars and canines, indicates that several of the Late Pleistocene samples (including KRM 41815) are outside the range of variation found in modern African and caucasoid populations, and in this respect, cannot be described as "anatomically modern", *sensu strictu*. There appears to be a trend in the process of modernisation, from very flared dental arcades (notably in the case of the Kabwe skull, representing "archaic" *H. sapiens*), through moderately flared arcades (as found in Late Pleistocene "nearly modern" samples) towards a less flared condition which is found in modern Africans and caucasoids.

KEY WORDS: "Anatomically modern man", Late Pleistocene, human evolution.

INTRODUCTION

Discoveries of so-called "anatomically modern" *Homo sapiens* at Late Pleistocene sites in southern Africa have played a key role in current debate on modern human origins (Beaumont *et al.* 1978; De Villiers 1973, 1976; Deacon 1989; Rightmire 1989; Rightmire and Deacon 1991; Singer and Wymer 1982). Controversy regarding the origin(s) of "anatomically modern" people has been fueled by analyses of mitochondrial DNA (Cann *et al.* 1987; Stringer and Andrews 1988; Stoneking and Cann 1989; Templeton 1992; Hedges *et al.* 1992). However, one of the principal problems in this debate concerns the definition of what constitutes "anatomically modern", when the fossil evidence itself is fragmentary and sparse. The problem is addressed in the present study by focussing on mandibles, one of the most common skeletal elements of Late Pleistocene hominids represented at southern African sites. We plot the spatial distribution of molars, premolars and canines in a Cartesian plane, and show that several of the Late Pleistocene samples differ from modern specimens by having a more flared dental arcade, outside the range of variation in modern African negroes and caucasoids. In this respect some of the Late Pleistocene samples cannot necessarily be regarded as "anatomically modern".

MATERIALS AND METHOD

Fossil specimens in this study include six mandibles

from three sites: Border Cave (Beaumont *et al.* 1978; De Villiers 1973, 1976), Klasies River Mouth (Deacon 1989; Rightmire 1989; Rightmire and Deacon 1991) and Tuinplaas, otherwise known as Springbok Flats (Broom 1929; Hughes 1990). The exact dating of such fossils is problematic since they are generally outside the range of the conventional radiocarbon dating technique (Beaumont and Vogel 1972; Beaumont 1980; Deacon and Geleijnse 1988; Clark 1989). However, for purposes of this study it is sufficient to note that all are reported to have been associated with Middle Stone Age cultural material and are generally considered to be of Late Pleistocene date. A Middle Pleistocene cranium from Kabwe (Broken Hill) (Tobias *et al.* 1977) has also been included in this study. Unfortunately this specimen is not associated with a mandible, but analysis of the maxillary dental arcade of this Middle Pleistocene specimen is considered to be sufficiently important for inclusion in this study, bearing in mind differences that may exist in the dental arcades of upper and lower dentition within individuals.

For comparative purposes, modern specimens of Khoisanoid "Bushmen", "Griqua", South African Negroes and caucasoids were examined, using the Dart Collection at the University of the Witwatersrand (Department of Anatomy and Human Biology), supplemented by material in the Broom Collection at the Transvaal Museum, Pretoria. Males and females

are represented in both collections. Although sex is not known for all specimens, males and females are represented in approximately equal proportions.

Quantifying variability in shape of the dental arcade

Extensive research has previously been undertaken on variability in shape of the dental arcade in hominid evolution (e.g. Simons and Pilbeam 1965; Walker and Andrews 1973; McKee and Molnar 1988; Roth 1985, 1986, 1988; Halazonetis *et al.* 1991; Roth and Simon 1992). In this study, shape of the arcade was documented simply by quantifying variability in the spatial distribution of molars, premolars and canines, as determined from x and y co-ordinates of "midpoints" of each tooth plotted in a Cartesian plane (Figure 1). "Midpoints" of molars and premolars represent the intersection of buccolingual and mesiodistal diameters. Midpoints of canines were determined by recording the intersection of maximum width and maximum length on occlusal surfaces. The mid-incisal point (intradentale prosthion) corresponds to (0,0) on a Cartesian plane, the dental arch being orientated to form a parabola with the turning point at (0,0), assuming symmetry of dentition (Figure 1). Co-ordinates for teeth of the left mandible were plotted in the quadrant where both x and y values are positive. Where possible, mid-points of missing teeth were estimated from antimeres or from alveolar sockets.

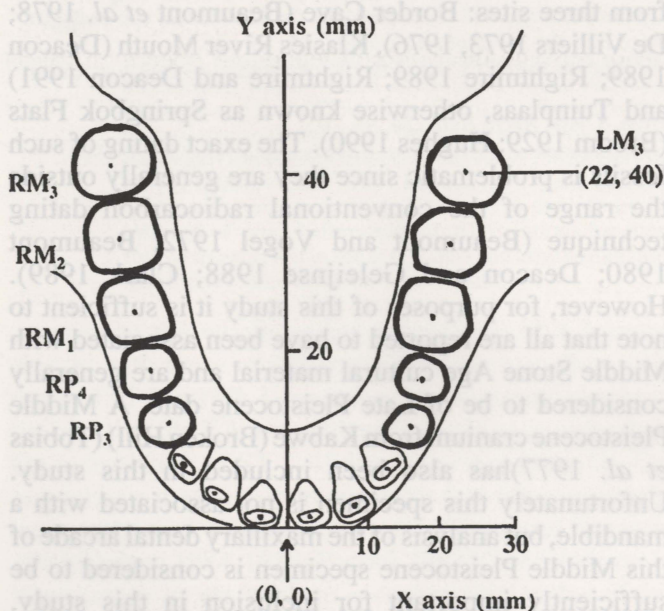


Figure 1. Diagram illustrating manner by which mid-points of left canines, premolars and molars were plotted in a cartesian plane, using (0,0) for the mid-incisal point (intradentale prosthion), assuming symmetry of dentition.

RESULTS

Results of this study are summarised in Table 1, and presented graphically in Figure 2.

TABLE 1

Mean values and standard deviations for x and y co-ordinates for canines, premolars and molars of *H. sapiens*; modern African samples include Khoisanoid and negroid specimens; modern caucasoid samples from the Raymond Dart and Robert Broom collections; Late Pleistocene specimens include specimens BC 2 and BC 5 from Border Cave; KRM 41815, KRM 13400 and KRM 21776 from Klasies River Mouth; and the Springbok Flats (Tuinplaas) mandible.

Modern Africans, southern Africa

	Mean X	s.d. X	Mean Y	s.d. Y	n
C	12.2	1.4	5.1	1.5	54
P3	15.9	1.5	10.7	2.0	54
P4	18.7	1.8	16.9	2.4	54
M1	21.6	1.9	25.1	3.0	54
M2	23.8	2.0	35.3	3.5	54
M3	25.4	2.1	45	4.5	54

Caucasoid

	Mean X	s.d. X	Mean Y	s.d. Y	n
C	12.8	1.0	6.5	1.6	20
P3	16.4	0.9	12.8	2.0	20
P4	19.0	1.1	19.6	2.2	20
M1	21.6	1.3	28.4	2.9	20
M2	24.3	1.4	38.0	3.1	20

Late Pleistocene *H. sapiens*, Southern Africa (Klasies River Mouth, Border Cave, Tuinplaas)

	Mean X	s.d. X	Mean Y	s.d. Y	n
C	11.8	2.2	4.1	1.3	6
P3	17.2	2.1	8.9	2.6	6
P4	20.3	2.5	14.5	2.8	6
M1	24.2	1.8	23.1	2.7	6
M2	26.8	1.5	33.0	2.9	6
M3	29.1	1.4	42.1	0.9	5

DISCUSSION AND CONCLUSIONS

As reflected by mean values and standard deviations of x and y co-ordinates for molars and premolars, the dental arcade in modern negroes and Khoisanoid samples from southern Africa is not significantly different from that of modern caucasoid samples (Table 1). By contrast, the dental arcade of Late Pleistocene samples (including KRM 41815 and KRM 13400) tends to be more flared than that of modern samples (Figure 2).

These findings support the claim that hominid fossils from Klasies River Mouth include samples that are not entirely modern in morphology (Wolpoff and Caspari 1990; Caspari and Wolpoff 1990; Klein 1992). A notable exception is the dental arcade of KRM 21776. Although broken and fragmentary, this specimen has x and y co-ordinates of mandibular teeth that correspond closely to the average values obtained for modern African samples (Table 1). KRM 21776 was excavated from deposits near the base of the MSA II culture-stratigraphic unit (Singer and Wymer 1982), thought to date around 90,000 years B.P. (Deacon 1989; Deacon and Geleijnse 1988).

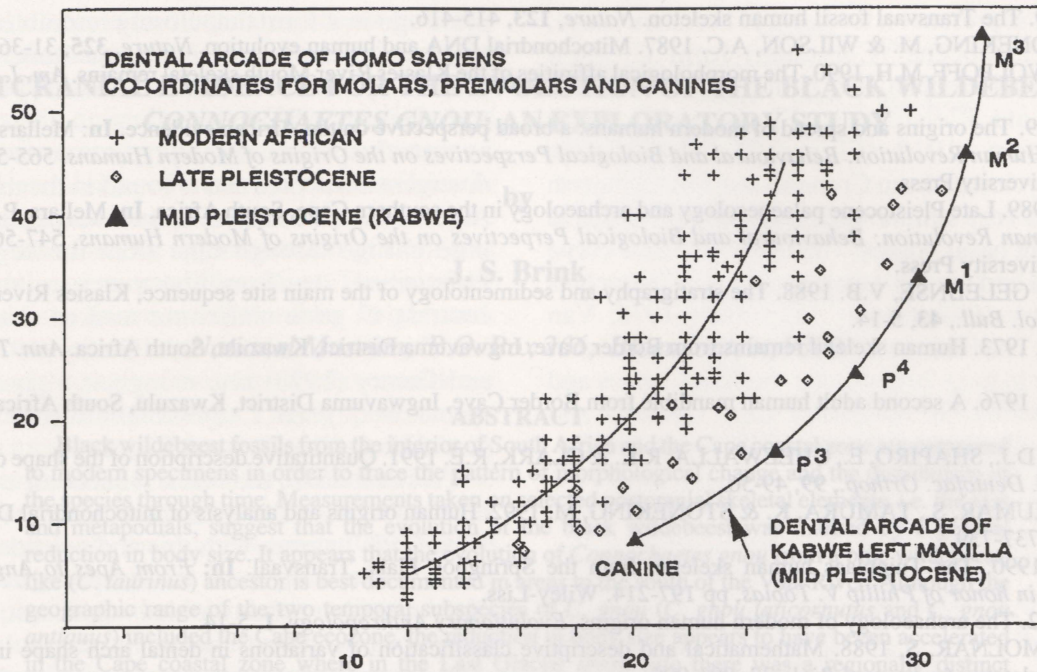


Figure 2. Co-ordinates for mid-points of lower molars, premolars and canines of modern, Late Pleistocene and Middle Pleistocene samples of *Homo sapiens* (modern Africans from southern Africa), compared to values for Late Pleistocene specimens from Klasies River Mouth (KRM 41815, KRM 21776, and KRM 13400), Border Cave (BC 2 and BC 5); and Springbok Flats ("Tuinplaas"), and a Middle Pleistocene specimen from Kabwe (Broken Hill). All data from mandibles, with the exception of the Kabwe specimen.

The dental arcade of the Kabwe maxilla is markedly more flared than that of mandibles of Late Pleistocene specimens from Klasies River Mouth, Border Cave and Tuinplaas (Figure 2). It is improbable that the scale of difference can be attributed to the fact that the Kabwe measurements have been obtained from maxillary dentition, whereas the Late Pleistocene specimens are all from mandibular dentition. This view is based on comparisons between the mean co-ordinates for upper and lower third molars of the same individuals of modern *H. sapiens*, indicating no significant difference at $P=0.05$. The significant difference (at the same level of probability) between the M^3 co-ordinates of the Kabwe specimen, compared to the mean values for the co-ordinates of lower third molars of Late Pleistocene *H. sapiens* from southern Africa (Table 1) is not likely to be attributable to differences in upper and lower dentition alone, although this may have contributed to some extent to the observed differences between Late and Middle Pleistocene specimens.

Although there are differences in mean values of x and y co-ordinates of teeth in modern and Late Pleistocene samples, the range of variation in x and y co-ordinates of Late Pleistocene material is comparable

to that found in the modern samples. In general, the Late Pleistocene specimens have dental arcades which are morphologically intermediate between those of modern mandibles and the Middle Pleistocene specimen from Kabwe (Figure 2). Although the available Pleistocene sample is small, the changes in dental arcade may be regarded as a reflection of a trend in the process of modernisation towards "anatomically modern" *H. sapiens* in Africa, pointing to gradual evolution as found also from studies of dental arcade variation in Middle and Late Pleistocene specimens of *H. sapiens* from Europe and Asia (Roth 1985, 1986, 1988, Roth and Simon 1992).

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REFERENCES

- BEAUMONT, P.B. 1980. On the age of Border Cave hominids 1-5. *Palaeont. afr.* **23**, 21-33.
 BEAUMONT, P.B. & VOGEL, J.C. 1972. On a new radiocarbon chronology for Africa south of the equator. *African Studies* **31**, Pt. I, 65-89; Pt. II, 155-182.
 BEAUMONT, P.B., De VILLIERS, H. & VOGEL, J.C. 1978. Modern man in sub-Saharan Africa prior to 49 000 B.P.: a review and evaluation with particular reference to Border Cave. *S. Afr. J. Sci.*, **74**, 409-419.

- BROOM, R. 1929. The Transvaal fossil human skeleton. *Nature*, **123**, 415-416.
- CANN, R.L., STONEKING, M. & WILSON, A.C. 1987. Mitochondrial DNA and human evolution. *Nature*, **325**, 31-36.
- CASPARI, R. & WOLPOFF, M.H. 1990. The morphological affinities of the Klasies River Mouth skeletal remains. *Am. J. Phys. Anthropol.*, **81**, 203.
- CLARK, J.D. 1989. The origins and spread of modern humans: a broad perspective on the African evidence. In: Mellars, P. & Stringer, C., Eds., *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*, 565-588. Edinburgh, Edinburgh University Press.
- DEACON, H.J. 1989. Late Pleistocene palaeoecology and archaeology in the southern Cape, South Africa. In: Mellars, P. & Stringer, C., Eds., *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*, 547-564. Edinburgh, Edinburgh University Press.
- DEACON, H.J. & GELEIJNSE, V.B. 1988. The stratigraphy and sedimentology of the main site sequence, Klasies River, South Africa. *S. Afr. Archaeol. Bull.*, **43**, 5-14.
- De VILLIERS, H. 1973. Human skeletal remains from Border Cave, Ingwavuma District, Kwazulu, South Africa. *Ann. Trans. Mus.*, **28**, 229-256.
- De VILLIERS, H. 1976. A second adult human mandible from Border Cave, Ingwavuma District, Kwazulu, South Africa. *S. Afr. J. Sci.*, **72**, 212-215.
- HALAZONETIS, D.J., SHAPIRO, E., GHEEWALLA, R.K. & CLARK, R.E. 1991. Quantitative description of the shape of the mandible. *Am. J. Orthod. Dentofac. Orthop.*, **99**, 49-56.
- HEDGES, S.B., KUMAR, S., TAMURA, K. & STONEKING, M. 1992. Human origins and analysis of mitochondrial DNA sequences. *Science*, **255**, 737-739.
- HUGHES, A.R. 1990. The Tuinplaas human skeleton from the Springbok Flats, Transvaal. In: *From Apes to Angels: Essays in Anthropology in honor of Phillip V. Tobias*, pp 197-214. Wiley-Liss.
- KLEIN, R.G. 1992. The archaeology of modern human origins. *Evolutionary Anthropology*, **1**, 5-14.
- McKEE, J.K. & MOLNAR, S. 1988. Mathematical and descriptive classification of variations in dental arch shape in an Australian aborigine population. *Archs. oral Biol.*, **33**, 901-906.
- RIGHTMIRE, G.P. 1989. Middle Stone Age humans from eastern and southern Africa. In: Mellars, P. & Stringer, C., Eds., *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*, 109-122. Edinburgh, Edinburgh University Press.
- RIGHTMIRE, G.P. & DEACON, H.J. 1991. Comparative studies of Late Pleistocene human remains from Klasies River Mouth, South Africa. *J. Hum. Evol.*, **20**, 131-156.
- ROTH, H. 1985. Morphometric study of the evolution of mandibular arcades. *J. Hum. Evol.*, **14**, 563-571.
- ROTH, H. 1986. Evolution of mandibular arcades: a statistical study. *International Journal of Anthropology*, **1**, 169-176.
- ROTH, H. 1988. Morphometric study of fossil mandibles: numerical representation of dental arcades by a biometric method. In: Trinkaus, E., Ed. *L'Homme de Neandertal*, Vol 3, 111-123. L'Anatomie, Liege.
- ROTH, H. & SIMON, C. 1992. The relationship of Pleistocene and modern mandibles evaluated by principal component analysis of the arcade dimensions. In: Toussaint, M., Ed., *Five million years, the human adventure*, 111-124. ERAUL 56.
- SIMONS, E.L. & PILBEAM, D.R. 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthroipoidea). *Folia Primat.*, **3**, 81-152.
- SINGER, R. & WYMER, J. 1982. *The Middle Stone Age at Klasies River Mouth in South Africa*. Chicago, University of Chicago Press.
- STONEKING, M. & CANN, R.L. 1989. African origins of human mitochondrial DNA. In: Mellars, P. & Stringer, C., Eds., *The Human Revolution: Behavioural and Biological Perspectives on the Origins of Modern Humans*, 17-30. Edinburgh, Edinburgh University Press.
- STRINGER, C. & ANDREWS, P. 1988. Genetic and fossil evidence for the origin of modern humans. *Science*, **239**, 1263-1268.
- TEMPLETON, A.R. 1992. Human origins and analysis of mitochondrial sequences. *Science*, **255**, 737.
- TOBIAS, P.B., COPLEY, K. & BRAIN, C.K. 1977. South Africa. In: Oakley, K.P., Campbell, B.G., & Molleson, T.I., Eds., *Catalogue of Fossil Hominids. Part I: Africa*, second edition, 95-151. London, Trustees of the British Museum (Natural History).
- WALKER, A. & ANDREWS, P. 1973. Reconstruction of the dental arcades of *Ramapithecus wickeri*. *Nature*, **244**, 314-323.
- WOLPOFF, M.H. & CASPARI, R. 1990. Metric analysis of the skeletal material from Klasies River Mouth, Republic of South Africa. *Am. J. Phys. Anthropol.*, **81**, 319.