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Human mandibular incisors from the late Middle Pleistocene locality of Hoedjiespunt 1, South Africa

The Hoedjiespunt 1 locality is an archaeological and palaeontological site located on the Hoedjiespunt Peninsula at Saldanha Bay, South Africa. In 1996 two human teeth, a left central mandibular incisor and a left lateral mandibular incisor, were discovered during excavations in the late Middle Pleistocene palaeontological layers. These teeth are described and are found to belong to a single subadult individual. Despite their developmental stage, these incisors already display early signs of wear. Their crown diameters are larger than modern and archaeological African comparative material and are most closely comparable with crown diameters of an early Middle Pleistocene and late Middle Pleistocene dental sample from Africa, Europe and Asia. In the light of this metrical evidence, data on two previously excavated maxillary molars, most probably belonging to the same individual, were re-examined. It was found that the Hoedjiespunt 1 hominid possessed dental metrical features (large anterior teeth and small molars) comparable with other African and European hominids referred to the Middle Pleistocene.

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Introduction

Hoedjiespunt 1 (HDP1) ($33^{\circ}01'45''\text{S}$, $17^{\circ}57'37''\text{E}$) is located on the southern edge of the Hoedjiespunt Peninsula, at Saldanha Bay on the West Coast of South Africa (Figure 1). The peninsula, which projects eastwards from the northwest corner of Saldanha Bay, is part of a large fossil dune landscape that houses several archaeological and palaeontological sites. Among these is the important Late Pleistocene site of Sea

Harvest, which, in addition to yielding an extensive mammalian fauna (Klein, 1983), also yielded human skeletal material in the form of a manual distal phalanx and a maxillary premolar (Grine & Klein, 1993).

Fossils from the Hoedjiespunt Peninsula were first reported by Klein (1983), who, together with scientists from the South African museum, collected bones as they weathered out of a sandstone cliff face, about 10 m from the present day site of HDP1. Subsequently this cliff had been

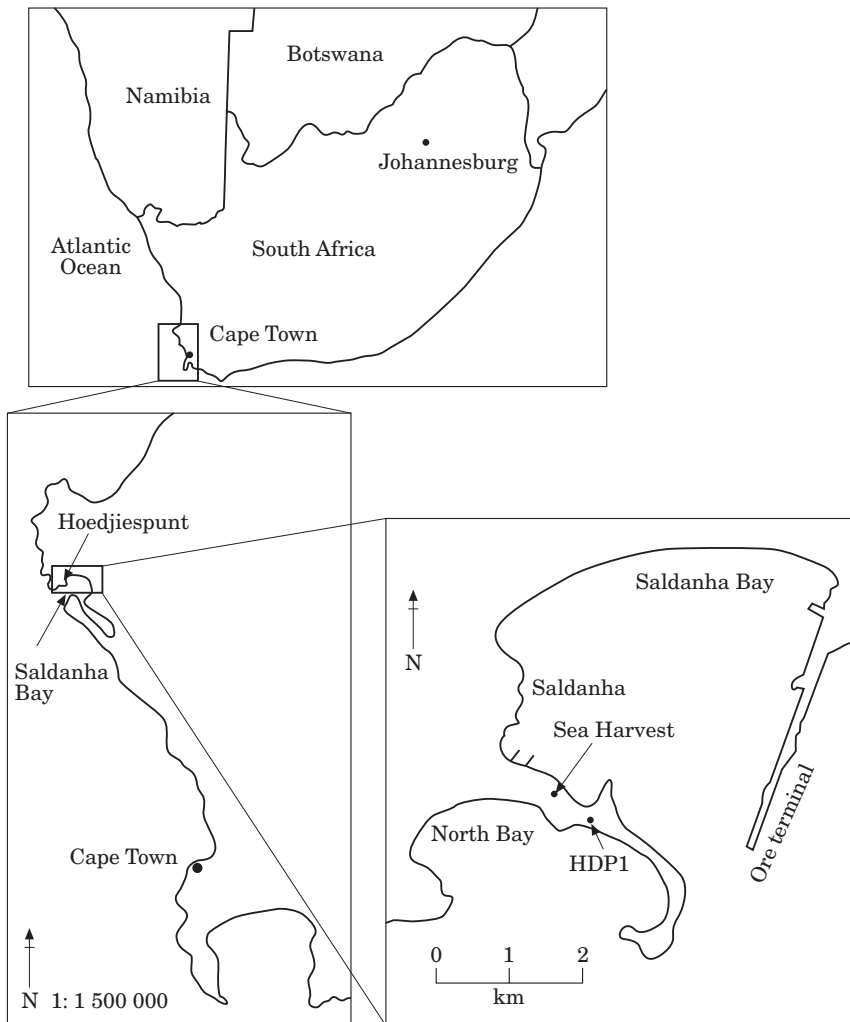


Figure 1. Position of the Hoedjiespunt peninsula and the sites of Hoedjiespunt 1 and Sea Harvest.

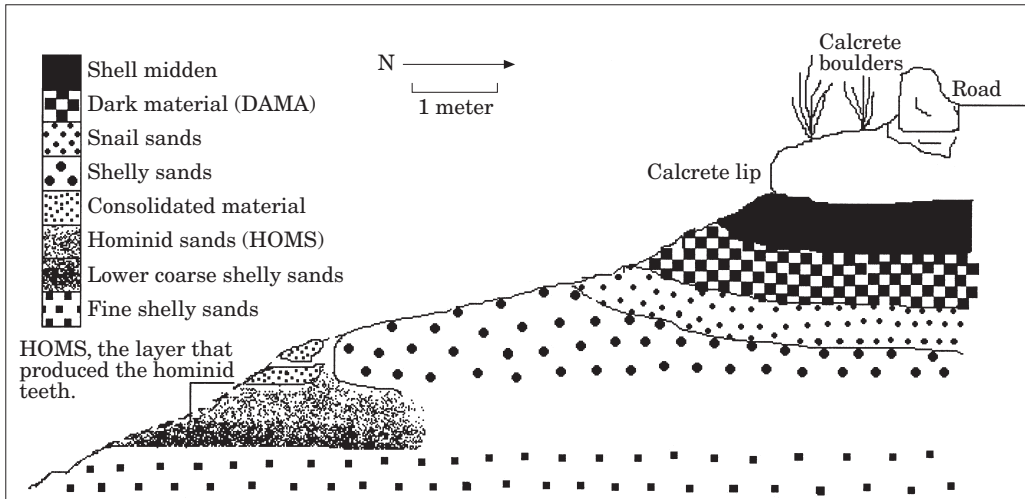


Figure 2. The Hoedjiespunt 1 stratigraphic sequence and the layer that yielded the human teeth (HOMS).

bevelled, thus exposing further archaeological and palaeontological material. In 1993, this abundance of exposed material prompted scientists and students from the University of Cape Town and the University of the Witwatersrand to carry out a limited surface survey of fossil material on the peninsula and surrounding area. The discovery of several fragments of a human left maxillary second molar (HDP1-1) in the course of this survey preceded the first systematic excavation of HDP1 in 1994. Excavations yielded an additional human tooth, a right maxillary third molar (HDP1-2, field no. 49). According to Berger & Parkington (1995) these molars probably date from the late Middle Pleistocene and belong to a single individual that died in its early teens.

Subsequent excavations in 1996 have led to the discovery of two additional human teeth—a left central mandibular incisor (HDP1-3, field no. 937) and a left lateral mandibular incisor (HDP1-4, field no. 3150). A human tibia was recovered in 1998 and has recently been described (Churchill *et al.*, 2000). In this paper, we present a

description and analysis of the two incisors. Their possible relation to the molars is also investigated.

The Hoedjiespunt 1 locality

Stratigraphy

The HDP1 locality consists of an archaeological site stratified above a palaeontological site. The stratigraphic sequence is capped by about two meters of calcrete carapace (Figure 2). A firmly cemented shell midden containing Middle Stone Age (MSA) stone tools, ostrich eggshell fragments, ochre, marine shell (mostly *Patella* spp.) and burnt animal bone, is situated at the base of the carapace. Below this is a dark, loamy archaeological layer (DAMA) that contains bone, ostrich eggshell and MSA quartz artefacts. Marine vertebrates, such as the jackass penguin (*Spheniscus demersus*) and the Cape cormorant (*Phalacrocorax capensis*), are abundant. Terrestrial vertebrates are present in lower numbers and are dominated by small species such as the angulate tortoise (*Chersina angulata*) (Stynder, 1997).

Two shelly sand bodies largely sterile of mammalian fossils separate the archaeological site from the palaeontological site below. The main bone-bearing layer of the palaeontological site (HOMS) is densely packed with bone. It is sandwiched between a shelf of consolidated material above and two less densely packed bone-bearing layers below. Grazing ungulates such as the black wildebeest (*Connochaetes gnou*) and red hartebeest (*Alcelaphus buselaphus*), and carnivores such as the black-backed jackal (*Canis mesomelas*), dominate this assemblage (Stynder, 1997). Marine animals are rare. The lack of any artefacts or archaeological features in the deposit, as well as the presence of a considerable number of hyena coprolites and gnawed bones, suggest that hyenas, most probably the brown hyena (*Hyaena brunnea*), accumulated these faunal remains.

Age

The presence of informal MSA stone tools is consistent with an age of between 40 ka and 240 ka for the archaeological site. Infrared stimulated luminescence (IRSL) and thermoluminescence (TL) dates on sediments from DAMA place the age of this horizon at ca. 117 ka, sometime during the Last Interglacial (isotope stage 5e) (Woodborne, 2000). The abundance of shellfish and marine vertebrate remains in these layers is consistent with accumulation during the Last Interglacial.

The age of the palaeontological site is less secure. IRSL and TL dates on sediments from HOMS suggest accumulation during the Middle Pleistocene, with a maximum age of ca. 550 ka (Woodborne, 2000). Analysis of the foraminiferal assemblage from HOMS indicates an age of between ca. 180 ka and ca. 480 ka (McMillan, personal communication). The fauna, most of which derive from the HOMS layer, is typical of the Florisbad Faunal Span. This places a maximum age of around 250 ka (Grün *et al.*, 1996) on the assemblage.

Based on these dates and our stratigraphic observations, we suggest that the palaeontological site was most probably deposited between 200 ka and 300 ka ago, sometime during the late Middle Pleistocene.

Location of teeth

All the teeth (HDP1-3 and HDP1-4 as well as HDP1-1 and HDP1-2) were found *in situ* in the HOMS layer of the palaeontological site. All four teeth were situated in a relatively small area of about 1.5 m in length by 1 m in breadth. The maximum difference in depth between the highest and lowest tooth was approximately 200 mm.

Anatomical descriptions

HDP1-3 LI₁ (Figure 3). This is a complete, well-preserved, permanent left central mandibular incisor. The corrected mesiodistal (MD) diameter of the crown is 6.4 mm and the buccolingual (BL) diameter is 7.2 mm. Crown height is ca. 8.1 mm and root length is 15.1 mm. Wear is marked with a broad rim of dentine exposed along the incisal edge [Figure 3(a)]. The distal interproximal wear facet (IWF) is placed slightly lingual to the midline. A clearly defined mesial IWF is not evident. The crown outline, as seen in lingual view, is asymmetrical, with the weak cervical eminence skewed distally. Very faint mesial and distal marginal ridges create a faint shovelling [Figure 3(b)]. Enamel polishing is evident along its entire length. The labial face is slightly convex inciso-cervically (IC). Numerous scratches are evident on the entire surface. An irregular band of hypoplastic enamel is present on the incisal third of the face [Figure 3(c)]. Remnants of dental calculus are evident on the cervical third of the crown. The root is long and thin, MD compressed, tapering inferiorly.

HDP1-4 LI₂ (Figure 4). This is a complete, well-preserved, permanent left lateral mandibular incisor. The corrected MD diameter of the crown is 7.7 mm and the BL

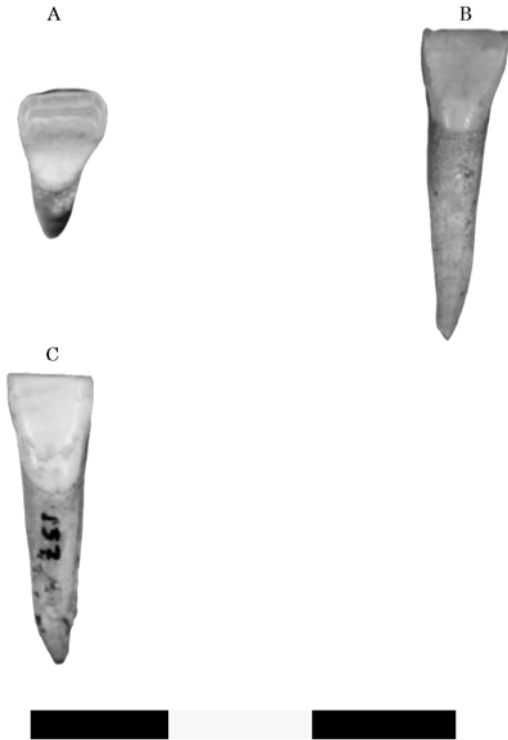


Figure 3. (a) Incisal edge, (b) lingual view and (c) labial view of HDP1-3, a left central mandibular incisor. The scale is in centimetres.

diameter is 7.2 mm. Crown height is 10.3 mm and root length ca. 13.5. Wear is marked by a subtriangular rim of dentine exposed on the incisal edge, tapering distally [Figure 4(a)]. No dentine is exposed on the disto-incisal corner. The mesial IWF has a rough surface and it is labially placed to the midline. No clear distal IWF is evident. The crown outline, as seen in lingual view, is subtriangular, with the mesio-incisal edge reduced by wear. Marked mesial and distal marginal ridges merge at the level of the very faint cervical eminence [Figure 4(b)]. On the labial face, many tiny scratches are present, especially near the incisal edge. A large area of hypoplastic enamel is present on the disto-incisal edge of the crown, extending onto the distal face [Figure 4(c)]. Smaller areas of enamel hypoplasia are

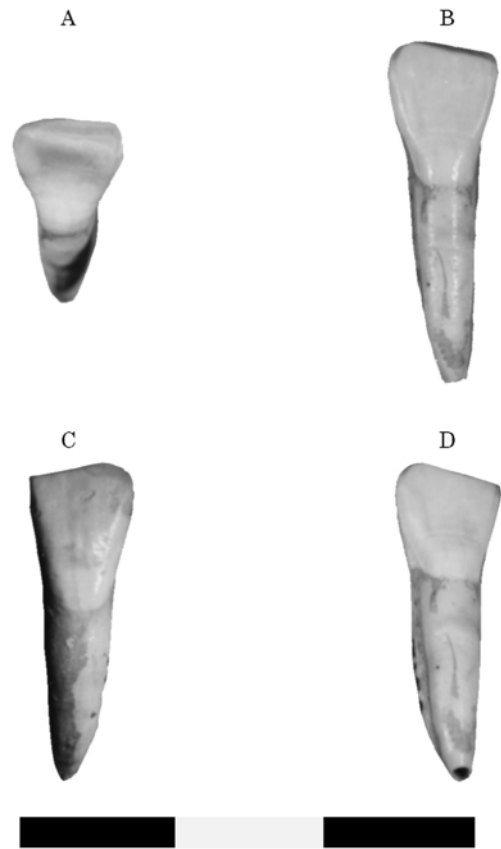


Figure 4. (a) Incisal edge, (b) lingual view, (c) labial view and (d) root apex of HDP1-4, a left lateral mandibular incisor. The scale is in centimetres.

evident on the mesio-labial edge, near the incisal margin, and on the cervical third of the crown. The root is long, strongly compressed MD with marked longitudinal grooves. The root apex is still open, suggesting that root development was not yet complete [Figure 4(d)].

Discussion

There is a strong possibility that HDP1-3 and HDP1-4 derive from a single individual. Both incisors display similar degrees of wear on their respective incisal edges. There are also matching interproximal wear facets, situated distolingually on HDP1-3 and

mesiolabially on HDP1-4. Based on the respective positions of these wear facets on each tooth, there appears to have been some degree of crowding in the anterior teeth of the mouth(s) from which they derive.

If these teeth do derive from a single individual, it is possible, on the basis of dental development, to give an estimate of the age at death of this individual. In this respect, only HDP1-4 can be used, since it still has the root apex open. Following Smith (1991), its stage of development is scored at Rc—A $\frac{1}{2}$ (root complete—apex half open) resulting in a predicted mean age of between 8 and 9 years at death, with a range of 6.5 and 10.5 years if we take into account age variation of formation stages (Moorrees *et al.*, 1963).

The existence of two human molars from the site (HDP1-1 with HDP1-2) (Berger & Parkington, 1995) raised the question of whether the two sets of teeth derive from the same individual. Since HDP1-1 and HDP1-2 were found in the same stratigraphic level as HDP1-3 and HDP1-4, and also belonged to a subadult individual (Figure 5—see also Figures 2 and 3 in Berger & Parkington, 1995), this was a distinct possibility. In order to address this issue, the developmental stages of the two molars have also been assessed. The same standards as those applied to the incisors were followed here with an acknowledgement that those standards relate to mandibular teeth.

The root of HDP1-1, a LM², reflects a level of development comparable to stage A₂¹, resulting in a predicted age of approximately 14 years (range 10–15). The root of HDP1-2, a RM³, is at a developmental stage equivalent to stage R₄¹ to R₂¹, resulting in an age estimate of 15 years (range 12–18). Thus on the basis of modern human standards of dental development, there appears to be a marked difference in age estimates between the incisor and the molars.

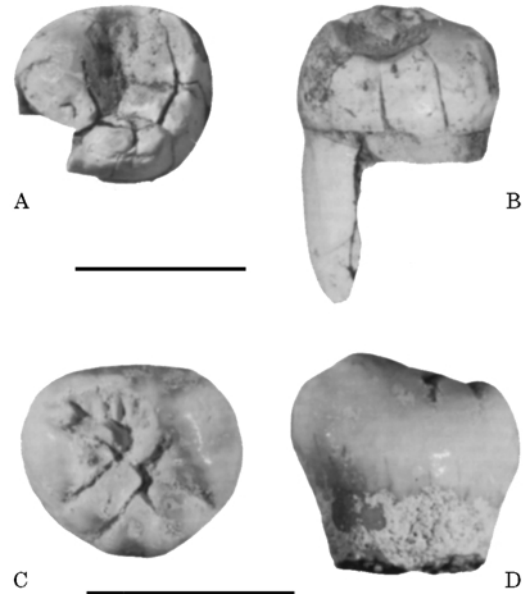


Figure 5. The Hoedjiespunt 1 molars: (a) occlusal and (b) mesial view of HDP1-1, a left maxillary second molar; (c) occlusal and (d) buccal view of HDP1-2, a right maxillary third molar. The scale is in centimetres.

However, some caution is required when interpreting this evidence. First, most standards of dental development are derived from modern European populations. This is not an ideal situation, as marked variability exists among living populations in terms of tooth formation (Tompkins, 1996a and references therein). For example, Tompkins (1996a) has demonstrated that molar teeth (in particular the M3) in African populations display advanced relative development compared with Europeans. Similar conclusions were reached by Dean *et al.* (1993) in their analysis of incremental markings in the enamel and the dentine of a West African individual. It has been suggested that this variability may be due to population differences in the timing of dental and skeletal development (Tompkins, 1996a). Second, it is well established that the third molar is very variable in its development (Garn *et al.*, 1962; Anderson *et al.*, 1976).

The scant data presently available on the dental development of Pleistocene hominids provide additional information. [Bermúdez de Castro *et al.*, \(1999b\)](#) described an essentially modern human pattern of dental development in the Lower Pleistocene hominids from the site of Atapuerca TD6. However, they also found that the third molar teeth displayed a pattern of advanced relative development compared to modern populations. An advanced relative development of the upper and lower third molars has also been described in a Middle Pleistocene specimen from Atapuerca-Sima de los Huesos ([Bermúdez de Castro & Rosas, 2001](#)). In addition to these data, [Tompkins \(1996b\)](#), in a study of relative dental development in Upper Pleistocene hominids (Neanderthals/archaic *Homo sapiens* and Early Modern/Upper Paleolithic), has demonstrated an advanced relative development of M2 and M3 in these fossil groups. At the same time, there also appeared to have been a relative delay in central incisor development compared with modern human populations.

Given this evidence, the observed discrepancy in age estimates between the HDP1 lateral incisor and the molars may well be related to a difference in the dental developmental patterns of this specific population and that of modern humans. Thus it seems reasonable to suggest that the two molars, HDP1-1 and HDP1-2, and the two incisors, HDP1-3 and HDP1-4, belonged to the same individual.

One of the most remarkable features of HDP1-4 is the simultaneous presence of a developing root and of marked incisal attrition comparable to wear stage 4 in the Murphy system [as modified by [Smith \(1984\)](#)] [[Figure 4\(a\)](#)]. A similar stage of wear is also evident on HDP1-3 [[Figure 3\(a\)](#)]. Enamel polishing, as well as numerous scratch marks more commonly associated with the incisal edge occur on the labial surfaces of both teeth. Heavy wear of

the anterior teeth with a tendency for the development of labial rounding, is often seen in people pursuing a hunter-gatherer lifestyle, and has been attributed to the habitual nonmasticatory utilization of anterior teeth ([Hinton, 1981](#)). It is possible that the HDP1 incisors are displaying the early stages of habitual nonmasticatory utilization. To shed light on this issue, a detailed analysis of the microwear patterns on these teeth is presently underway.

A comparative analysis of the metrical features of the HDP1 incisors provides additional information. [Tables 1 and 2](#) report the MD and BL diameters of central and lateral mandibular incisors respectively, in selected recent, archaeological and fossil human specimens. Crown shape index (CSI = $BL/MD \times 100$) values are also provided.

The MD and BL diameters of HDP1-3 are larger than the mean values of a sample of recent and archaeological African central incisors. The MD diameter of HDP1-3 is within the range of *Homo ergaster* (KNM-WT 15000 and KNM-ER 820) and *Homo erectus* (the Zhoukoudian sample and Sangiran 11), and only slightly smaller than *Homo habilis* (OH 7 and OH 16). The BL diameter of HDP1-3 is exceeded only by European specimens from Fontana Ranuccio (an approximate value by [Segre & Ascenzi, 1984](#)) and Atapuerca-TD6-52, the latter attributed to the species *Homo antecessor* by [Bermúdez de Castro *et al.* \(1999a\)](#), and with a suggested age of greater than 780 ka.

The MD and BL diameters of HDP1-4 are larger than the mean values of a sample of modern and archaeological African lateral incisors. The MD diameter of HDP1-4 is close to the values of *H. habilis* and among the largest in the sample of Early and Middle Pleistocene hominid lateral incisors from Africa, Europe and Asia. The BL diameter of HDP1-4 is larger than the mean value for the *H. erectus* specimens from Zhoukoudian, as well as the individual dimensions of the

Table 1 Mesiodistal (corrected) and buccolingual diameters (in mm) and crown shape index (CSI) of HDP1-3 and of central mandibular incisors in selected recent, archaeological and fossil humans from Africa, Europe and Asia

	<i>n</i>	MD	S.D.	<i>n</i>	BL	S.D.	Crown height	Root length	CSI	References
HDP1-3		6.4			7.2		(8.1) worn	15.1	112.5	Personal data
OH 7		6.8			6.6		9.2		97.1	Tobias (1991)
OH 16		6.5			7		10.6		107.7	Tobias (1991)
SKX 2355				6	—					Personal data
KNM-WT-15000		6.6			6.8		10.1	19.9	103.0	Brown & Walker (1993)
KNM-ER-820		6.1			6.3				103.3	Wood (1991)
Dmanisi		6.2			5.9				95.2	Gabunia & Vekua (1995)
Sangiran 11		7.4			6.5				87.8	Wood (1991)
Sangiran Bs 9706		6.0			5.8		9.9		96.7	Baba <i>et al.</i> (2000)
Zhoukoudian	5	6.3	0.26	5	6.4	0.42	9.0		101.6	Wood (1991)
Ternifine		5.7		6	6.6				115.8	Bermúdez de Castro (1986)
Rabat					7				116.7	Bermúdez de Castro (1986)
Atapuerca-TD ATD6-52		—			7.6					Bermúdez de Castro (1986)
Mauer		5.5			7.1				129.1	Bermúdez de Castro (1986)
Fontana Ranuccio		6.5 ca.			7.5 ca.		9.5 ca.	19.0		Segre & Ascenzi (1984)
Atapuerca-SH	5	5.5	0.08	5	6.5	0.43			118.2	Bermúdez de Castro (1986, 1988, 1993)
Border Cave 5		—			6.6					Personal data
Nubia, "Mesolithic", males	8	5.80	0.35	11	6.43	0.39			110.9	Calcagno (1989)
Nubia, "Mesolithic", females	12	5.48	0.34	14	6.31	0.39			115.1	Calcagno (1989)
San, males	6	5.4	0.47	—	5.3	0.27			98.1	van Reenen (1982)
San, females	5	5.4	0.84	—	5.6	0.61			103.7	van Reenen (1982)
San	—			5	5.2	—	6.8	12	104.0	Drennan (1929)
S. A. blacks, males	181	5.33	0.42	—	5.83	0.39			109.4	Jacobson (1982)
S. A. blacks, females	61	5.3	0.35	—	5.71	0.42			107.7	Jacobson (1982)
S. A. blacks, males	56	5.43	0.45	—	6.2	0.32			114.2	Kieser <i>et al.</i> (1987)
S. A. blacks, females	49	5.48	0.56	—	5.96	0.49			108.8	Kieser <i>et al.</i> (1987)
S. A. blacks	—	5.9	—	6	6	—	7.8	12.4	101.7	Shaw (1931)

Table 2 Mesiodistal (corrected) and buccolingual diameters (in mm) and crown shape index (CSI) of HDP1-4 and of lateral mandibular incisors in selected recent, archaeological and fossil humans from Africa, Europe and Asia

	<i>n</i>	MD	S.D.	<i>n</i>	BL	S.D.	Crown height	Root length	CSI	References
HDP1-4		7.7			7.2		10.3	13.5 inc.	93.5	Personal data
OH 7		7.7			7.4		10.1		96.1	Tobias (1991)
OH 16		7.8			7.5		11.7		96.2	Tobias (1991)
SKX 2354		6.9			—					Personal data
SKX 21204		7.1			—					Personal data
KNM-WT 15000		7.5			8.3		11.1	20.5	110.7	Brown & Walker (1993)
KNM-ER 820		7.3			6.9		10.8		94.5	Wood (1991)
KNM-ER 992		7.2			7				97.2	Wood (1991)
KNM-ER 1812		7.1			6.6				93.0	Wood (1991)
Dmanisi		6.4			6.3				98.4	Gabunia & Vekua (1995)
Zhoukoudian	7	6.8	0.4	—	6.9	0.3			101.5	Bermúdez de Castro <i>et al.</i> (1999 <i>a</i>)
Ternifne 3		6.3			7.3				115.9	Bermúdez de Castro <i>et al.</i> (1999 <i>a</i>)
Rabat		7.0			7.5				107.1	Bermúdez de Castro (1986)
Atapuerca-TD ATD6-2		7.0			7.8			17.8	111.4	Bermúdez de Castro <i>et al.</i> (1999 <i>a</i>)
Atapuerca-TD ATD6-48		7.6			7.7				101.3	Bermúdez de Castro <i>et al.</i> (1999 <i>a</i>)
Mauer		6.0			7.8				130.0	Bermúdez de Castro (1986)
Atapuerca-SH	14	6.6	0.3	—	7.3	0.4			110.6	Bermúdez de Castro <i>et al.</i> (1999 <i>a</i>)
Jebel Irhoud 3		—			7.2					Day (1986)
Nubia, "Mesolithic", males	14	6.31	0.53	15	6.86	0.26			108.7	Calcagno (1989)
Nubia, "Mesolithic", females	15	5.95	0.44	16	6.62	0.51			111.3	Calcagno (1989)
San, males	8	5.9	0.5	—	5.6	0.32			94.9	van Reenen (1982)
San, females	7	5.7	0.25	—	5.7	0.54			100.0	van Reenen (1982)
San	—	5.6	—	—	5.6	—	7.1	13.4	100.0	Drennan (1929)
S. A. blacks, males	223	6.06	0.47	—	6.27	0.37			103.5	Jacobson (1982)
S. A. blacks, females	83	5.99	0.42	—	6.12	0.4			102.2	Jacobson (1982)
S. A. blacks, males	52	6.43	0.51	—	6.56	0.46			102.0	Kieser <i>et al.</i> (1987)
S. A. blacks, females	48	6.11	0.55	—	6.45	0.28			105.6	Kieser <i>et al.</i> (1987)
S. A. blacks	—	6	—	—	6	—	8.4	13.2	100.0	Shaw (1931)

sample of *H. ergaster* specimens (excluding KNM-WT 15000). The BL dimensions are similar to other African Middle Pleistocene hominids (Tighenif 3 and Rabat) and within the range of the *Homo heidelbergensis* sample from Atapuerca-SH. Buccolingual dimensions are smaller than *H. habilis* and specimens from Atapuerca-TD6.

The large size of HDP1-3 and HDP1-4 relative to the other samples is also evident in bivariate plots of crown measurements [Figure 6(a) and (b)]. Both HDP1-3 and HDP1-4 fall outside the distribution of *H. erectus* and *H. heidelbergensis*. Their positions in the plots compare most closely to specimens of *H. habilis* and Atapuerca-TD ATD6-48 (in the case of HDP1-4).

When the overall shape of the incisors (as expressed by the CSI) is considered, HDP1-3 shows a marked degree of BL expansion, whereas this doesn't seem to be the case for HDP1-4 (Tables 1 and 2). Bermúdez de Castro *et al.* (1999a) describe BL expansion of the mandibular incisors as one of the evolutionary trends of hominid evolution from the Lower Pleistocene through the Middle Pleistocene. This trend is exemplified by the Atapuerca TD6 hominids and later in time, by the Mauer specimen and the Atapuerca SH hominids. They also hypothesized that the African Middle Pleistocene hominids may have increased the BL dimensions of the mandibular incisors. The evidence from HDP1 provides contrasting results in this respect. In terms of absolute size, both HDP1-3 and HDP1-4 display large BL size. In terms of relative BL expansion, the value of the CSI for HDP1-3 seems to follow a trend also evident in other African Middle Pleistocene hominids (Tighenif and Rabat). However, despite its large absolute size, HDP1-4 seems to retain a primitive condition in contrast to other African Middle Pleistocene specimens.

The results of the metrical analysis of HDP1-3 and HDP1-4, as well as the avail-

ability of a more expanded data set than that available to Berger & Parkington (1995), prompted us to re-examine the crown dimensions of the two molars, HDP1-1 and HDP1-2. Bivariate plots of the dental dimensions of HDP1-1 and HDP1-2 are displayed in Figure 7(a) and (b). Specimens and samples analysed are listed in the footnotes.

A different pattern appears to emerge in this analysis. In the case of HDP1-1 (LM²), the dimensions fall well inside the distribution of both *H. erectus* and *H. heidelbergensis*, and are smaller than specimens of *H. habilis* and *H. ergaster*. In the case of HDP1-2 (RM³), the dimensions are also smaller than specimens of *H. habilis* and *H. ergaster* and fall just outside the distribution of *H. erectus* and *H. heidelbergensis*. Both HDP1-1 and HDP1-2 fall towards the lower end of the distribution for African Middle Pleistocene specimens. Overall, both molars appear to be relatively small when compared with the other fossil samples examined in this study. Size reduction of the posterior teeth seems to be a common trend in Lower and Middle Pleistocene hominids (Bermúdez de Castro & Nicolás, 1995; Bermúdez de Castro *et al.*, 1999a), and the molars from HDP1 appear to fit this trend.

The results of the metrical analyses of the HDP1 incisors and molars suggest that we are looking at an individual that displays a pattern of dental metrical features (large anterior teeth and small molars) that is comparable with that seen in other African and European Middle Pleistocene hominids, e.g. Atapuerca (Bermúdez de Castro, 1993) and Fontana Ranuccio (Ascenzi & Segre, 1996).

A taxonomic attribution based on a few dental remains is more problematic, especially when dealing with specimens from the African Middle Pleistocene, that are presently subject to debate (see McBrearty & Brooks, 2000 for a review). Churchill *et al.* (2000) suggested that

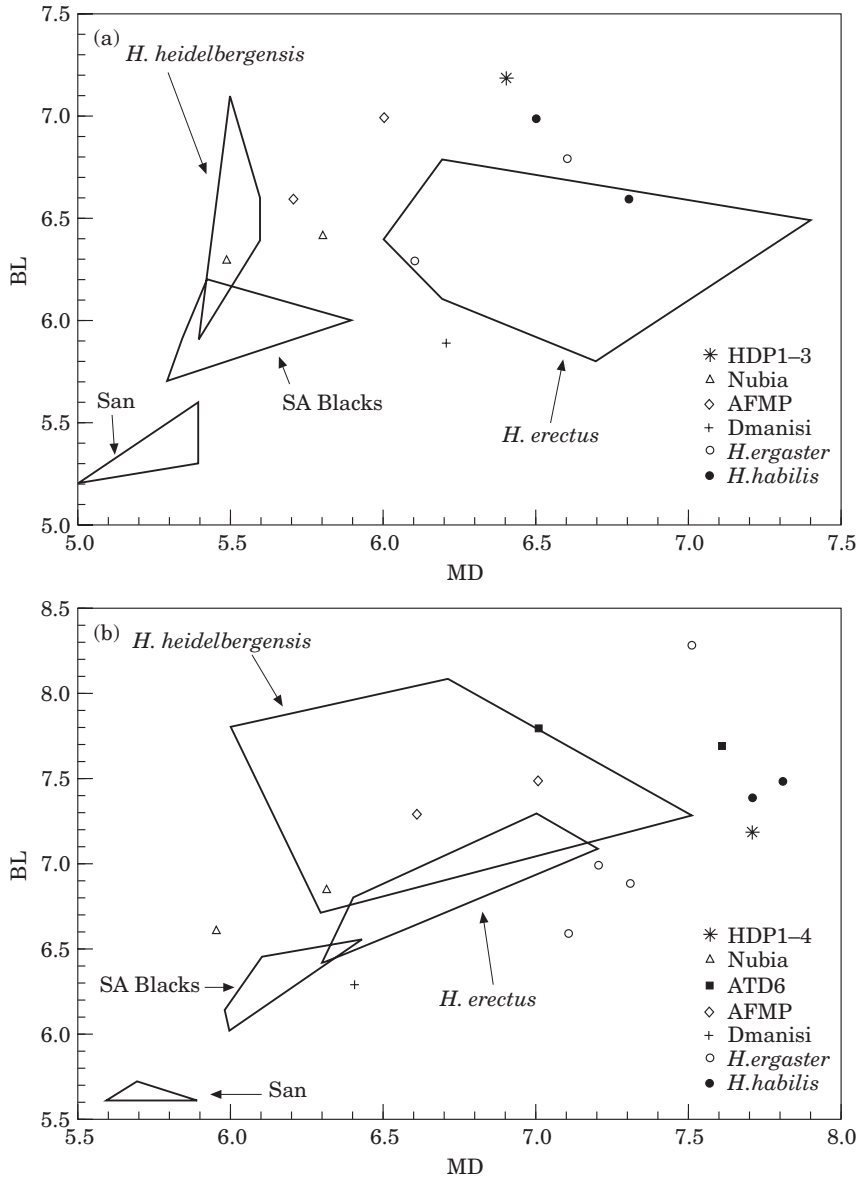


Figure 6. Bivariate plots comparing the dental dimensions of (a) HDP1-3 and (b) HDP1-4 to those of selected archaeological and fossil humans from Africa, Europe and Asia. Specimens included and references are listed in Tables 1 and 2. *H. habilis* includes OH 7, OH 16. *H. ergaster* includes KNM-WT 15,000, KNM-ER 820, KNM-ER 992, KNM-ER 1812. *H. erectus* includes the Khoukoudian sample and Sangiran 11. *H. heidelbergensis* includes the Atapuerca sample and the Mauer mandible. The African Middle Pleistocene sample (AFMP) includes Tighenif and Rabat. ATD6 indicates Atapuerca TD6 hominids. Fontana Ranuccio has not been included because measurements given are approximate.

the tibia recovered from HDP1 might be attributed to *H. heidelbergensis* in view of its morphological similarities to the Boxgrove

tibia. This view lends support to the idea by Rightmire (1998) of a geographically broad distribution of this Middle Pleistocene

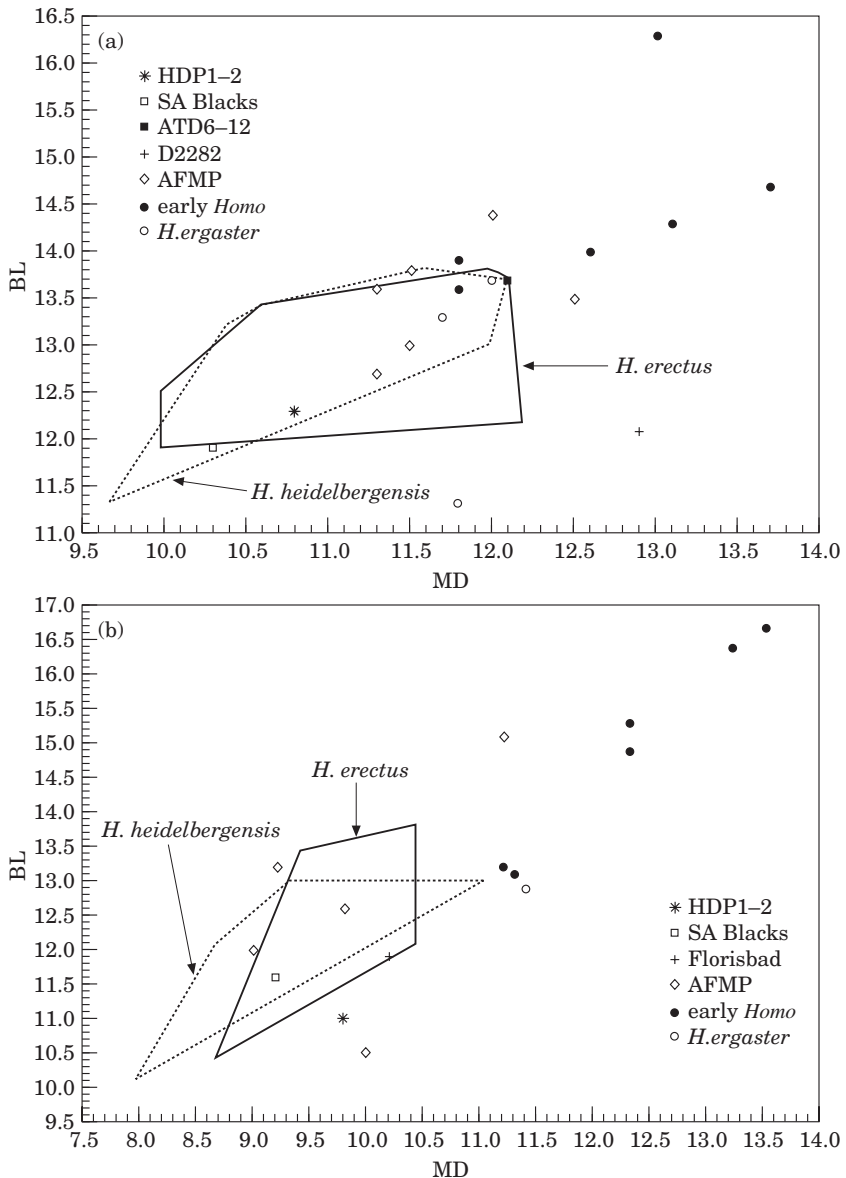


Figure 7. Bivariate plots comparing the dental dimensions of (a) HDP1-1 and (b) HDP1-2 to those of selected recent and fossil humans from Africa, Europe and Asia. Specimens included: South African Blacks (Jacobson, 1982). Atapuerca TD6 (Bermúdez de Castro *et al.*, 1999a,b). Dmanisi D2282 (Gabunia *et al.*, 2000). African Middle Pleistocene (AFMP): Kabwe (Day, 1986); Rabat (Bermúdez de Castro, 1986); Thomas III (Bermúdez de Castro, 1986); Sale' (Day, 1986); Lainyamok (Shipman *et al.*, 1983); Dagadle' (de Bonis *et al.*, 1984); Laetoli H 18 (Day *et al.*, 1980). Florisbad, personal data. *H. heidelbergensis*: Atapuerca SH (Bermúdez de Castro, 1986, 1988, 1993); Petralona (Bermúdez de Castro, 1986); Arago XXI (Bermúdez de Castro, 1986). *H. erectus*: Zhoukoudian (Wood, 1991); Sangiran (Wood, 1991). *H. ergaster*: (KNM ER 807, ER 1808, ER 3733) (Wood, 1991); KNM WT 15,000 (Brown & Walker, 1993). Early *Homo*: *H. habilis* (OH 13, OH 15, OH 16, OH 24, OH 39, ER 1813) (Tobias, 1991; Wood & Richmond, 2000); South African early *Homo* (SE 1508, SK 27, SK 847) personal data.

species. Other authors, however, contend that the species *H. heidelbergensis* is part of an exclusively European lineage leading to *Homo neanderthalensis*, whereas another lineage with an African distribution rooted in the species *H. antecessor* would have given rise to *H. sapiens* (Bermúdez de Castro *et al.*, 1997, 1999a). In this respect, it is interesting to note that the dental remains from HDP1 seem to display some of the traits described by Bermúdez de Castro *et al.* (1999a) as characteristic of a group of hominids which include, among others, the ATD6 human remains. These traits include size reduction of the third molars and increase of the BL dimensions of the mandibular incisors. However, the available evidence is still insufficient to point to closer affinities of the HDP1 sample with either the African or European Middle Pleistocene hominids.

Conclusion

The human remains from HDP1 (two maxillary molars, two mandibular incisors and a tibia) probably date from the late Middle Pleistocene. The analysis presented here suggests that the two incisors and the two molars belong to a single individual. The incisors display early signs of a wear pattern often seen in people pursuing a hunter-gatherer lifestyle. These incisors are also larger than a sample of modern and archaeological African dental remains. They are comparable in size with dentition from African, European and Asian early Middle and late Middle Pleistocene humans. The metrical evidence from these incisors in conjunction with a re-examination of metrical data from the molars, suggest that the Hoedjiespunt 1 hominid possessed dental metrical features (large anterior teeth and small molars) comparable with other African and European Middle Pleistocene hominids.

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References

- Anderson, D. L., Thompson, G. W. & Popovich, F. (1976). Age of attainment of mineralization stages of the permanent dentition. *J. Forensic Sci.* **21**, 191–200.
- Ascenzi, A. & Segre, A. G. (1996). Artefacts and human teeth at the Fontana Ranuccio Middle Pleistocene site (Central Italy). *Anthropologie (Brno)* **34**, 39–46.
- Baba, H., Aziz, F., Narasaki, S., Sudijono, Kaifu, Y., Suprijo, A., Hyodo, M., Susanto, E. E. & Jacob, T. (2000). A new hominid incisor from Sangiran, Central Java. *J. hum. Evol.* **38**, 855–862.
- Berger, L. R. & Parkington, J. E. (1995). Brief communication: A new Pleistocene hominid-bearing locality at Hoedjiespunt, South Africa. *Am. J. phys. Anthropol.* **98**, 601–609.

- Bermúdez de Castro, J. M. (1986). Dental remains from Atapuerca (Spain). I. Metrics. *J. hum. Evol.* **15**, 265–287.
- Bermúdez de Castro, J. M. (1988). Dental remains from Atapuerca/Ibeas (Spain) II. Morphology. *J. hum. Evol.* **17**, 279–304.
- Bermúdez de Castro, J. M. (1993). The Atapuerca dental remains. New evidence (1987–1991 excavations) and interpretations. *J. hum. Evol.* **24**, 339–371.
- Bermúdez de Castro, J. M. & Nicolás, M. E. (1995). Posterior dental size reduction in hominids: the Atapuerca evidence. *Am. J. phys. Anthrop.* **96**, 335–356.
- Bermúdez de Castro, J. M. & Rosas, A. (2001). Pattern of dental development in Hominid XVIII from the Middle Pleistocene Atapuerca-Sima de los Huesos site (Spain). *Am. J. phys. Anthrop.* **114**, 325–330.
- Bermúdez de Castro, J. M., Arsuaga, J. L., Carbonell, E., Rosas, A., Martínez, I. & Mosquera, M. (1997). A Hominid from the Lower Pleistocene Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* **276**, 1392–1395.
- Bermúdez de Castro, J. M., Rosas, A. & Nicolás, M. E. (1999a). Dental remains from Atapuerca-TD6 (Gran Dolina site, Burgos, Spain). *J. hum. Evol.* **37**, 523–566.
- Bermúdez de Castro, J. M., Rosas, A., Carbonell, E., Nicolás, M. E., Rodríguez, J. & Arsuaga, J. L. (1999b). A modern human pattern of dental development in Lower Pleistocene hominids from Atapuerca-TD6 (Spain). *Proc. Natn. Acad. Sci. USA* **96**, 4210–4213.
- Brown, B. & Walker, A. (1993). The dentition. In (A. Walker & R. E. Leakey, Eds) *The Nariokotome Homo erectus skeleton*, pp. 161–192. Berlin: Springer Verlag.
- Calcagno, J. M. (1989). Mechanisms of human dental reduction. A case study from Post-Pleistocene Nubia. *University of Kansas Publications in Anthropology* **18**. Lawrence: University of Kansas.
- Churchill, S. E., Berger, L. R. & Parkington, J. E. (2000). A Middle Pleistocene human tibia from Hoedjiespunt, Western Cape, South Africa. *S. Afr. J. Sci.* **96**, 367–368.
- Day, M. H. (1986). *Guide to Fossil Man*. 4th edn. London: Cassell.
- Day, M. H., Leakey, M. D. & Magori, C. (1980). A new hominid fossil skull from the Ngaloba Beds, Laetoli, northern Tanzania. *Nature* **284**, 55–56.
- Dean, M. C., Beynon, A. D., Reid, D. J. & Whittaker, D. K. (1993). A longitudinal study of tooth growth in a single individual based on long- and short-period incremental markings in dentine and enamel. *Int. J. Osteoarch.* **3**, 249–264.
- de Bonis, L., Geraads, D., Guerin, G., Haga, A., Jaeger, J. J. & Sen, S. (1984). Decouverte d'un Hominide fossile dans le Pleistocene de la Republique de Djibouti. *C. r. Acad. Sci. Paris* **299**, 1097–1100.
- Drennan, M. R. (1929). The dentition of a Bushman tribe. *Ann. S. Afr. Mus.* **24**, 61–87.
- Gabunia, L. & Vekua, A. (1995). A Plio-Pleistocene hominid from Dmanisi, East Georgia, Caucasus. *Nature* **373**, 509–512.
- Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher III, C. C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S. C., Bosinski, G., Jöris, O., de Lumley, M. A., Majsuradze, G. & Mouskhelishvili, A. (2000). Earliest Pleistocene hominid cranial remains from Dmanisi, Republic of Georgia; taxonomy, geological setting, and age. *Science* **288**, 1019–1025.
- Garn, S. M., Lewis, A. B. & Bonne, B. (1962). Third molar formation and its development course. *Angle Orthodontist* **32**, 270–279.
- Grine, F. E. & Klein, R. G. (1993). Late Pleistocene human remains from the Sea Harvest site, Saldanha Bay, South Africa. *S. Afr. J. Sci.* **89**, 145–152.
- Grün, R., Brink, J. S., Spooner, N. A., Taylor, L., Stringer, C. B., Franciscus, R. G. & Murray, A. S. (1996). Direct dating of Florisbad hominid. *Nature* **382**, 500–501.
- Hinton, J. (1981). Form and patterning of anterior tooth wear among aboriginal human groups. *Am. J. phys. Anthrop.* **54**, 557–564.
- Jacobson, A. (1982). *The Dentition of the South African Negro*. Anniston: Higginbotham.
- Kieser, J. A., Groeneveld, H. T. & Cameron, N. (1987). Evidence for a secular trend in the Negro dentition. *Ann. Hum. Biol.* **14**, 517–532.
- Klein, R. G. (1983). Palaeoenvironmental implications of Quaternary large mammals in the Fynbos Biome. *South African National Science Progress Report* **75**, 116–138.
- McBrearty, S. & Brooks, A. S. (2000). The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. hum. Evol.* **39**, 453–563.
- Moorrees, C. F. A., Fanning, E. A. & Hunt, E. E. (1963). Age variation of formation stages for ten permanent teeth. *J. Dent. Res.* **42**, 1490–1502.
- Rightmire, G. P. (1998). Human evolution in the Middle Pleistocene: the role of *Homo heidelbergensis*. *Evol. Anthrop.* **6**, 218–227.
- Segre, A. G. & Ascenzi, A. (1984). Fontana Ranuccio: Italy's earliest Middle Pleistocene hominid site. *Curr. Anthrop.* **25**, 230–233.
- Shaw, J. C. M. (1931). *The Teeth, the Bony Palate and the Mandible in Bantu races of South Africa*. London: John Bull, Sons & Danielsson.
- Shipman, P., Potts, R. & Pickford, M. (1983). Lainyamok, a new middle Pleistocene hominid site. *Nature* **306**, 365–368.
- Smith, B. H. (1984). Patterns of molar wear in hunter-gatherers and agriculturalists. *Am. J. phys. Anthrop.* **63**, 39–56.
- Smith, B. H. (1991). Standards of human tooth formation and dental age assessment. In (M. Kelley & C. S. Larsen, Eds) *Advances in Dental Anthropology*, pp. 143–168. New York: Wiley-Liss.
- Stynder, D. D. (1997). The use of faunal evidence to reconstruct site history at Hoedjiespunt 1 (HDP1), Western Cape. M.A. Thesis. Department of Archaeology, University of Cape Town.

- Tobias, P. V. (1991). *Olduvai Gorge, Volume IV. The Skulls, Endocasts and Teeth of Homo habilis*. Cambridge: Cambridge University Press.
- Tompkins, R. L. (1996a). Human population variability in relative dental development. *Am. J. phys. Anthropol.* **99**, 79–102.
- Tompkins, R. L. (1996b). Relative dental development of Upper Pleistocene hominids compared to human population variation. *Am. J. phys. Anthropol.* **99**, 103–118.
- van Reenen, J. F. (1982). The effects of attrition on tooth dimensions of San (Bushmen). In (B. Kurtén, Ed.) *Teeth: Form, Function and Evolution*, pp. 182–203. New York: Columbia University Press.
- Wood, B. A. (1991). *Koobi Fora Research Project IV: Hominid Cranial Remains from Koobi Fora*. Oxford: Clarendon Press.
- Wood, B. A. & Richmond, B. G. (2000). Human evolution: taxonomy and paleobiology. *J. Anat.* **196**, 19–60.
- Woodborne, S. (2000). Luminescence dating of the Middle Stone Age in South Africa. Report to the National Science Foundation.