Hominid fossils from Kromdraai: a revised list of specimens discovered since 1938

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Hominid fossils from Kromdraai B, situated in the Sterkfontein valley in the province of Gauteng, South Africa, recovered from excavations conducted by Broom, Brain, Vrba, Thackeray and Berger, are reassessed. All specimens are attributed to *Australopithecus* (*Paranthropus*) *robustus.* Nine individuals are identified from 27 specimens. Four of these individuals are recognized as juveniles, one as a subadult and four as young adults.

Keywords: Pleistocene, *Australopithecus, Paranthropus.*

INTRODUCTION

The early Pleistocene site of Kromdraai is situated approximately 2 km east of Sterkfontein on the southern side of the Bloubank stream in the province of Gauteng, South Africa. It was from this site that the type specimen of *Australopithecus (Paranthropus) robustus* was recovered (Broom, 1938*a*, 1950*a*). The site comprises two separate deposits, Kromdraai A (KA), also known as the 'faunal site', and Kromdraai B (KB), also known as the 'hominid site'. KA, situated approximately 30 m to the west of KB (Fig. 1), has a much higher concentration of bone in calcified deposits, but as yet has not yielded hominid fossils. Stone artefacts have been recovered from KA, indicating a hominid presence associated with an Early Acheulean or Developed Oldowan technology (Kuman *et al.*, 1997). A polyhedral core from Kromdraai B (KB 5501) could perhaps be Oldowan but the sample size from KB is too small to allow firm conclusions regarding the industry represented there (Thackeray, 1999). On the basis of faunal comparisons and seriation (McKee *et al.*, 1995), it appears that KA may be slightly younger than KB, and that both fall within the period 2,0–1,5 mya.

The type specimen of *Australopithecus* (*Paranthropus*) *robustus* from KB (TM 1517) is morphologically similar to robust australopithecines from Swartkrans, which Broom (1950*b*) had attributed to *Paranthropus crassidens.* Some researchers prefer to maintain a specific distinction between the hypodigms represented at Swartkrans and Kromdraai (Howell, 1978; Grine, 1981, 1982*a,b*), in accordance with Broom's (1950*b*) recognition of *Paranthropus crassidens* from Swartkrans as distinct from *Paranthropus robustus* from Kromdraai. Others (e.g., Tobias, 1968; de Ruiter, 1995; Kaszycka, 1995; Keyser *et al.*, 2000) recognize a single, variable species, *Australopithecus (Paranthropus) robustus* at the two sites.

In this paper we provide a brief history of work conducted at Kromdraai, and list all hominid fossils recovered from this site, providing a revised estimate for the minimum number of individuals attributable to *Australopithecus (Paranthropus) robustus* from the KB assemblage.

HISTORY OF DISCOVERIES AT KROMDRAAI

In 1938 a new hominid fossil locality was brought to the attention of Robert Broom as a result of the activity of a local schoolboy who had discovered several teeth belonging to a partial skull (TM1517). Broom recognized that although hominid, the teeth were much more robust than those known at the time from Sterkfontein (Broom, 1950*a*). He began excavations at the site, and recovered several more hominid fossils over the following years. These were given catalogue numbers with the Transvaal Museum's TM prefix (see below).

Broom (1938*a*) erected a new genus and species, *Paranthropus robustus,* to accommodate the hominid fossils from Kromdraai. His primary morphological distinction between the newly discovered *Paranthropus* and the previously discovered *Australopithecus* material from Sterkfontein was the morphology of the fourth premolar. Based on analysis of the fauna from Kromdraai, Broom (1941*a*) felt that the Kromdraai fossils were of a much younger geological age than the Sterkfontein fossils.

The first hominid postcranial material from Kromdraai was discovered in 1938. Broom (1938*b*)

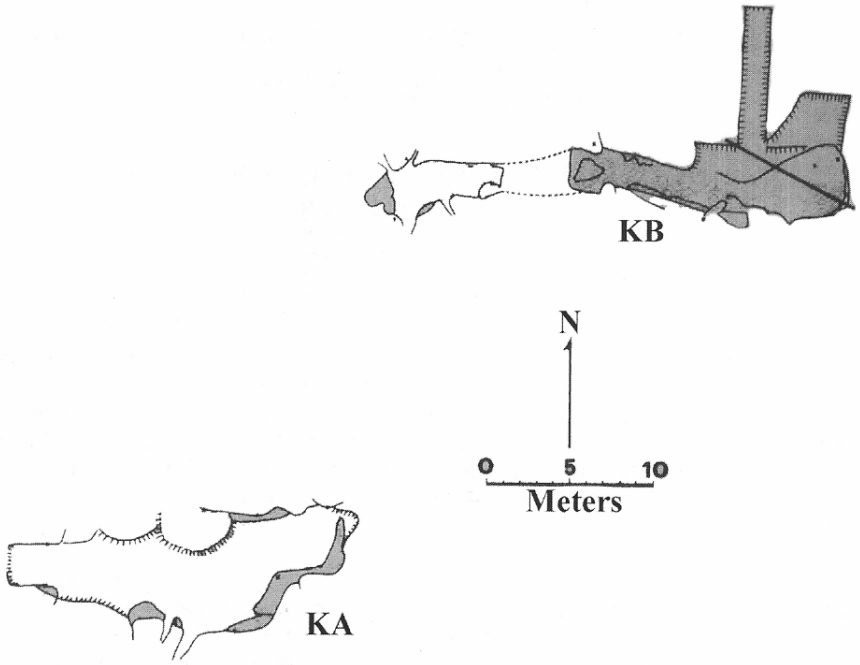

Fig. 1
Map of Kromdraai A and Kromdraai B. Modified from Brain (1981).

noted that the morphology of these postcranial elements was similar to that of modern humans. However, some of the postcranial elements originally thought by Broom (1942) to belong to the same individual as the TM 1517 skull were subsequently shown to belong to a non-hominid primate, most likely a baboon (Day, 1978; Day and Thornton 1986).

Soon after these early fossil finds, Broom (1941*b*) discovered juvenile hominid specimens from Kromdraai, allowing the first age-related comparisons to be made with the Taung skull. Broom considered that the deciduous dentition of hominids from Taung, Sterkfontein and Kromdraai represented three different genera. He even went so far as to suggest that the hominids from Kromdraai and Sterkfontein should be placed in separate subfamilies (Broom, 1950*b*).

Broom and Schepers (1946) noted dental and cranio-facial differences between specimens attributed to *Australopithecus* (*Plesianthropus*) and *Paranthropus.* In particular, they highlighted as typical of *Paranthropus* the characteristic concavity of the face, and extreme buttressing and cresting of the cranium, as well as the enlarged post-canine dentition.

When Broom and John Robinson discovered 'Mrs Ples' (Sts 5, an adult cranium of *Australopithecus africanus*) at Sterkfontein in 1947, they focused their attention on this site, and never resumed work at Kromdraai. In 1955, C. K. Brain of the Transvaal Museum recommenced work at Kromdraai B, increasing the sample of both robust australopithecine hominids, as well as non-hominid fauna. He implemented a new fossil numbering system that incorporated the prefix 'KB'.

The bovid fossils from the Sterkfontein valley were the focus of a study by Vrba (1976). She also undertook excavations at Kromdraai B and discovered additional hominid material (Grine 1982*a,b*) associated with ungulates, primates and carnivores (Vrba, 1980). The non-hominid fauna was used to draw inferences regarding palaeoecology, chronology and agents of accumulation (Vrba 1976; Vrba and Panagos, 1982). Partridge (1982) divided the Kromdraai B deposits into five members. The Kromdraai B hominids are confined to Member 3.

Hominid fossils discovered in 1949 at the nearby site of Swartkrans confirmed Broom's conclusions regarding the morphological differences between the 'robust' australopithecines from Kromdraai and the 'gracile' australopithecines from Sterkfontein and Taung. Broom, however, believed that the hominids from Kromdraai and Swartkrans were differentiated at species level (Broom, 1950*b*; Broom and Robinson, 1952), a view supported by Grine (1981, 1982*a,b*) and Howell (1978). However, Robinson (1954) rejected this opinion, and instead

preferred to see them as variable members of the same species. This latter interpretation has been supported by the 'robust' hominid fossil material recently recovered from the site of Drimolen (Keyser *et al.,* 2000).

Since 1993, excavations conducted at Kromdraai by the Transvaal Museum, in collaboration with the University of the Witwatersrand (Berger *et al.,* 1994) and Harvard University (Young *et al.,* 1997), have yielded artefacts from both Kromdraai A and B (Kuman *et al.,* 1997), and a right deciduous second molar (Rdm_2) attributable to *Paranthropus (Australopithecus) robustus* (KB 5503). Sediments have been studied for variability in trace-element concentrations, with special reference to vanadium, which shows interesting temporal changes (Thackeray *et al.,* 1995; Young *et al.,* 1997). Attempts are currently being made to obtain absolute dates by electron spin resonance, uranium-series and palaeomagnetic dating techniques. Faunal dating suggests that Kromdraai B is penecontemporaneous with Bed I at Olduvai (McKee *et al.,* 1995).

Early *Homo* is apparently not represented at Kromdraai. J.F.T. has suggested that morphometric analysis of TM 1517 from Kromdraai and OH 5 from Olduvai Gorge indicates a high probability of conspecificity (Thackeray, 1997). D.J.D. and L.R.B. do not support this interpretation.

HOMINID LIST

The list below is a summary of hominid material attributed here to *Paranthropus (Australopithecus) robustus* from Kromdraai B. Mann (1975) previously provided age estimates of the hominids assuming human rates of dental development.

If the rates of development in robust australopithecines were different from those typical of *Homo sapiens* as suggested by Dean *et al.* (1993), the individual ages for robust australopithecines should be revised to give younger values in absolute terms. Age estimates are therefore provided in both human and chimpanzee terms. Human rates of eruption are based on Schour and Massler (1941 *in* Hillson, 1986), and chimpanzee rates of eruption are based on Conroy and Kuykendall (1995) and Kuykendall *et al.* (1992).

List of Kromdraai hominid material

KB542	Metacarpal, mature individual (Fig. 2)
KB3133	Left cuboid, mature individual (Fig. 2)
KB3297	Right calcaneous, mature individual (Fig. 2)
KB5063	A very small molar, probably RM^1; coming into occlusion, crown beginning to wear; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 3)
KB5222	LM^3; coming into occlusion, crown beginning to wear mesially; age estimate: human 18 ± 1 years, chimpanzee 10 years ± 9 months (Fig. 3)
KB5223	Isolated mandibular teeth; Ld_c, Ldm_1, Ldm_2, LI_1, LI_2, L_C, LM_1, Rdm_2, RI_1, RI_2, RM_1; Ldm_1 shows moderate wear, dm^2 coming into occlusion and showing light wear, M1 coming into occlusion but essentially unworn; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 4)
KB5226	LM_3; crown fragment showing moderate wear; age estimate; human 21+ years, chimpanzee 11+ years (Fig. 3)
KB5383	RM^1; coming into occlusion, crown beginning to wear mesially; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 3)
KB5503	Rdm_2; coming into occlusion but essentially unworn; age estimate: human 2 years ± 6 months, chimpanzee 1 year ± 6 months (Fig. 5)
TM1517a	Cranium with LP^3 LM^2 + associated isolated RP^3–RM^3; M^3 erupting and coming into occlusion; age estimate: human 18 ± 1 years, chimpanzee 10 years ± 9 months (Fig. 6)
TM1517b	Mandible with RP_3–M_3 + associated isolated LP_3 and LP_4; probably derived from the same individual as TM1517a cranium; M^3 erupting and coming into occlusion; age estimate: human 18 ± 1 years, chimpanzee 10 years ± 9 months (Fig. 7)
TM1517c	Number representing several isolated teeth attributed to cranium and mandible above; consists of RP^3, RP^4, a probable RM^1 fragment, RM^2, RM^3, LP_3, and LP_4, plus an isolated enamel fragment (Fig. 8)
TM1517d	Right talus; presumed to be derived from same individual as cranium and mandible (Fig. 2)
TM1517e	Proximal right ulna; articulates with TM1517f; presumed to be derived from same individual

	as cranium and mandible (Fig. 2)
TM1517f	Right distal humerus; articulates with TM1517e; presumed to be derived from same individual as cranium and mandible (Fig. 2)
TM1536	Right mandible with RI_1 (unerupted), Rdi_2, Rdc, Rdm_{1-2}, RM_1, Ldc, Ldm_1; both dm_1 show slight wear, dm_2 in occlusion, M_1 also coming into occlusion; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 9)
TM1600	Left mandible fragment with LP_3, LM_2–LM_3; light wear of third molar; age estimate: human 18 ± 1 years, chimpanzee 10 years ± 9 months (Fig. 10)
TM1601a–f,	Mann (1975) believed these to be derived from two individuals, with TM1601a and TM1601e representing one, and TM1601b, c, d representing the other. However, TM1601e probably does not derive from the same individual as TM1601a. TM1601f was not previously catalogued.
TM1601a	Rdm_1; coming into occlusion; age estimate: human 2 years ± 6 months, chimpanzee 1 year ± 6 months (Fig. 11)
TM1601b	LP_3; unerupted; age estimate: human 10 years ± 9 months, chimpanzee 7 years ± 6 months (Fig. 11)
TM1601c	L_c; age estimate: human 10 years ± 9 months, chimpanzee 8 years ± 9 months (Fig. 11)
TM1601d	LP_4; unerupted; age estimate: human 10 years ± 9 months, chimpanzee 7 years ± 6 months (Fig. 11)
TM1601e	LM^1; coming into occlusion but essentially unworn; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 11)
TM1601f	Rd_c; this specimen was not previously catalogued, but is a right deciduous hominid mandibular canine; it is possible that this tooth comes from the same individual as TM1601c, and would have been replaced by the latter permanent canine when it errupted; it is lightly worn and slightly damaged at the mesial edge of the occlusal surface; age estimate: human 10 years ± 9 months, chimpanzee 8 years ± 9 months (Fig. 11)
TM1602	Right maxillary fragment with roots of RP^4–RM^2; RM^3 hypothesized to be forming in crypt; age estimate inconclusive without crowns present; however, this does appear to be an adult that cannot be matched to any other adult present, and therefore probably represents a separate individual (Fig. 12)
TM1603	LM^3; coming into occlusion; referred to as an antimere to TM1517a; age estimate: human 18 ± 1 years, chimpanzee 10 years ± 9 months (Fig. 8)
TM1604	Ldm_2; light wear; age estimate: human 6 years ± 9 months, chimpanzee 3 years ± 6 months (Fig. 5)
TM1605	Iliac fragment of mature individual, preserving a portion of the acetabulum but lacking the iliac crest (Fig. 13)
TM3601	Left distal femur of mature individual (uncertain provenance, but probably from Kromdraai) (Fig. 2). Suzman (1978) identified as a felid.

Adult individuals

Individual 1	TM1517 + TM1603: M^3s antimeres
Individual 2	TM1600 + KB5222
Individual 3	TM1602
Individual 4	KB5226

Subadult individual

Individual 5	TM1601b,c,d,f

Juvenile individuals (not yet at reproductive maturity)

Individual 6	TM1536 + KB5063
Individual 7	TM1601a + KB5503
Individual 8	TM1601e + TM1604
Individual 9	KB5223 + KB5383

Table 1
Comparison of antimere molar sizes from undistorted Swartkrans dentitions (in mm).

	LM1	RM1	Difference
	SK14	**SK14**	
MD length	12.67	12.71	0.04
BL breadth	13.86	13.61	0.25
	SK48	**SK48**	
MD length	12.32	12.14	0.18
BL breadth	14.01	13.86	0.25
	SK49	**SK49**	
MD length	12.34	12.36	0.02
BL breadth	14.89	15.10	0.23
	TM1601e	**KB5383**	
MD length	12.56	13.06	0.47
BL breadth	13.17	14.10	0.93

Table 2
Mesiodistal (MD) and bucco-lingual (BL) tooth diameters of Kromdraai hominid deciduous dentition (in mm).

Tooth	Specimen	MD	BL
di2	TM1536	4.62	3.83
dc	TM1536	4.83	5.14
	TM1601f		
dm1	TM1601a	10.17	8.28
	KB5223	–	7.84
	TM1536 (L)	9.91	8.11
	TM1536 (R)	9.92	8.02
dm2	TM1604	–	10.12
	KB5503	12.84	10.27
	KB5223 (L)	12.43	10.25
	KB5223 (R)	12.35	10.21
	TM1536	12.36	9.81

Some of our age estimates disagree with previous reports as a result of a taphonomic phenomenon at Kromdraai. Several of the isolated teeth lack roots, which had previously been considered to be unformed. However, attrition of the crowns indicated that these specimens were significantly older than would be hypothesized based on root formation (or lack thereof). It was then recognized that the missing roots probably were extant at the time of deposition, but that a subsequent diagenetic process had eroded the roots and dentine away, leaving only hollowed enamel caps. As a result, root formation was used with extreme caution when diagnosing the age at death of individuals.

We have grouped the hominids together into what we believe to be discrete individuals. Groupings are based on stage of development, dental attrition, and occlusal morphology, to the exclusion of state of preservation or colouration. Individual associations between the TM-numbered hominid material from Kromdraai have been discussed previously (Broom and Schepers, 1946; Brain, 1981). Mann (1975) believed the TM1601a–e fossils were derived from two separate individuals: TM1601a and TM1601e representing one, and TM1601b, c, d representing the other. Our analysis of these fossils indicates that TM1601a and TM1601e probably come from different individuals as well. TM1601f is a hominid deciduous canine that had not been previously catalogued, but probably belongs to the same individual as TM1601b, c and d.

When KB5383 was discovered, it was thought to be an antimere to TM1601e. Three maxillae from Swartkrans possess both left and right maxillary first molars in a similar state of dental attrition as KB5383 and TM1601e. Table 1 lists their respective measurements. The Kromdraai teeth exhibit a significantly larger difference in size between the left and right teeth than do the Swartkrans fossils. Even though KB5383 is damaged, it is still the larger of the two teeth. KB5383 and TM1601e are therefore held to belong to separate individuals.

CONCLUSIONS

On the basis of dentition, we conservatively estimate a minimum number of nine hominid individuals representing *Paranthropus (Australopithecus) robustus* in the Kromdraai B assemblage. This number includes four young adults, four juveniles and one subadult. On the basis of epiphyseal fusion, we conclude that all of the hominid postcranial material from Kromdraai B represent adult individuals. Since no duplication of elements is evident, it is possible that all are derived from one individual. Broom and Schepers (1946) considered the postcranial material from TM1517 to belong to the same individual as the cranial material from TM1517 based on their close provenance *in situ*.

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Table 3
Mesiodistal (MD) and bucco-lingual (BL) tooth diameters of Kromdraai hominid permanent dentition (mm).

Maxillary tooth	Specimen	MD length	BL breadth	
P3	TM1517 (L)	10.16	13.77	
	TM1517 (R)	10.27	–	
P4	TM1517 (L)	10.70	15.24	(MD estimated)
	TM1517 (R)	10.83	–	
M1	TM1517 (L)	13.14	14.41	
	TM1601e	12.59	13.17	
	KB5383	13.06	14.10	(damaged, estimated)
	KB5063	11.16	12.77	
M2	TM1517 (R)	13.73	15.86	
	TM1517 (L)	13.66	15.84	
M3	TM1603	13.96	15.97	
	TM1517	14.40	16.04	
	KB5222	14.82	16.73	
Mandibular tooth	**Specimen**	**MD length**	**BL breadth**	
I1	KB5223 (L)	4.79	4.06	
	KB5223 (R)	4.87	4.05	
I2	KB5223 (L)	5.58	–	
	KB5223 (R)	5.64	5.72	
C	TM1601c	7.48	8.09	
P3	TM1517 (L)	10.36	12.59	
	TM1517 (R)	10.46	12.49	(BL estimated)
	TM1600	10.12	12.46	
	TM1601d	9.23	11.21	
P4	TM1517 (L)	11.71	13.17	
	TM1517 (R)	11.57	13.13	
	TM1601b	10.84	12.05	
M1	KB5223 (L)	14.33	12.47	
	KB5223 (R)	13.98	12.57	
	TM1517 (R)	14.48	13.03	
	TM1536	12.80	11.80	(MD estimated)
M2	TM1600	14.77	14.74	
	TM1517 (R)	–	14.08	
M3	TM1600	15.95	14.69	
	TM1517 (R)	16.19	13.86	

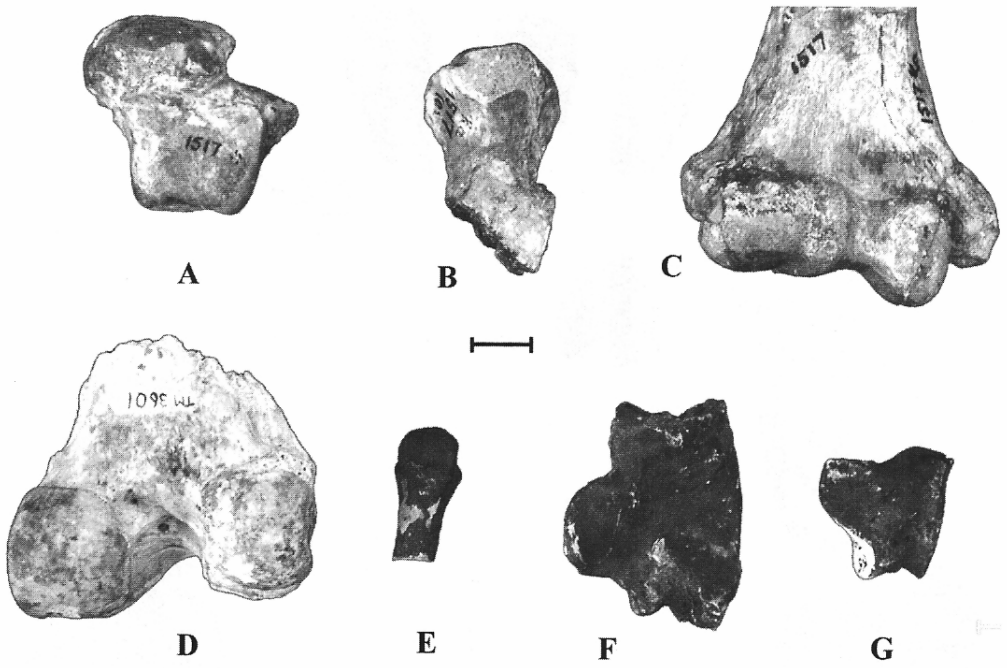

Fig. 2

Hominid postcranial remains from Kromdraai. **A**: TM1517d, right talus, superior aspect; **B**: TM1517e, proximal end of right ulna, anterior aspect; **C**: TM1517f, distal end of right humerus, anterior aspect; **D**: TM3601, distal articular condyles of left femur, posterior aspect; **E**: KB542, distal half of metacarpal, dorsal aspect; **F**: KB3297, fragment of right calcaneous, articular surface; **G**: KB3133, complete left cuboid, medial aspect. Scale bar = 1 cm.

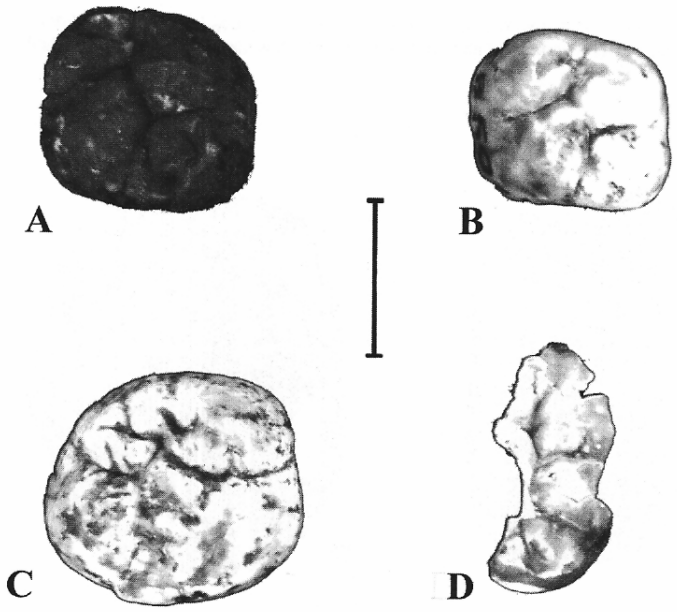

Fig. 3

Isolated hominid molar teeth from Kromdraai. **A**: KB5383, RM^1; **B**: KB5063, RM^1; **C**: KB5222, LM^3; **D**: KB5226, LM_3. Scale bar = 1 cm.

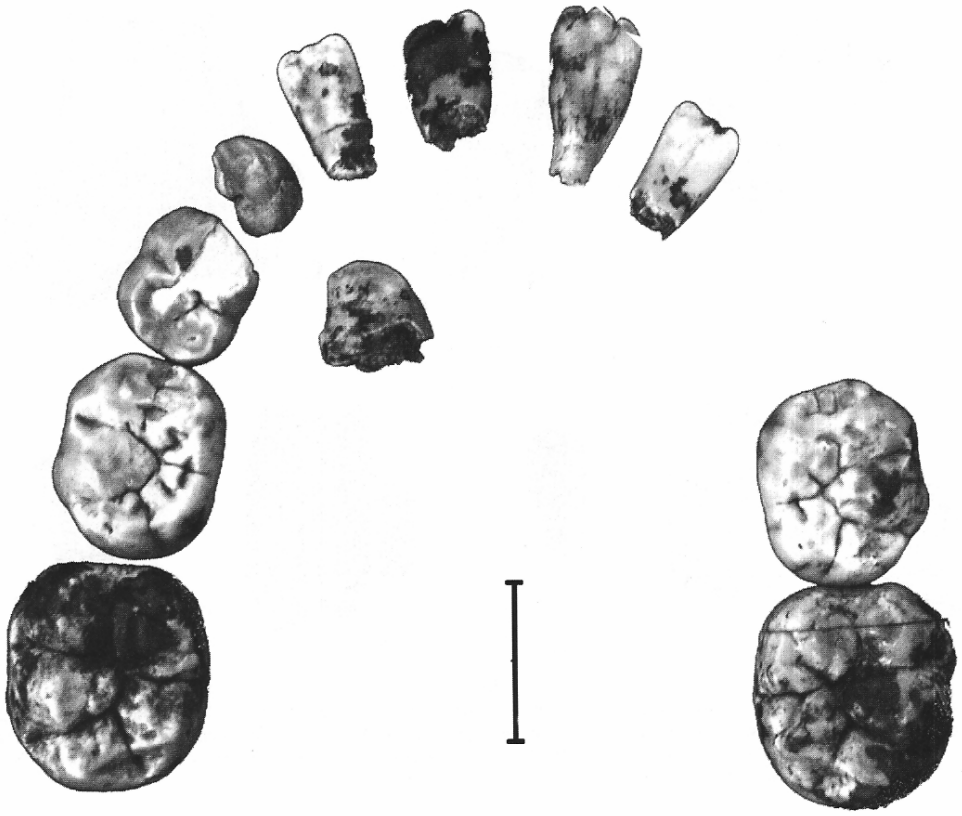

Fig. 4

KB5223 fragmented juvenile mandible from Kromdraai. Teeth include LI_1, LI_2, Ld_c, L_C (unerupted), Ldm_1, Ldm_2, RI_1, RI_2, Rdm_1 and Rdm_2. Several small fragments of mandibular bone are also present for this specimen (not figured). Scale bar = 1 cm.

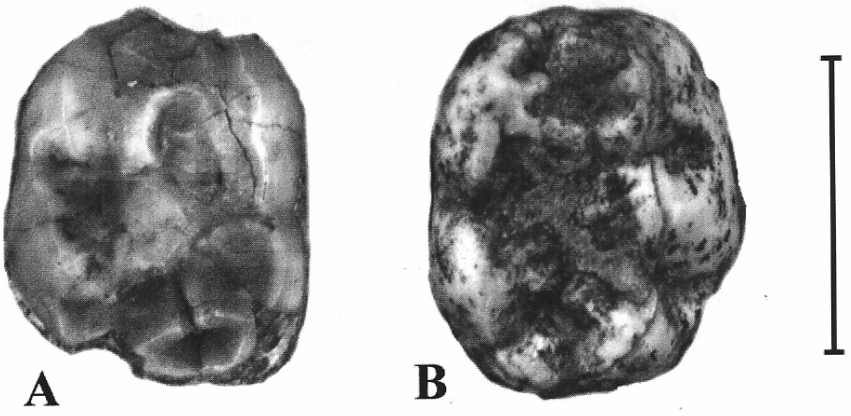

Fig. 5

Isolated deciduous molars from Kromdraai. **A**: TM1604, Ldm_2; note that distal surface of the tooth has been damaged, removing a portion of enamel; **B**: KB5503, Rdm_2. Scale bar = 1 cm.

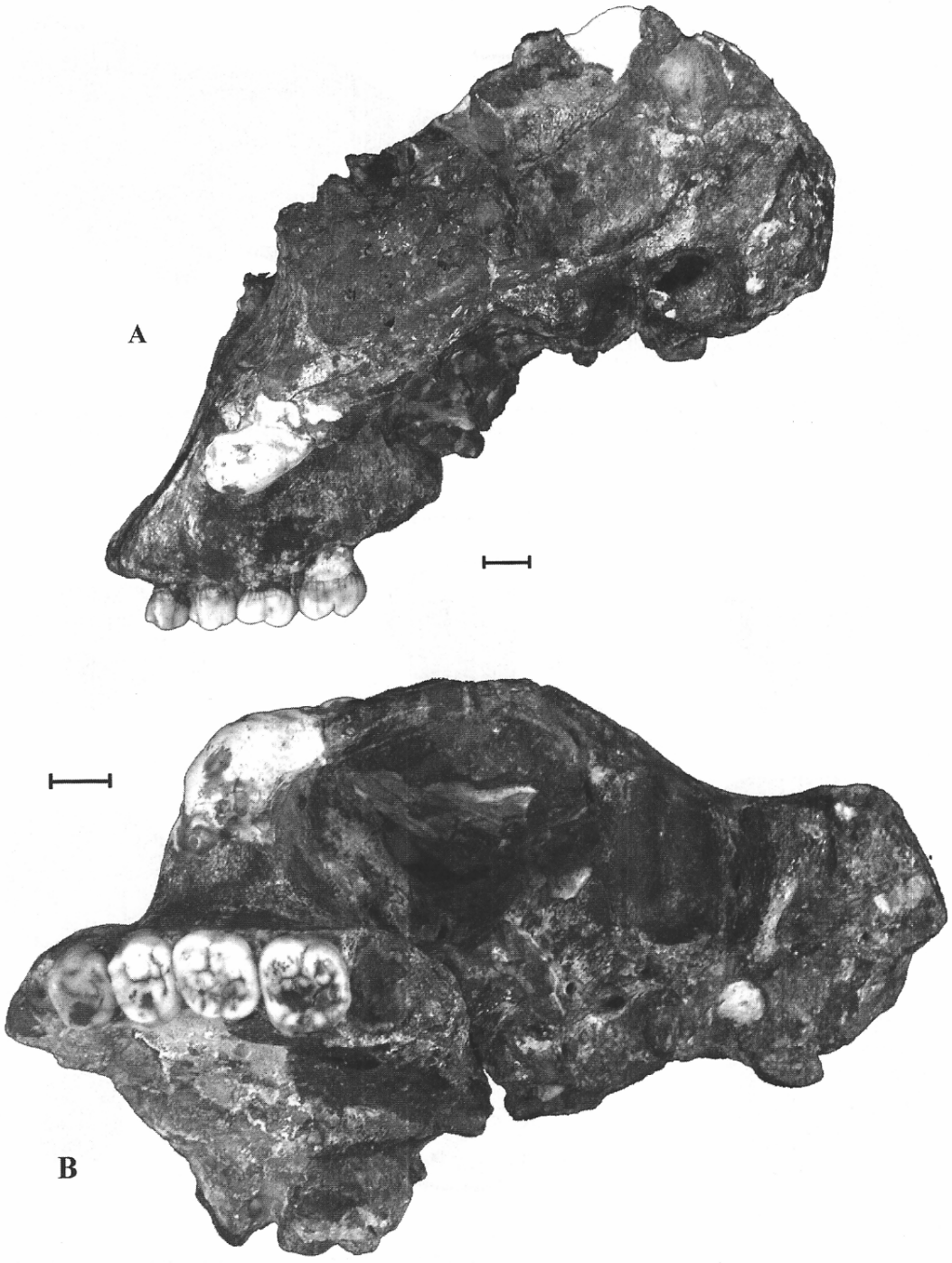

Fig 6

TM1517 type specimen of *Paranthropus robustus* from Kromdraai. **A**: left lateral view of cranium; **B**: view of cranium in norma basalis, displaying dentition. Teeth present include LP^3, LP^4, LM^1 and LM^2. Scale bar = 1 cm.

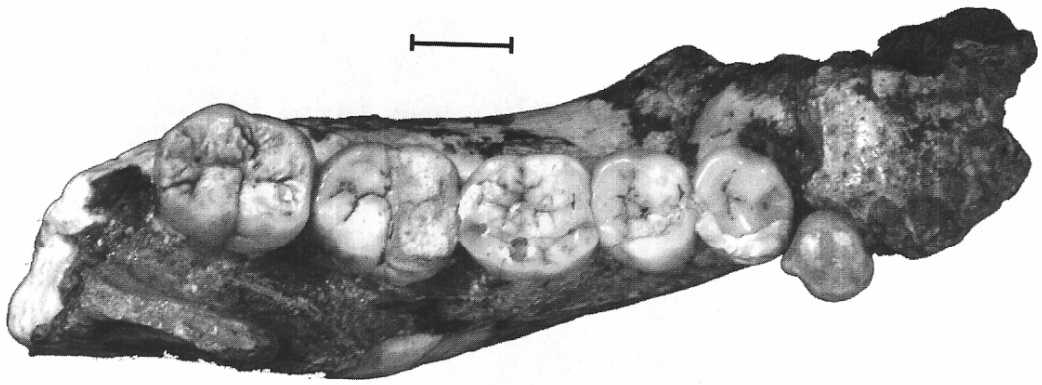

Fig. 7

Right hemi-mandible of TM1517 in occlusal view. The canine has been reconstructed out of plaster. Damage to the buccal side of both premolars and the mesial half of the second molar has been repaired with plaster. Teeth present include RP_3, RP_4, RM_1, RM_2 and RM_3. Scale bar = 1 cm.

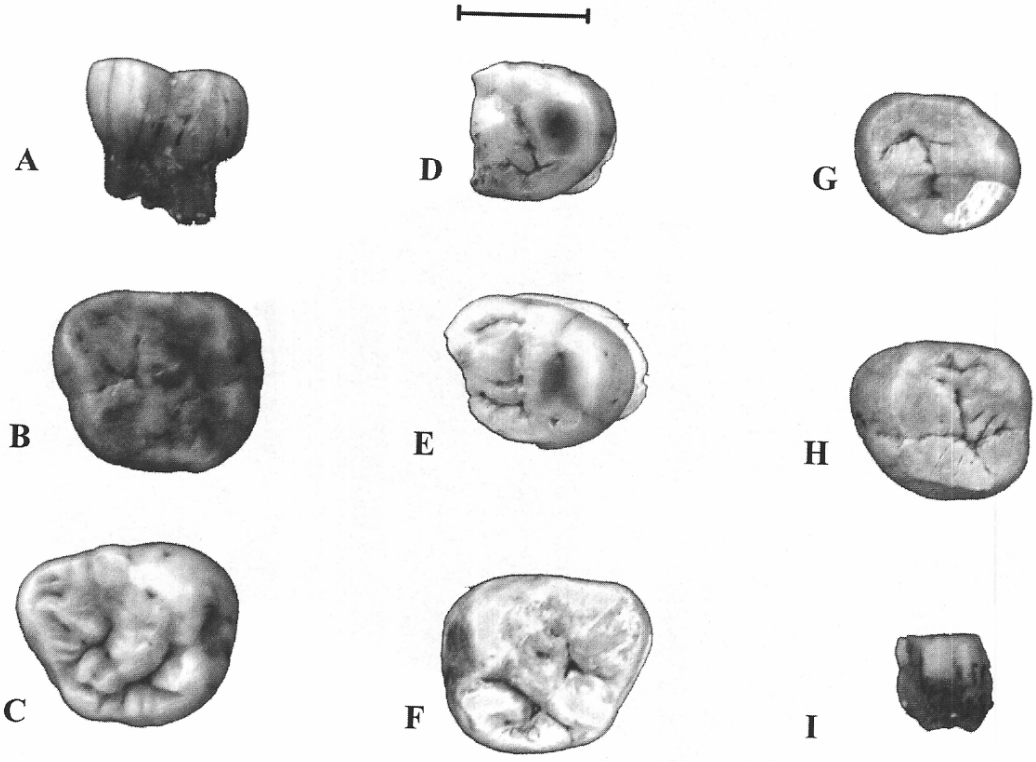

Fig. 8

TM1517c, isolated teeth and tooth fragments belonging to the individual TM1517, all in occlusal view, except (A) and (I) in lingual view. All teeth but (F) were derived from the same block as the TM1517 cranium and mandible, and all are consistent with being antimeres to their respective *in situ* teeth in the jaws. **A**: TM1517c, RM^1 fragment; **B**: TM1517c, RM^2; **C**: TM1517c, RM^3; **D**: TM1517c, RP^3; **E**: TM1517c, RP^4; **F**: TM1603, LM^3 probable antimere to (C); **G**: TM1517c, LP_3; **H**: TM1517c, LP_4; and **I**: TM1517c, enamel fragment, may be part of (A). Scale bar = 1cm.

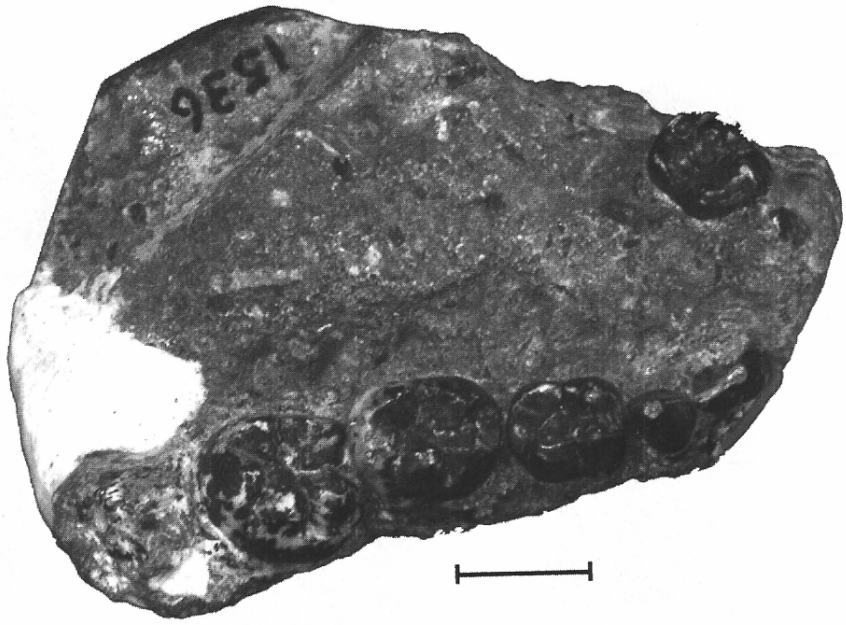

Fig. 9

TM1536, juvenile mandible from Kromdraai. The bone has eroded away, leaving the isolated teeth in approximate anatomical position. Teeth present include RI_1 (unerupted), Rdi_2, Rd_c, Rdm_1, Rdm_2, RM_1, Ld_c and Ldm_1.

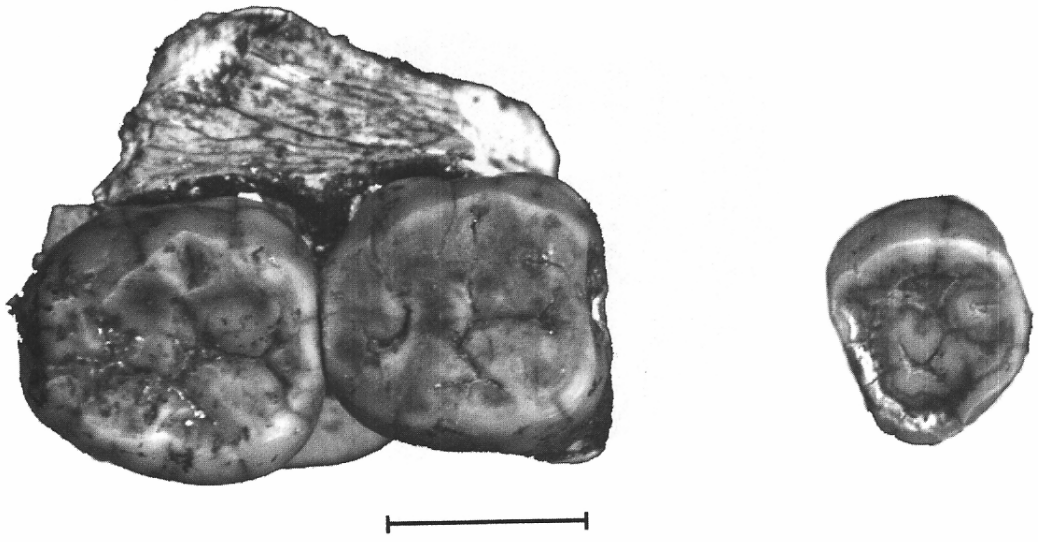

Fig. 10

TM1600, fragmented left hemi-mandible from Kromdraai. Teeth present include LP_3, LM_2 and LM_3. Scale bar = 1cm.

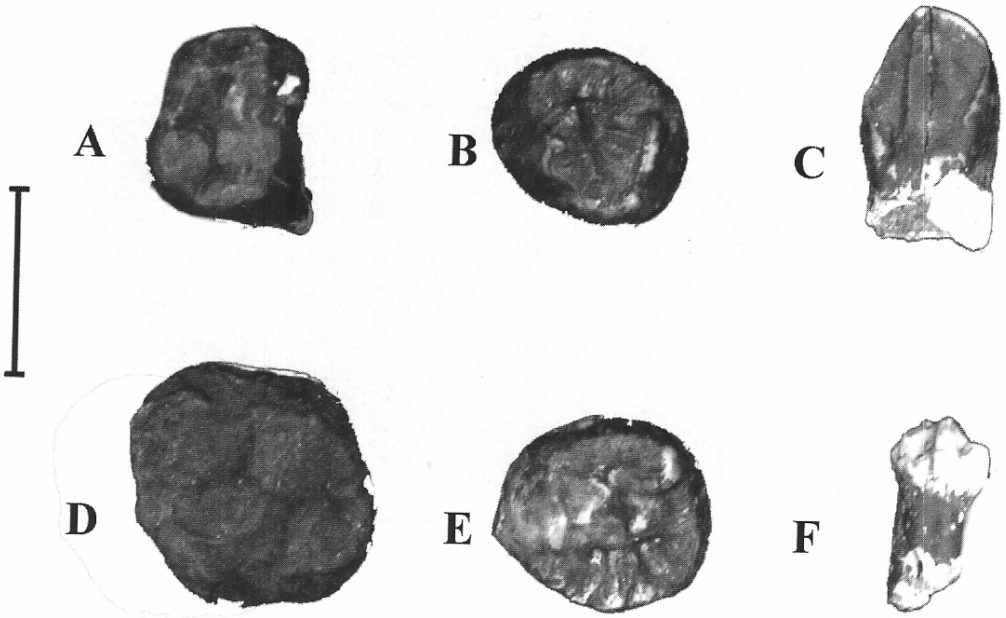

Fig. 11

TM1601, isolated teeth from several individuals at Kromdraai. **A**: TM1601a. Rdm_1; **B**: TM1601b. LP_3; **C**: TM1601c. L_C; **D**: TM1601e, LM^1; **E**: TM1601d, LP_4; and **F**: TM1601f, Rd_c. Scale bar = 1cm.

Fig. 12

TM1602, right maxillary fragment from Kromdraai. The crowns of the teeth have been broken away, but the roots of the RP^4, RM^1 and RM^2 are present. The RM^3 is possibly forming in the crypt. Scale bar = 1 cm.

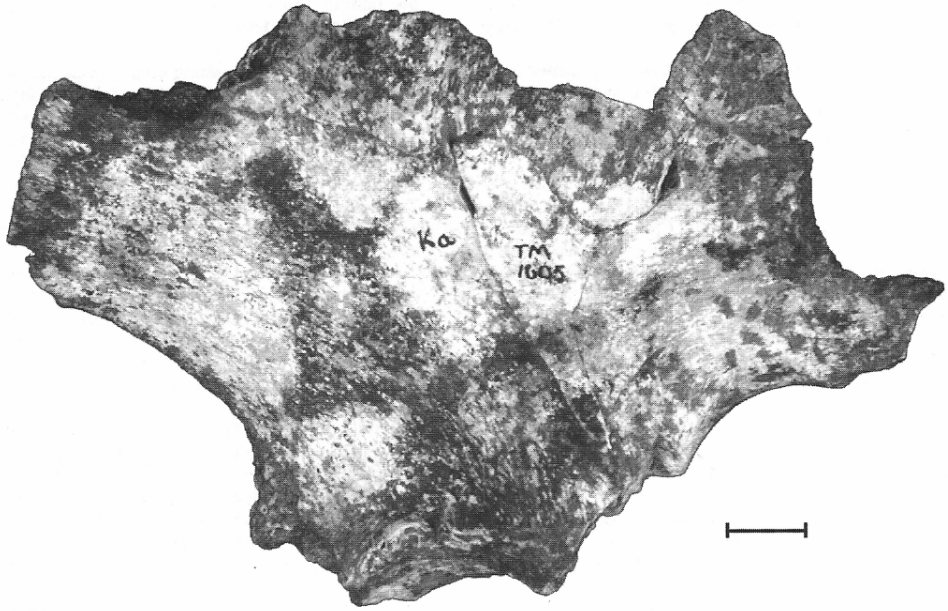

Fig 13

TM1605, iliac fragment from Kromdraai with a portion of the acetabulum preserved, but lacking the iliac crest. Scale bar = 1 cm.

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