her many sacrifices, especially during the first two years of the excavation when I had to fund the project myself. R. Smith and Babcock Africa Ltd are thanked for help during the initial phase of the excavation. I am most grateful to S.R. Loth, M. Henneberg, C. Menter, S. Cobb, C. Steininger, J. Moggi-Cecchi and T. Pickering for advice on the description of the skull and for a critical reading of the manuscript. P. Tobias and R. Clarke are thanked for their assistance, advice and encouragement. I thank C. Menter for indispensable help with the excavation and faunal analysis during the last three years, T. Pickering for help with the taphonomy and faunal analysis, and J. Moggi-Cecchi and C. Menter who assisted with the preliminary reconstruction of the skull. This work was funded by the Palaeo-Anthropology Scientific Trust of South Africa, the National Geographic Society of Washington, D.C., the L. S. B. Leakey Foundation and the Cultural Division of Foreign Affairs of the Republic of France.

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Drimolen: a new hominid-bearing site in Gauteng, South Africa

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The co-occurrence of *Paranthropus robustus* and early *Homo* in South Africa has so far been firmly documented only at the site of Swartkrans.[1–4] Our analysis of a sample of 79 early hominid fossil specimens from the newly discovered cave site of Drimolen confirms that *Paranthropus* [*Australopithecus*] *robustus*[5] was contemporaneous with early *Homo* in South Africa during the Plio-Pleistocene. In addition, analysis of the large number of robust australopithecine dental remains from Drimolen demonstrates the considerable variability in this taxon. The sub-sample of deciduous *P. robustus* teeth from Drimolen encompasses a wide range of the metrical and morphological variation observed in the robust australopithecine samples from Swartkrans and Kromdraai. This finding supports the idea of a single, variable species of robust australopithecine in South Africa during the Plio-Pleistocene. At the same time, it weakens the hypothesis of the existence of two separate robust australopithecine species (namely, *P. robustus* from the site of Kromdraai and *P. crassidens* from Swartkrans) in South Africa, as first proposed by Broom[6] and later supported by others.[7–12]

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Drimolen, located approximately 7 km north of the well-known Sterkfontein Valley caves, is a relatively rich hominid-bearing site discovered by one of us (A.W.K.) in 1992. Like the other Gauteng sites, Drimolen is a former cave system that formed in the impure dolomitic limestone of the Monte Christo Formation. Figure 1 summarizes the site's stratigraphy and provides a reconstruction of its formation. Radioisotopic dating is not yet possible at Drimolen and the recovered fauna contains few time-sensitive mammals, including a remarkable absence of suids and equids (Table 1). However, the overall composition of the macromammalian assemblage suggests a Plio-Pleistocene age of 2.0 to 1.5 Myr.

The hominid fossils recovered thus far from Drimolen are listed in Table 2, along with our provisional taxonomic allocations. It is clear that the site preserves numerous remains of a robust australopithecine species[13] and several specimens of one or more non-robust species (DNH 35, 45, 49, 70, 71), including *Homo* sp. In particular, DNH 35, a right mandible with dm_1, dm_2 and developing M_1, displays a number of features in its deciduous dentition that are incompatible with robust australopithecine morphology and are, instead, comparable to non-robust hominids. These deciduous features include: a Y-shaped fovea anterior, skewed lingually; a low lingual end of mesial marginal ridge; a protoconid mesially positioned to the metaconid; and a shallow buccal groove. More important, the M_1 of DNH 35 preserves features that have been described in specimens of early *Homo* from Swartkrans, such as relative MD elongation, high cusps and buccal and lingual faces that are almost vertical.[4,14] Overall, the expression of these traits in DNH 35 argues for the specimen to be allocated to the genus *Homo.* Thus, the Drimolen evidence is important because it confirms the co-existence of robust australopithecines and early *Homo* in South Africa during the Plio-Pleistocene. Before the discovery of Drimolen such evidence was known only from the nearby and broadly like-aged site of Swartkrans.[1–4]

The Drimolen hominid fossil assemblage, with its relatively large sample of deciduous teeth, is also relevant to the debate over the taxonomic unity or disunity of the South African robust australopithecines. Following Broom,[6] both Howell[7] and Grine[8–12] have made a species-level distinction between the robust australopithecine fossils from Kromdraai and Swartkrans,

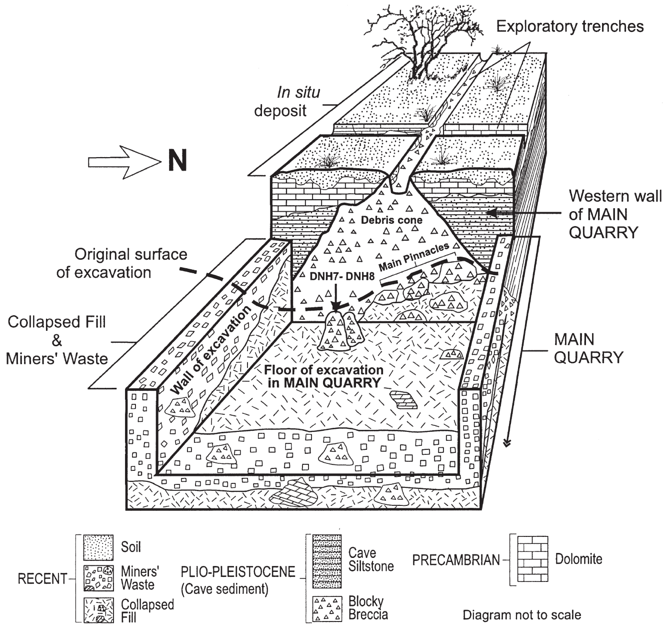

Fig. 1. Block diagram showing the stratigraphic relations of the cave sediments. The Drimolen fossil site is a former cave within the dolomites of the Monte Christo Formation of the Malmani Subgroup of the Chunniespoort Group. The Drimolen cave is similar in form and formation to the dolomitic caves in the Sterkfontein Valley area.[19,20] The site was mined for calcite (flowstone) during the first half of the present century. Cave sediment is exposed in about twenty holes that were blasted out by the miners. Most of the ceiling of the cave had been removed by weathering and erosion. The fossiliferous sediments of the site have been divided into two groups: *in situ* deposits and Collapsed Fill. Figure 1 illustrates the Collapsed Fill in the eastern aspect and *in situ* sediments to the west. Two *in situ* fossil bearing lithologies are recognized: the Blocky Breccia and the Cave Siltstone. The Blocky Breccia was deposited as an elongated debris cone and is clast supported with a pinkish brown sandy matrix. The clasts are composed of dolomite and chert. This unit is highly fossiliferous and all the hominids derive from this genetic increment. This cone was deposited through a fissure that is now exposed in the longer of the two exploratory trenches. The Cave Siltstone is reddish brown, thinly laminated and shows ripple marks and desiccation cracks on bedding planes. It formed around the debris cone and fills all the side passages of the original cave. The Cave Siltstone is much less fossiliferous than the Blocky Breccia and mostly contains fossils of micromammals. From the field relations of the two lithologies it appears that the distal cave silts represent finer material washed out of the debris cone and that both lithologies were deposited contemporaneously. The east–west exploratory trench approximately follows the fissure through which the sediment entered the main chamber. The sediment was most likely derived from an upper chamber that was frequented by carnivores and possibly hominids that accumulated the bones. This upper stratified deposit was then washed down into the lower chamber by catastrophic flash floods. The Collapsed Fill only occurs in the Main Quarry. All the hominid fossils derive from this part of the site. This deposit is comprised of collapsed blocks of dolomite and chert and large boulders of the Blocky Breccia and the Cave Siltstone of various sizes, some as large as 5 metres in diameter. The voids between the blocks were filled with dark brown dolomitic soil derived from the hill slope to the west of the site. Some of the collapsed blocks of cave sediment have been decalcified by the roots of vegetation growing into the Collapsed Fill. It appears likely that part of the fill of the main chamber collapsed into a younger cave that formed under the deposit and that the fill constitutes the collapse of a sinkhole. The miners dug deep pits along the edges of the Main Quarry in order to look for the stalagmitic floor of the cave and dumped the decalcified material into the centre of the sinkhole. Large numbers of fossils, including hominids, are being recovered from the dumped material; however, the majority of hominids have been found in the Collapsed Fill.

Table 1. Macromammalian taxa from Drimolen.

Primates		
	Hominidae	
		Paranthropus robustus
		Homo sp.
	Cercopithecidae	
		Papio robinsoni
		Cercopithecoides williamsi
Carnivora		
	Felidae	
		Dinofelis sp. aff. *piveteaui*
		Felis caracal
		Felidae indet. (large)
	Hyaenidae	
		Hyaenidae indet.
	Canidae	
		Canis sp.
	Viverridae	
		Herpestinae indet.
		Viverridae indet.
Artiodactyla		
	Bovidae	
		Gazella sp. aff. *vanhoepini*
		Oreotragus sp.
		Neotragini indet.
		Antidorcas recki
		Pelea sp.
		cf. *Redunca* sp.
		Damaliscus sp.
Connochaetes sp.		
Megalotragus sp.		
Tragelaphus sp.		

based in part on morphological and metrical differences in the dentition between the two samples. The Kromdraai sample is referred to as *Paranthropus* [*Australopithecus*] *robustus*,* and is supposedly distinguished from the Swartkrans sample (referred to as *P.* [*A.*] *crassidens*) by its larger premolars, smaller deciduous molars, and by an overall 'less morphologically derived' dentition.

It is generally accepted that hominoid deciduous teeth are more conservative morphologically than adult dentition, and are thus relatively more useful for distinguishing specimens at various taxonomic levels.[15–17] Morphological features of the dm_1 employed by Grine[10] to differentiate robust australopithecine specimens from Kromdraai and Swartkrans at the species level include the reduction of the tuberculum molare, relative cusp size and the presence or absence of a mesioconulid. The Drimolen hominid assemblage includes single, individual dm_1 specimens that display similarities with the Kromdraai sample in some morphological features and similarities with the Swartkrans sample in other features (Table 3). Thus, it appears that these traits are more variable within a single population then previously supposed, and, as a result, their systematic value needs to be reconsidered.

In addition, our metrical data do not show a consistent pattern (Fig. 2a,b). Both the MD and BL diameters of the dm_2 sample show similarities to the Kromdraai mean and range. The data on the dm_1 sample, however, display a mean value for the MD diameter closer to the Swartkrans mean, but with a range that is largely overlapping with both the Kromdraai and Swartkrans distributions.

*Four of us (C.G.M., J.M.-C., L.R.B & T.R.P.) object to the use of *Paranthropus robustus*, and prefer the use of *Australopithecus robustus*.

Table 2. List of hominid fossils from Drimolen.

Catalogue Number	Element	Estimated age	Provisional taxonomic allocation	Measurements* (MD, BL)
DNH 1	LM^2	Adult	*P. robustus*	(15.0), 16.0
DNH 2	Ldm_2	Juvenile	*P. robustus*	11.6, 10.1
DNH 3	Left maxilla with M^2, M^3	Adult	*P. robustus*	M^2, 12.4, 14.1 M^3, 13.6, 16.3
DNH 4	LM^1	Adult	*P. robustus*	14.1, 15.2
DNH 5	Right ascending ramus of mandible	Adult	*P. robustus* ?	
DNH 6	Crushed right mandible with RM2, M3 and LM2, M3	Adult	*P. robustus*	n.d.
DNH 7	Cranium (a) and mandible (b), both with complete dentition	Adult	*P. robustus*	*
DNH 8	Mandible with complete dentition	Adult	*P. robustus*	*
DNH 9	Phalanx	Adult	?	
DNH 10	Right mandibular fragment with M3	Adult	*P. robustus*	(15.7), 14.7
DNH 11	Lower molar fragment		?	
DNH 12	Right mandibular fragment with M_3 – two pieces	Adult	*P. robustus*	
DNH 13	Left distal hallucal phalanx		?	
DNH 14	RM^1	Adult	*P. robustus*	(12.9), 14.4
DNH 15	(a) LM^3 (b) RM^3	Adult	*P. robustus*	LM^3, (14.8), 16.4 RM^3, (14.2), 16.1
DNH 16	RM^1	Adult	*P. robustus*	
DNH 17	LP^3	Adult	*P. robustus*	(9.0), 13.4
DNH 18	RM_3	Adult	*P. robustus*	(17.2), 15.7
DNH 19	Left mandibular body with P3, P4, M1, M2, M3	Adult	*P. robustus*	P_3, (11.0), – P_4, (12.3), 13.2 M_2, (16.6), 15.2
DNH 20	Partial skull	Adult	*P. robustus*	
DNH 21	Left mandibular body with M2, M3	Adult	*P. robustus*	M_2, (15.3), 13.9 M_3, (14.3), 13.7
DNH 22	Right maxillary fragments with associated P4, M2, M3; right petrous part of temporal bone, calvaria fragments	Subadult	*P. robustus*	P^4, (9.8), 13.6 M^2, (13.4), 14.6 M^3, (12.8), 15.4
DNH 23	R lower dc	Juvenile	*P. robustus* ?	(6.2), 6.0
DNH 24	Rdi^2	Juvenile	*Homo* ?	(4.6), 4.1
DNH 25	LI^2	Adult	*P. robustus*	5.0, 5.4
DNH 26	RP_4	Subadult	*P. robustus*	(10.9)
DNH 27	LP_4	Adult	*P. robustus*	(11.2), 12.9
DNH 28	L$\underline{C}$	Adult	?	(7.9), 8.7
DNH 29	RP^4	Adult	*P. robustus*	(10.1), 13.9
DNH 30	Ldm^2	Juvenile	?	(11.8), 12.7
DNH 31	Ldi^2	Juvenile	?	(4.9), 3.7
DNH 32	Right distal humerus	Adult	?	
DNH 33	Thoracic vertebra	Adult	?	
DNH 34	Right petrous part of temporal bone and basioccipital	Juvenile	*Homo*	
DNH 35	Right mandible with dm_1, dm_2, M_1, Ldm_2, left radius and ulna	Juvenile	*Homo*	Rdm_1, 9.1, 7.5 Rdm_2, (11.6), 10.3 Ldm_2, 11.4, 9.7 RM_1, 14.3, 12.4
DNH 36	Rdm^1	Juvenile	*P. robustus*	9.8, 9.8
DNH 37	Molar fragment		?	
DNH 38	Ldi^2	Juvenile	*P. robustus* ?	(4.3), 3.9
DNH 39	RM^1	Juvenile	?	12.8, (13.0)
DNH 40	LM^3	Adult	*P. robustus*	(14.3), (15.1)
DNH 41	Left maxilla with I2, C, P3	Adult	*P. robustus*	I^2, (6.3), 7 C, (8.8), (9.9) P^3, (9.0), –
DNH 42	Rdm^2	Juvenile	*P. robustus* ?	–, (11.1)
DNH 43A	Fragmentary sacrum	Adult	?	
DNH 43B	Fragmentary pelvis	Adult	?	
DNH 44	(a) Right mandibular body with dc, dm1, dm2, (M1); (b) Right ulna	Juvenile	*P. robustus*	d_c, 3.9, 4.9 dm_1, 10.7, 8.8

Continued on p. 196

Table 2 continued from p. 195

Catalogue Number	Element	Estimated age	Provisional taxonomic allocation	Measurements* (MD, BL)
				dm_2, –, (10.3)
DNH 45	RI^2	Juvenile	*Homo* ?	6.4, 6.5
DNH 46	Right mandibular body with dm2, M1, M2	Juvenile	*P. robustus*	M_1, (14.7), (13.5)
DNH 47	Left maxilla with di1, dc, dm1, dm2, M1 (bud); right maxilla with di2, dm1, I1 (bud); Rdm_1	Infant	*P. robustus*	Ldi^1, (6.3), (4.3) Rdi^2, (4.3), 4 Ld^c, (5.7) Rdm^1, 10.1, 9.9 Ldm^2, 11.6, 12 LM^1, (12.1), (12.4) Rdm_1, (11.0), (8.6) RI^1, 8.9, –
DNH 48	Phalanx		?	
DNH 49	Rdi^2	Juvenile	*Homo* ?	–, 4.9
DNH 50	Right humerus	Neonate	?	
DNH 51	Right mandibular fragment with P3, P4, M1, M2, M3	Adult	*P. robustus*	P_3, (10.9), 11.3 P_4, (11.0), (12.5) M_1, (14.3), – M_2, (16.8), 13.9 M_3, (17.0), 13.9
DNH 52	R$\underline{C}$	Adult	?	–, (7.9)
DNH 53	L$\underline{C}$	Adult	?	9.9, (9.8)
DNH 54	LM^3	Adult	*P. robustus*	(14.0), 14.2
DNH 55	(a) Left temporal bone; (b) Right mandibular condyle	Adult	?	
DNH 56	(a) Ldm_2 (b) Rdm_2	Juvenile	*P. robustus*	Ldm_2, 11.5, 9.9 Rdm_2, 11.6, 10
DNH 57	(a) Ldm^2 (b) RM^1	Juvenile	*P. robustus*	Ldm^2, 11.1, 11.3 RM^1, 12.7, 13.6
DNH 58	LP_3	*P. robustus*		(11.3), –
DNH 59	RP^4	*P. robustus*		10.1, 13.9
DNH 60	Cranial fragments (Left, cf temporal bone fragment; right petrous part of temporal bone; cranial base fragment) and associated teeth (Rdm^1 fragment, LM^1, Rdm_1, Rdm_2, RM_1, RM_2 – bud)	Juvenile	*P. robustus*	dm^1, –, 9.0 dm_1, (9.4), 7.7 dm_2, (12.2), 10.1 M^1, 12.5, 13.6 M_1, 13.6, 11.9 M_2, 14.5, 13
DNH 61	Molar fragment		?	
DNH 62	LM^1 bud	Juvenile	?	13.9, 13.4
DNH 63	2nd Phalanx	Adult	?	
DNH 65	2nd Phalanx	Adult	?	
DNH 66	2nd Phalanx, fragmentary	Adult	?	
DNH 67	RM_1 bud	Juvenile	*P. robustus*	14.6, 12.2
DNH 68	Right mandibular body (fragments) with C (fragment), P3, P4, M1, M2, M3	Adult	*P. robustus*	P_3, (10.0), 12.9 P_4, 9.9, – M_1, (14.5), – M_2, (17.2), 14.3 min M_3, 14.7 min, –
DNH 70	LM^1	Juvenile	*Homo* ?	12.7, 13.1
DNH 71	RI^1 bud	Juvenile	*Homo* ?	9.4, –
DNH 72	L$\underline{C}$	Adult	*P. robustus* ?	–, 8.9 min
DNH 73	L$\underline{C}$	Adult	*P. robustus*	(8.8), 9.2
DNH 74	L upper molar	Adult	*P. robustus*	(13.0), 14
DNH 75	RM_3	Subadult	*P. robustus*	(17.3), 13.4
DNH 77	RI^1	Adult	*P. robustus*	(8.0), (6.5)
DNH 78	RP^3	Juvenile	*P. robustus*	9.7, 12.8
DNH 79	R_C	Juvenile	?	7.4, 8.5
DNH 80	LI_2	Adult	*P. robustus*	(7.8), 7
DNH 81	LM_1	Juvenile	?	14.6 min, 13
DNH 82	L_C	Juvenile	*P. robustus*	–, 8.1

*Measurements for the dentition of DNH 7 & 8 are in Keyser.[13] Dental dimensions are standard (in mm) and estimates are in brackets. MD is mesiodistal diameter and BL is buccolingual diameter. Probable associations: DNH 1 and 4; DNH 14, 15 and 17; DNH 34 and 35; DNH 70 and 71.

Table 3. Comparative dm_1 features for Drimolen (DNH), Swartkrans and Kromdraai.

Lower dm_1 features	Kromdraai	Swartkrans	DNH 44	DNH 47	DNH 60
Tuberculum molare	Reduced*	Very reduced*	Marked	Very reduced	Reduced
Cuspal height disparity	Little disparity	No disparity	—	Little disparity	—
Cusp size	ME ≈ PR	ME > PR	ME ≈ PR	ME > PR	ME ≈ PR
Mesioconulid	Absent	Present	Present	Absent	—

Dash indicates that this feature cannot be determined.
*As compared to *A. africanus.*

In summary, there is no consistent and exclusive pattern of metrical and morphological similarity between the Drimolen deciduous dentition and either the Kromdraai or Swartkrans deciduous samples. These findings effectively weaken the hypothesis of a species level distinction in the South African robust australopithecines, and support the proposition of a single, variable species, *P. robustus*. On a broader scale, these findings corroborate Suwa *et al.*'s[18] caution against the taxonomic splitting of fossil hominids based on a few characters for which the extent of intraspecific variation is poorly understood.

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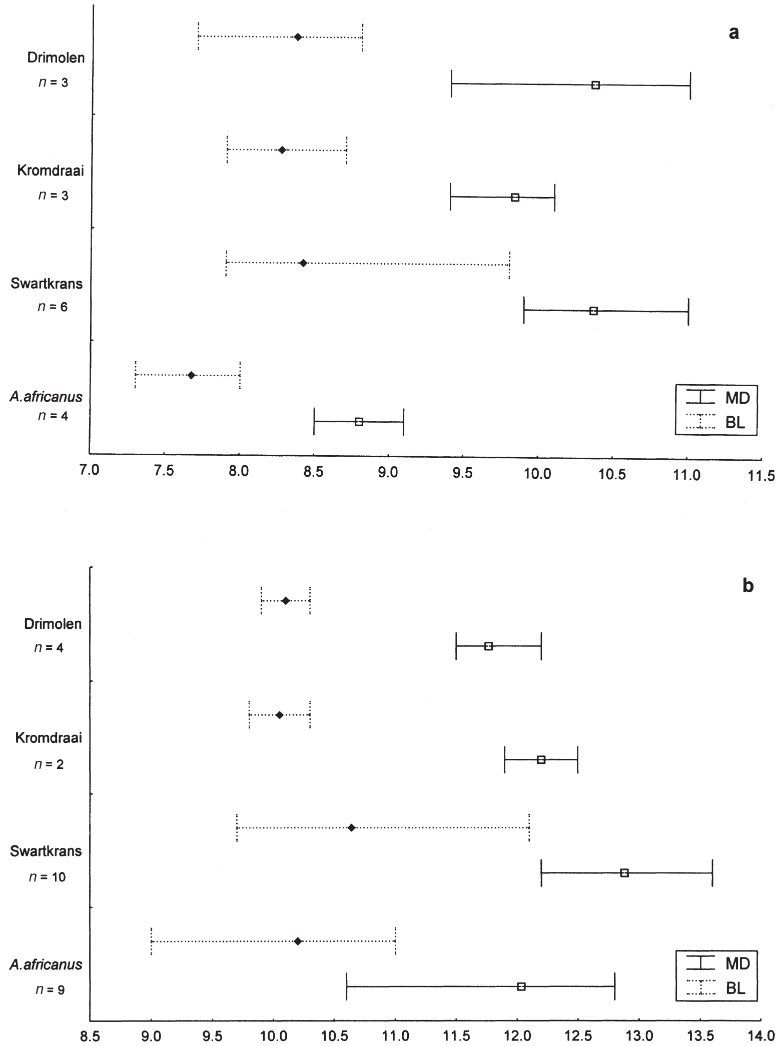

Fig. 2. Lower deciduous molar dimensions for *Paranthropus robustus* from Drimolen, Kromdraai and Swartkrans as well as *Australopithecus africanus.*[5] **a**, dm_1; **b**, dm_2. Mean value and range are indicated.

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