The Drimolen skull: the most complete australopithecine cranium and mandible to date

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I report on a well-preserved *Paranthropus robustus* skull and another mandible from the recently discovered dolomitic cave site of Drimolen, Krugersdorp District, South Africa. The skull (DNH 7), a presumed female, consists of the first cranium and articulated mandible with the most complete dentition yet described for this taxon. Found juxtaposed to the skull was a large and presumably male mandible, with almost complete dentition (DNH 8). *Paranthropus robustus* was described from Kromdraai in South Africa in 1938 and in 1948 from Swartkrans, and has until recently been definitively known only from these two sites.[1–3] Owing to the distortion of many of the Swartkrans crania, it has been suggested that *P. robustus* displays a smaller degree of intraspecific variability than the better preserved specimens of *Paranthropus boisei* from East Africa.[4,5] Owing to the excellent preservation of this new skull, it is now possible to demonstrate that *P. robustus* shows a greater degree of intraspecific variability in both morphology and size, indicating greater sexual dimorphism in this species, than was previously thought.[4]

Drimolen is one of the newest and potentially richest early hominid sites in South Africa and was discovered by the author on 9 July 1992. The site is located about 7 km north of the well-known Sterkfontein Caves in the Krugersdorp District of Gauteng Province, South Africa. The first hominid remains were found on the third visit to the site. Drimolen has yielded 79 hominid specimens thus far, most of which have been attributed to *Paranthropus robustus* but some specimens appear to belong to an as yet unidentified species of early *Homo.*[6]

The site itself is an exposed phreatic maze cave in the dolomites of the Chunniespoort Group.[7,8] Part of the breccia deposit collapsed into a sinkhole, where the blocks of calcified breccia were decalcified by the roots of vegetation growing in the fill of the sinkhole. The sinkhole section of the deposit is known as the Drimolen Main Quarry and has yielded all of the hominid remains found thus far. The age of the cave fill is estimated to be 1.5 to 2 million years, based on faunal correlation with other sites, especially Member 1 of Swartkrans,[6,9–11] approximately 7 km to the south. The associated fauna indicates a mixed environment with grassland.[6]

The complete skull (DNH 7) and other mandible (DNH 8) were exposed on 21 October 1994. One of a group of volunteers working at the site, R. Smith, was digging out a horncore when a trowel unearthed a piece of maxilla containing two molars. Recognizing these as hominid teeth, I immediately took over the excavation of the specimen. Brushing aside the soft, decalcified cave sediment revealed the outline of the skull and mandible, which were partially exposed over the following three days. These remains had been invaded by plant roots and a colony of ants. Unfortunately, the ants and roots entered the dipole of the calotte, resulting in the separation of the inner and outer tables. At this stage, R.J. Clarke and I removed the extraneous materials. Clarke then proceeded over the ensuing 5 years to glue the calotte and glabella together.

During the past few months, I re-assembled the sections Clarke had pieced together. A preliminary reconstruction was made to evaluate the condition of the specimen and obtain an appreciation of the form and characteristics of the complete skull. This procedure also serves as preparation for a more exacting reconstruction to be undertaken in the future to correct the present distortion in the vault.

DNH 7 is the most complete australopithecine skull yet discovered (Fig. 1). The face lacks only the left zygomatic arch, superolateral margins of the left orbit, and the nasal bones. The basicranium lacks the body of the sphenoid, including the pterygoid plates and the anterior portion of the occipital, including the margin of the foramen magnum. The internal walls of the orbits, ethmoid and greater and lesser wings of the sphenoid are crushed beyond repair. The skull has been slightly distorted by bilateral compression. The mandibular corpus of DNH 7 is well preserved, with the exception of the inferior margins, (Fig. 1; Fig. 2, left). The male mandible (DNH 8) is complete save for the right ramus (Fig. 2, right), and the left ramus is preserved but missing fragments prevent its attachment. Wear on third molars indicates that DNH 7 is a mature individual.

DNH 7 is noticeably smaller than SK 48, the only other well-preserved *P. robustus* cranium, and most of the other crania from Swartkrans. The overall size of DNH 7 is rather small; provisional measurements include bimastoid breadth: 119 mm, biporionic breadth: 105 mm, maxillo-alveolar breadth at M2: 62 mm, porion-bregma distance: 75 mm, and prosthion-opisthocranion: 163 mm. The maxillo-alveolar breadth of 62 mm is smaller than 7 of the 9 measurable specimens of *P. robustus*[12] (mean 67 mm. Comprehensive and more accurate measurements will be possible when the specimen is fully restored. The measurements are given to indicate the approximate size of the specimen.

Figure 1a shows that the lateral margins of the piriform aperture are rounded. While the length of the opening itself is greater than SK 12, it is approximately the same width. The face is not as deeply dished as in larger *P. robustus* specimens such as SK 48 and SK 83. The maxillary sinus extends to the superiormost portion of the bone, approaching the inferior margin of the orbit. Weakly developed anterior pillars are barely visible because of the absence of canine fossae on the adjacent maxilla. The maxillary fossula[13] originates between the roots of third and fourth premolars, and extends superiorly, ending just inferior to the maxillary sulcus,[13] where the structures are separated by a slight eminence (subforamen divide). The maxillary sulcus is very short. The canal of the infraorbital foramen runs vertically to emerge near the internal aspect of the inferior margin of the orbit. There is a shallow depression superior to the infraorbital foramen that narrows supero-medially as it approaches the superior aspect of the piriform aperture as in Sts 71,[4] *A. africanus*. A shallow zygomaticomaxillary fossa is present below the zygomatic prominence. There is also a double zygomaticofacial foramen.

The wide, guttered nasoalveolar clivus is situated between the roots of the canines. Inferiorly, it emerges close to the alveolar border and curves gently into the floor of the piriform aperture without the abrupt inferior nasal marginal ridge observed in *Homo.* There are no incisal eminences like those observed in other *P. robustus* specimens (e.g., SK 48 and SK 83). If the skull is

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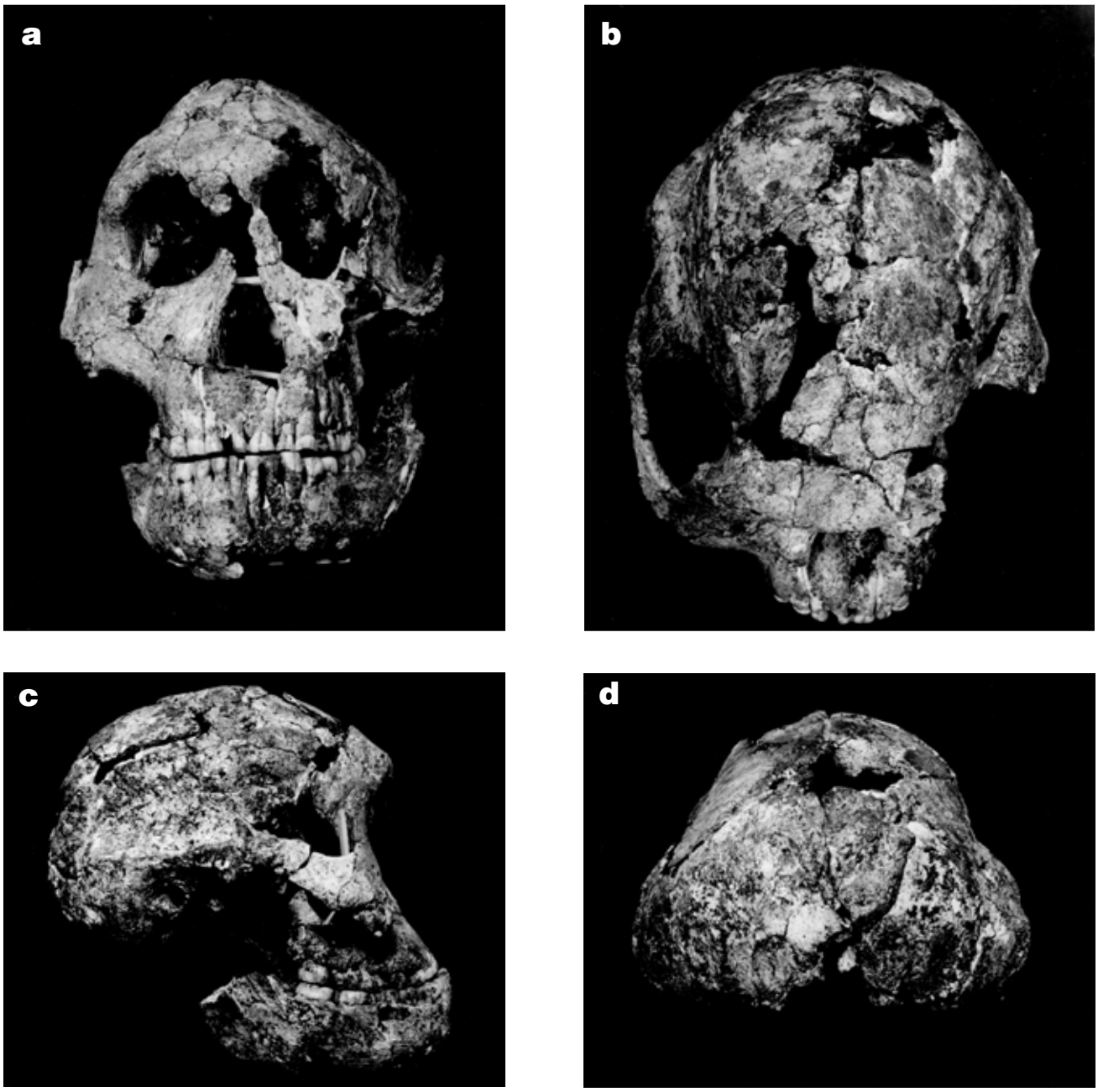

Fig. 1. The Drimolen skull (DNH 7). **a**, Norma frontali;, **b**, norma verticalis; **c**, norma lateralis, note underbite; **d**, norma occipitalis.

orientated in the Frankfurt Horizontal, the anterior surface of the zygomatic processes of the maxillae are more vertically orientated than in the assumed female *P. boisei,* KNM-ER 732.[4,12] The visor configuration as is evident in the *P. boisei* sample, except for the new skull from Konso, Ethiopia (KGA 10-525),[14] is not present in DNH 7, but is as seen in the *P. robustus* sample.[13] These features distinguish DNH 7 as *P. robustus.*

The supraorbital margins slope superolaterally like 'gull wings' from the glabella. The superior and superolateral margins of the orbits are smoothly rounded and 'rib-shaped'.[15] There is no apparent supraorbital torus, fissure or tubercle. The glabella is as prominent as in KNM-ER 732 and is accompanied by a distinct supraglabellar depression within the frontal trigone.[15] Lacking superciliary grooves, the superior margins of the orbits slope smoothly upward to the frontal squama.

The frontal squama slopes gently upward to its apex near bregma. The coronal and sagittal sutures can be traced but with difficulty because they are almost completely fused and nearly obliterated. The curvature and size of the vault approximates that of KNM-ER 732. The temporal lines are very faint across the frontal and parietal bones. They emerge from the superior margin of the zygomatic processes of the frontal bone to begin converging near the midline of the bone well anterior to bregma. On the parietals, the lines extend from the mastoid crest posterior to the mastoid process, continuing superoanteriorly past the squamous temporals. The inferoposterior portions of the parietals are relatively thick. Unlike males of this species, this specimen has no sagittal crest. The parietal articulation with the mastoid occurs well below asterion, much more inferiorly placed than in *Homo.*

On the occipital bone, inferior to lambda are hollows formed by the nuchal muscles, which are sharply demarcated superiorly. This condition is similar to many early hominid specimens, but this structure in DNH 7 is considerably reduced compared

with assumed *P. boisei* males, OH 5[16] and KNM-ER 406.[12]

The temporal bones have a noticeably long overlap with the parietals. The mastoid region expands laterally to a greater extent than in KNM-ER 732. The mastoid process is small, as in early *Homo.* There are small digastric fissures medial to the process with clear grooves for the occipital arteries. The external acoustic meatus is very large and circular with two shallow grooves on the inferior surface. It does not have the funnel-like 'megaphone' shape observed in *P. boisei.*[16,17] The glenoid fossa of the temporal bone is deep and rounded as in *P. robustus* and modern humans with a postglenoid process adjacent to the meatus. The tympanic portion of the temporal forms most of the posterior wall of the fossa. There is no spiral groove as in *P. boisei.*[16] In DNH 7, the glenoid fossa overlaps the brain case, in contrast to its more lateral placement in KNM-ER 732.

Fig. 2. Mandibles of presumed female DNH 7 (left) and male DNH 8 (right).

The articular eminence is essentially similar to that in modern hominids. It does not have an elevated tubercle at its medial end where it joins with the sphenoid or at its articulation with the sphenoid lateral to the foramen spinosum. The eminence is straight in the horizontal plane. A distinct, well-preserved foramen spinosum is visible, which is not commonly preserved in *P. robustus.* The stylomastoid foramen is small. There is a well-developed, well-preserved styloid process on the left petrosal — probably the most complete one known in australopithecines.

Endocranially, both left and right transverse venous sinuses are visible. It is clear from this configuration that the posterior cranial fossa is similar to that in *P. robustus* and *Homo.* The margins of the foramen magnum are not preserved. The roof of the petrous portion of the temporal bone is more rounded than in modern humans and the tegmen tympani not flattened. The groove for the superior petrosal sinus is shallow as is the floccular fossa. The slit of the vestibular aqueduct is visible above the sigmoid sulcus.

The molar tooth rows are nearly parallel with only slight anterior–posterior divergence. The anterior tooth rows show some anterior curvature and are not as straight as in OH 5.[16] The palate is wide and relatively shallow compared to *P. bosiei* specimens. It is badly preserved and the superior surface is eroded. Anterior and posterior teeth exhibit marked flat wear in both the mandible and maxilla. Only on the third upper molars, the cusps, though worn, are still evident. Upper and lower premolars are heavily molarized. Premolars are buccolingually widened, but the talonid portion of P_4 is larger than that of P_3, as described by Robinson.[18] The premolars are typical of robust australopithecines with the maximum dimension in the buccolingual direction. The upper molar cusps have the characteristic parallelogram arrangement common in most robust australopithecines with the protocone being the largest cusp. Molar size follows the robust australopithecine pattern, increasing distally (M1<M2<M3).[18,19] Dental measurements from the mandibles of DNH 7 and 8 appear in Table 1.

The anterior teeth, including the canines, are reduced as is typical of all robust australopithecines. The teeth have a peg-like appearance, exaggerated by heavy wear. When the molars are occluded, there is a distinct underbite (see Fig. 1c). The underbite may be explained by a 6 mm differential between the posterior tooth rows. The mandibular row measures 55.1 mm; the maxillary, 49.1 mm. A similar condition has been observed in the robust skull, KGA 10-525, from Konso, Ethiopia.[14]

Several characteristics of DNH 7 lead to the conclusion that it is probably female. Overall, it is relatively small and gracile, especially when compared with the visibly larger crania of SK 48 and SK 82. The face of DNH 7 is flat rather than dished, as in SK 48 and SK 82. This feature has been noted to distinguish sex within *P. boisei.*[4] As in KNM-ER 732, a presumed female of *P. boisei,*[4,12] there is no evidence of a sagittal crest in DNH 7 as is common in robust australopithecine males (e.g., SK 48 and SK 83).[12] Also, the mandible of DNH 7 is visibly smaller and more gracile than the presumed male mandibles of DNH 8 and SK 12.[3] Table 2 illustrates sexual dimorphism between presumed males and females. Size differences are also apparent in the dental measurements from these mandibles (Table 1). The molar and tooth row dimensions are in the range of robust australopithecine females.[18]

The distinctive dentition and morphology of the skull (DNH 7) and isolated mandible (DNH 8) leave little doubt that both specimens belong to *P. robustus.* Drimolen's other cranial and dental remains fall within the range of the combined metrics from the Swartkrans and Kromdraai samples.[6] Previously mentioned, morphological indicators of sexual dimorphism in DNH 7 indicate that the specimen is female. As with the newly described skull KGA10-525, which demonstrates greater intraspecific variation in *P. boisei*[14] than previously thought, DNH 7 also shows an increased degree of intraspecific variation but now in *P. robustus.* The characteristics of this new and most complete robust australopithecine skull support the contention that KNM-ER 732 and KNM-ER 407 are indeed *P. boisei* females.[12] The discovery of Drimolen and its large sample of hominid fossils adds to our knowledge of this phase of hominid evolution. The completeness of DNH 7 helps to elaborate the characteristics of robust australopithecine females.

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Table 1. Dental and mandibular dimensions (in mm) of DNH 7 and DNH 8.

		DNH 7 Upper dentition		DNH 7 Lower dentition		DNH 8 Lower dentition	
		Left	Right	Left	Right	Left	Right
I1	MD	(8.4)	–	–	–	–	–
	BL	6.7	–	6.1	6.3	–	–
I2	MD	(5.8)	(5.8)	–	–	–	(5.6)
	BL	5.9	5.6	–	(6.5)	–	5.9
C	MD	(7.9)	7.9	(7.3)	(7.0)	8.1	8.1
	BL	8.3	8.3	7.6	7.7	8.8	8.5
P3	MD	–	(9.1)	(9.2)	(8.9)	10.2	–
	BL	–	12.9	12.3	12.4	12.6	–
P4	MD	(9.2)	(9.9)	(10.3)	(10.1)	11.3	11.4
	BL	14.3	14.5	12.6	11.9	13.6	13.4
M1	MD	(12.0)	(12.1)	(13.4)	–	(15.7)	(15.2)
	BL	14.1	13.9	12.6	(12.7)	14.5	14.7
M2	MD	(11.6)	(11.9)	(13.4)	(14.2)	(15.9)	(15.5)
	BL	14.6	14.3	13.5	13.5	15.0	14.8
M3	MD	(12.1)	(12.2)	(15.2)	(15.4)	19.1	18.8
	BL	14.5	14.2	13.6	13.4	16.2	15.5
Combined length of lower premolar and molar tooth rows				55.1	55.1	67.7	68.5
Width of mandible at M1				20.9	–	25.3	26.5
Width of mandible at M2				29.1	–	32.3	30.2

Dental dimensions are standard and estimates are shown in brackets. MD is mesiodistal diameter and BL is buccolingual diameter.

Table 2. Distribution of derived robust australopithecine features for *Paranthropus robustus* and *Paranthropus boisei*.*

	DNH 7	SK 48 & SK 12	OH 5 KNM-ER 3032	KNM-ER 732
Development of a sagittal crest	–	+	+	–
Strong postorbital constriction	+	+	+	+
Extensive squamosoparietal overlap	+	+	+	+
Deep glenoid fossa	+	+	+	+
Temporomandibular joint lateral to cranial vault	(+)	+	+	(+)
Posteriorly orientated entoglenoid	–	–	+	+
Coronally orientated petrous	+	+	+	+
Vertically deep and plate-like tympanic	+	+	+	+
External auditory meatus obliquely elliptic	(+)	(+)	+	(+)
Laterally inflated mastoid with distinct supramastoid sulcus	+	+	+	+
Anterior position of zygomaxillary plane	(+)	+	+	+
Anterior orientation of zygomatic frontal process	+	+	+	+
High position of zygomatic temporal process	+	+	+	+
Visor-like zygomatic morphology	–	–	+	+
Zygomatic prominence	+	+	–	–
Zygomatic-maxillary fossa	+	+	–	–
Maxillary fossula and absence of canine fossa	+	+	–	–
Anterior pillar	–	+	–	–
Low position of infraorbital foramen	+	+	+	+
Rounded orbits	+	–	–	+
Rib-like supraorbital margins	+	+	+	+
Guttered nasoalveolar clivus	+	+	+	+
Deep palate	–	–	+	–
Absolutely and relatively tall mandibular ramus	+	+	+	–
Relatively thick and inflated mandibular corpus	+	+	+	–
Wide extramolar sulcus	+	+	+	–
Absolutely large postcanines	+	+	+	–
Relatively small anterior teeth	+	+	+	
Specialized lower 3rd premolar morphology	+	+	+	
Specialized lower 4th premolar morphology	+	+	+	
Lower molars with large distal cusps	+	+	+	
Thick enamel	+	+	+	–
Flat molar wear	+	+	+	–

*The characters here have been considered to be derived features for *Paranthropus robustus* and *Paranthropus boisei* relative to species of the genus *Australopithecus* conditions (modified after Suwa, G. *et al.*[14]). Brackets indicate intermediate or variable conditions. Because of the arbitrary boundaries of presence/absence criteria, variability within species and possible correlation of features, the tabulated data are not recommended for numerical cladistic analysis. The character list is intended to demonstrate differences between species of *Paranthropus* and sexual differences within the species. Presumed females include DNH 7 and KNM-ER 732 and presumed males include SK 48, SK 12 and OH 5.[3,12,16]

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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,

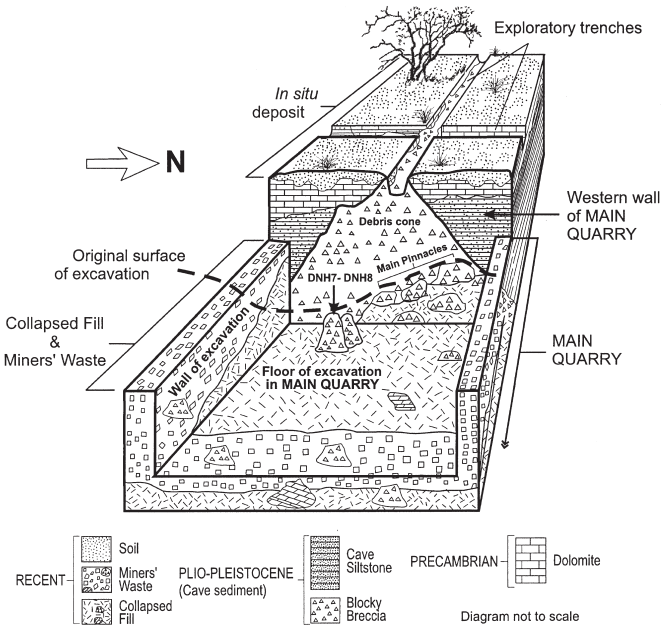

Fig. 1. Block diagram showing the stratigraphic relations of the cave sediments. The Drimolen fossil site is a former cave within the dolomites of the Monte Christo Formation of the Malmani Subgroup of the Chunniespoort Group. The Drimolen cave is similar in form and formation to the dolomitic caves 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<u>C</u>	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	RC	Adult	?	–, (7.9)
DNH 53	LC	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	LC	Adult	*P. robustus* ?	–, 8.9 min
DNH 73	LC	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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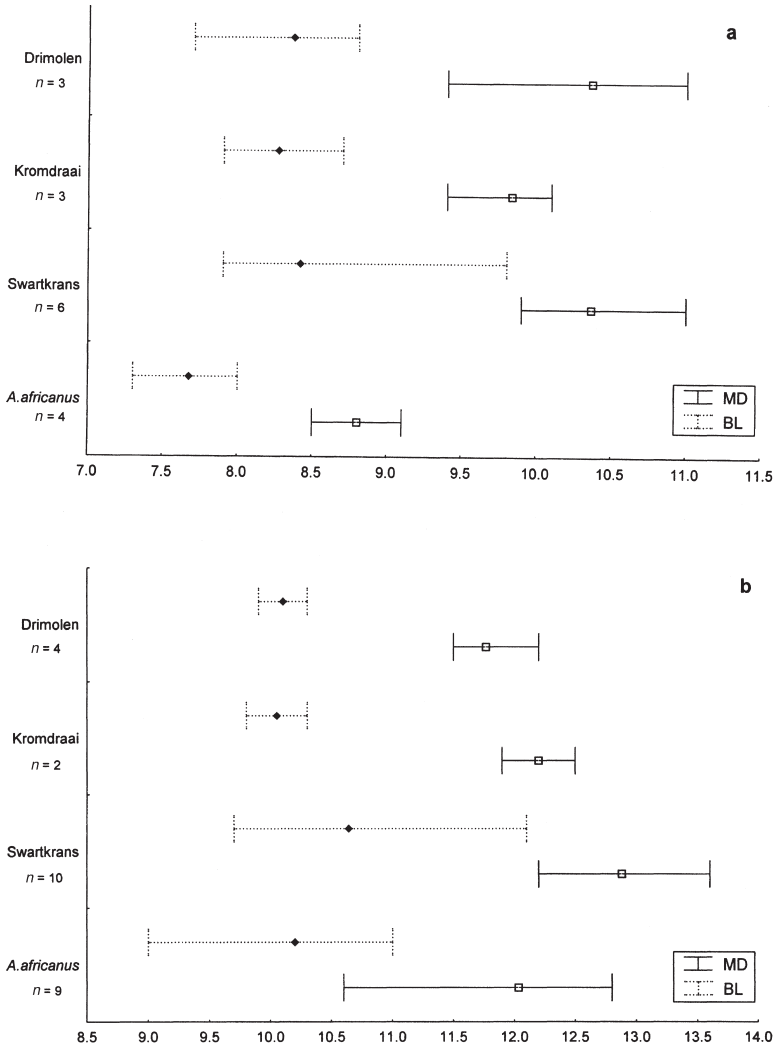

Fig. 2. Lower deciduous molar dimensions for *Paranthropus robustus* from Drimolen, Kromdraai and Swartkrans as well as *Australopithecus africanus*.[5] **a**, dm_1; **b**, dm_2. Mean value and range are indicated.

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