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First record of hominid teeth from the Plio-Pleistocene site of Gondolin, South Africa

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Introduction

We report here on recent excavation results from the Plio-Pleistocene fossil locality known as Gondolin, including recovery of the first fossil hominid teeth. Gondolin is located approximately 4 km SW of the town of Broederstroom and 35 km NW of Pretoria, in the North West Province, South Africa. The site lies on the farm *Broederstroom 481 JQ* (25°49.837′S, 27°51.857′E) on the rocky slope of the Skurweberg mountain range, and is about 20 km north-west of the well-known hominid sites of Sterkfontein, Swartkrans and Kromdraai.

The site complex, which is an abandoned limeworks, was first noted by MacKenzie in 1977 (MacKenzie, 1994) and, following this, Vrba initiated a brief 3-week research project in February 1979 (Vrba, 1982; Watson, 1993). Vrba's excavation (Vrba, 1982; Watson, 1993) removed an estimated 2 m^3 of a highly fossiliferous siltstone remnant exposed in the eastern wall of the site (Figure 1). The recovered fossil assemblage was analysed by Watson (1993) and was shown to contain a substantial mammalian fauna with 27 identified taxa. Based mainly on the presence of *Metridiochoerus andrewsi*, which is similar to material known from Swartkrans Member 1 and Koobi Fora, Cooke suggested as a "tentative approximation" an age between 1·5 and 1·9 m.y.a. (quoted in Watson, 1993, p. 37).

A single hominid tooth, a right P_3 (G14018), attributed to *Homo sapiens*, was originally reported (Watson, 1993) as being recovered during Vrba's excavation. However, it has since been shown that this tooth was intrusive (Thackeray, personal communication; MacKenzie, 1994). Watson (1993) noted that no other primate fossils were recovered.

Aims of current research

While Vrba's excavation removed a considerable sample of *in situ* fossiliferous siltstone, these materials derive from only one small area of the cave and from only two of the several deposits at the site. As there are several fossiliferous dumps at the site that had not been sampled, we re-opened excavations in November 1997 with these aims: (1) to intensively sample all the sediment types contained in one of the more extensive mining dumps and (2) to survey and map the site in order to achieve a

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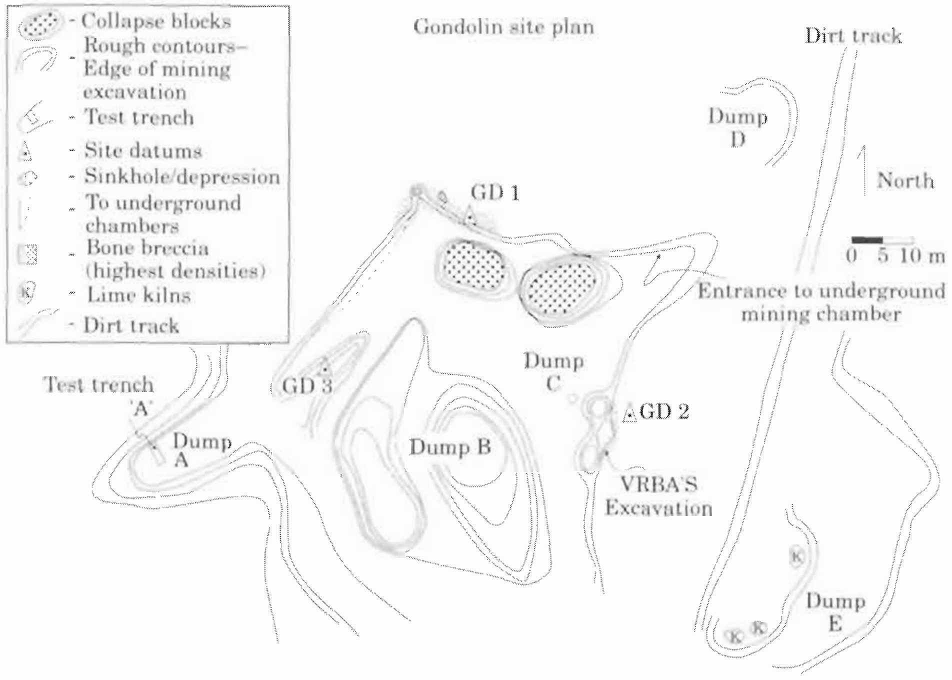

Figure 1. Gondolin Site Plan.

basic understanding of the original cave's geological and lithostratigraphic features.

Site geology

During the Plio-Pleistocene, Gondolin was a large cave that formed an Precambrian dolomitic rocks of the Eccles Formation of the Malmani Subgroup of the Chunniespoort Group (South African Committee for Stratigraphy, 1980). Gondolin is the second cave in the Eccles Formation to yield fossil hominid remains, the other being Gladysvale (Berger *et al.*, 1993). The other well-known hominid sites of Sterkfontein, Swartkrans and Kromdraai and the new hominid site of Drimolen are all in the Monte Christo Formation.

Our interpretation of the cave formation and accumulation of Gondolin follows the general model as described by Brain (1958, 1981, 1993), Brink & Partridge (1965) and Keyser & Martini (1990). The preserved cave sediment at Gondolin accumulated in a large chamber that followed the regional dip of the dolomite and included several smaller side passages. There may have been an upper chamber in this system which is no longer preserved. Sediment entered the chamber through an opening that formed in the northwestern corner of the cave by a dome-shaped collapse of the ceiling.

Our interpretation of the sedimentary succession [see Figure 2(b)] at Gondolin is based on the preserved section of the north and west walls of the cave. The succession begins with a basal breccia that is derived from collapse of the dolomite ceiling. This basal collapse breccia is made up of large blocks of dolomite, some of which may be over 5 m in size, with the voids between the large blocks containing smaller blocks. Most of the basal collapse breccia is cemented by calcite flowstone. No discrete basal flowstone unit can be recognised because the flowstone formation occurs within the basal

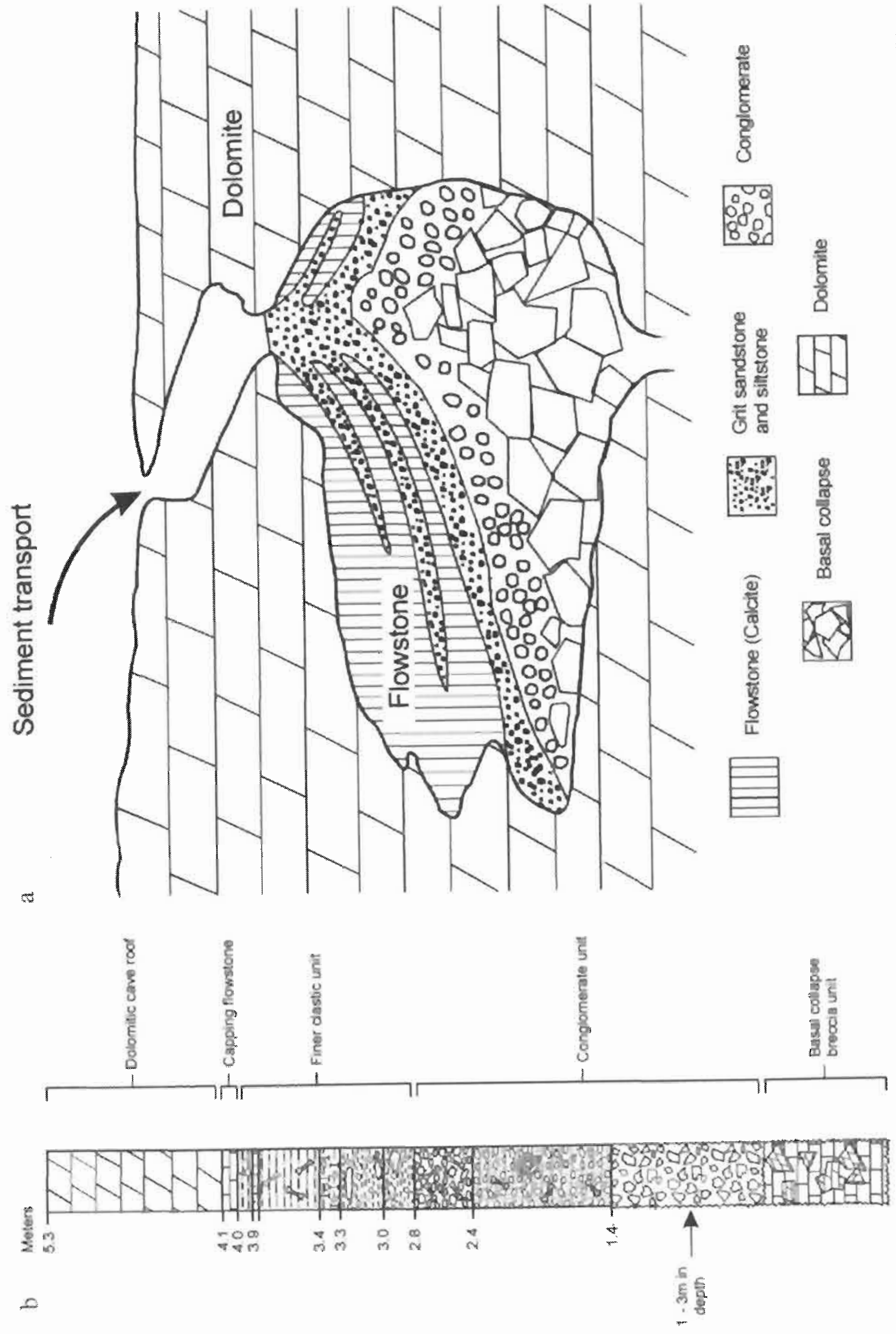

Figure 2. (a) Schematic reconstruction of the Gondolin main chamber to show the relationship of the main sediment types (not to scale). (b) Generalized section of the intersection of the North and West walls.

collapse. The basal collapse formed a debris cone that constitutes the base upon which subsequent sedimentation took place.

Subsequently, sediment was introduced into the cave, probably by flash flooding which carried sediment into a lower chamber from the upper cave system. This occurred through an opening in the northeastern corner of the main chamber and deposited the sediment on the debris cone. Flowstone formation continued contemporaneously with the deposition of the cave sediment.

In the northeastern part of the chamber the collapsed cone is covered with a conglomerate layer with a minimum thickness of 2·8 m. This Conglomerate Unit shows clear evidence of sorting with an average clast size of about 10 cm and fines upward. The clasts are angular with distinct rounding of the edges, indicating that the sediment could have been introduced to the cave entrance by a stream, since such clasts could have been transported only as the bed load of a stream. The finer grained upper part of the Conglomerate Unit is fossiliferous.

The Conglomerate Unit is followed by a succession of finer sediments including grits, sandstones and siltstones that are all richly fossiliferous and make up the Finer Clastic Unit. A capping flowstone completes the succession. Finer sediment, mainly silt, washed out of the debris cone, accumulated around the base of the debris cone and against the walls of the chamber. These distal siltstones are highly fossiliferous in places, such as in Vrba's excavation area. Since flowstone was actively forming during the accumulation of the distal sediments, the siltstone layers must have interdigitated with the accumulating floor flowstone.

During the subsequent mining operation the miners sorted out the fossiliferous clastic sedimentary layers and dumped the material on the extensive dumps around the site. Thus, we interpret the clastic sediment to have accumulated on a debris cone in the corner of a large chamber while the rest of the chamber was filled with flowstone that was subsequently removed by mining.

Excavation results

As mentioned above, our testing strategy focused on one of the larger breccia dumps (designated Gondolin Dump A or GDA), which is a mixed deposit containing highly fossiliferous blocks, dolomite blocks, flowstone and miners' rubble from many if not most of the stratigraphic units represented at the site. Thus, it may not be possible to determine the exact temporal or stratigraphic relationship of this sample to that analysed by Watson (1993), but preparation of these materials is continuing, and in due course the fauna from this mixed deposit will be fully analysed and compared with the previous sample.

The hominid teeth

Two hominid teeth were recovered from GDA during the 1997 field season. The first was recovered while A.W.K. was sorting breccia blocks, and the second by a member of the excavation team (L. Dihasu) during manual reduction of breccia excavated from the test trench. Both teeth were recovered from sediments of the Finer Clastic Unit. Detailed descriptions and comparisons are forthcoming (Kuykendall and Conroy, in prep.), but preliminary observations and interpretations are offered below.

Observations and discussion

The first tooth (GDA-1) recovered is a partial crown of a left mandibular first or second molar [see Figure 3(a–c)], preserving the distolingual section of the crown including the complete entoconid. Parts of the mesial and buccal cusps are missing due to fractures, so no metrical observations relating to overall crown size can be obtained. The cusps show moderate wear with distinct

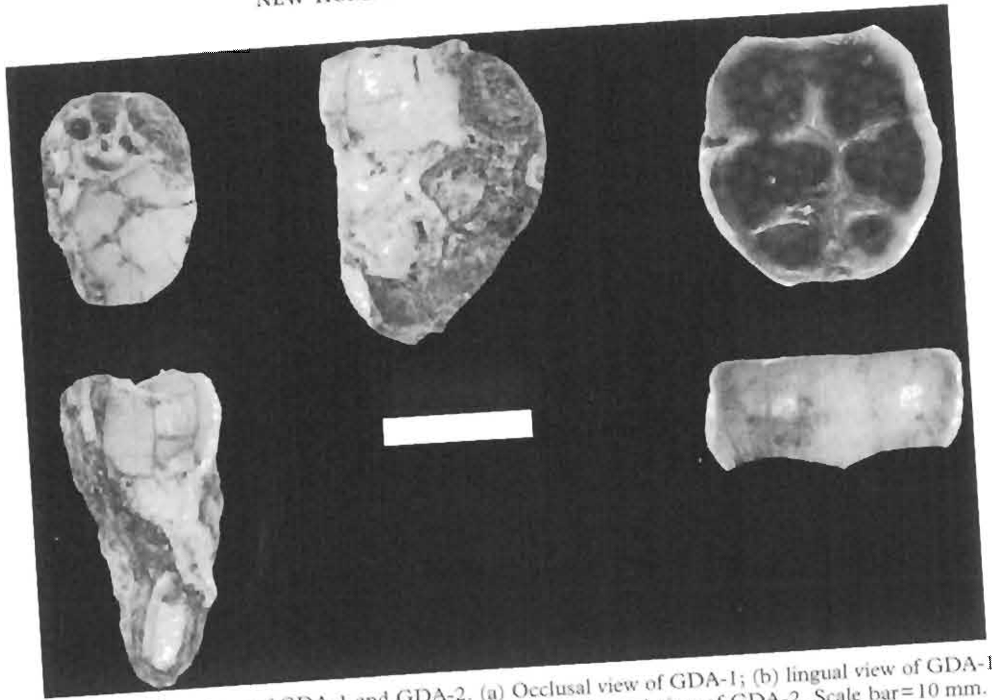

Figure 3. Surface views of GDA-1 and GDA-2. (a) Occlusal view of GDA-1; (b) lingual view of GDA-1; (c) distal view of GDA-1; (d) occlusal view of GDA-2; (e) lingual view of GDA-2. Scale bar = 10 mm.

wear facets, but no dentinal exposures, and wear appears to be slightly greater on what remains of the buccal cusps. Though worn, all cusps project occlusally, and the occlusal wear is characterized by relief rather than a flattened surface. No accessory cusps appear to be present. On this evidence, it is not possible to attribute this tooth to any taxon, other than to conclude that it is probably not a "robust" australopithecine.

The second tooth (GDA-2) is a virtually complete left permanent mandibular second molar, possessing both mesial and distal interproximal wear facets [see Figure 3(d–e)]. The distal wear facet precludes this tooth from being a third molar, and the tooth's large size argues against it being a first molar. The uncorrected mesiodistal (MD) and buccolingual (BL) diameters are 18·8 mm and 18·1 mm, respectively, and the calculated crown base area (MD × BL) is thus 340·3 mm^2. Our estimate of the MD diameter corrected for interproximal wear is 19·6 mm. Both the diameters and the crown base area place this tooth within the recorded size ranges for "robust", rather than "gracile", australopithecines (Wood & Abbott, 1983; Suwa *et al.*, 1994, 1996). Other distinguishing morphological features of this tooth include low and bulbous cusps, with the transition from occlusal surface to the vertical crown margin being smoothly rounded. The occlusal surface is moderately worn and flat, and the buccal cusps (protoconid and hypoconid) show two pinpoint dentinal exposures. However, distinct wear facets are not visible on the individual cusps. A C6 cusp (tuberculum sextum), as well as a distoconulid (Grine, 1984, p. 46) are also present.

The size of this tooth is perhaps its most notable trait, and may be of taxonomic interest. According to Wood & Abbott (1983, p. 204, Table 5, referring to computed crown base areas using the uncorrected mesiodistal diameter), no known gracile australopithecine possesses a

Table 1 **Comparative measurements for australopithecine and paranthropine lower second molars**

	n	Mean	S.D.	S.E.	Observed range
Mesiodistal diameter					
A. afarensis	19	14·06	1·05	0·24	12·1–15·4
A. africanus	13	15·70	1·00	0·28	14·4–17·0
East African robusts	19	18·01	1·67	0·38	15·0–20·5
South African robusts	17	16·38	0·86	0·21	15·0–18·0
Gondolin (uncorrected)	1	18·80	—	—	—
Gondolin (corrected estimate)	1	19·60	—	—	—
Buccolingual diameter					
A. afarensis	18	13·51	1·01	0·24	12·1–15·2
A. africanus	15	14·52	0·69	0·18	13·2–15·5
East African robusts	18	16·68	1·22	0·29	14·5–18·8
South African robusts	19	14·99	0·92	0·21	13·1–16·5
Gondolin	1	18·10	—	—	—

Measurements have been compiled from the literature from Wood (1991) and Grine (1993). Table 1 includes some specimens (e.g., SKX 19892) with only MD or BL (not both) diameters which are not included in Figure 4.

second mandibular molar with a crown base area as large, and the Gondolin tooth falls above the reported maximum of 290 mm^2 for the South African robust group and within the East African robust group range of 275–378 mm^2. This comparison alone suggests that the Gondolin tooth represents a robust australopithecine.

Other comparisons of size dimensions between the Gondolin M_2 and other South African and East African hominids from published sources are presented in Table 1 and Figure 4 (comparative data from Wood, 1991; Grine, 1993; see table and figure descriptions for details of the samples). The data in Table 1 show that the Gondolin M_2 is completely outside (above) the recorded size ranges for all known "gracile" australopithecine samples, as well as for South African "robusts" (SAR). In addition, this tooth exceeds the mean size of the East African robust sample (EAR). In particular, our corrected mesiodistal diameter is more than three standard deviations above the SAR mean, and the buccolingual diameter is more than three standard deviations above the SAR mean, though it falls just within one standard deviation of the mesiodistal diameter and just above one standard deviation of the buccolingual diameter for the EAR sample.

On their own, measures of overall tooth crown size are considered to have limited usefulness as precise, diagnostic taxonomic indicators (Wood & Abbott, 1993; Suwa *et al.*, 1996), due to highly overlapping sample ranges among hominid species. However, as part of a combined criteria approach utilizing traits such as absolute crown size, cusp area proportions, presence/absence of C6 and C7, wear patterns and enamel thickness (Suwa *et al.*, 1996), distinctions between robust and nonrobust taxa appear reliable (see also Wood & Abbott, 1983; Wood *et al.*, 1983) in assessing individual teeth. Thus, our provisional comparisons based on our description, and those provided by others (Robinson, 1956; Tobias, 1967, 1991; Grine 1981, 1993; Clarke, 1985, 1994; Wood & Abbott, 1983; Wood & Chamberlain, 1987; Wood *et al.*, 1983; Suwa *et al.*, 1996), lead us to assignthis tooth to the genus *Paranthropus* (*Paranthropus* sp. indet.).

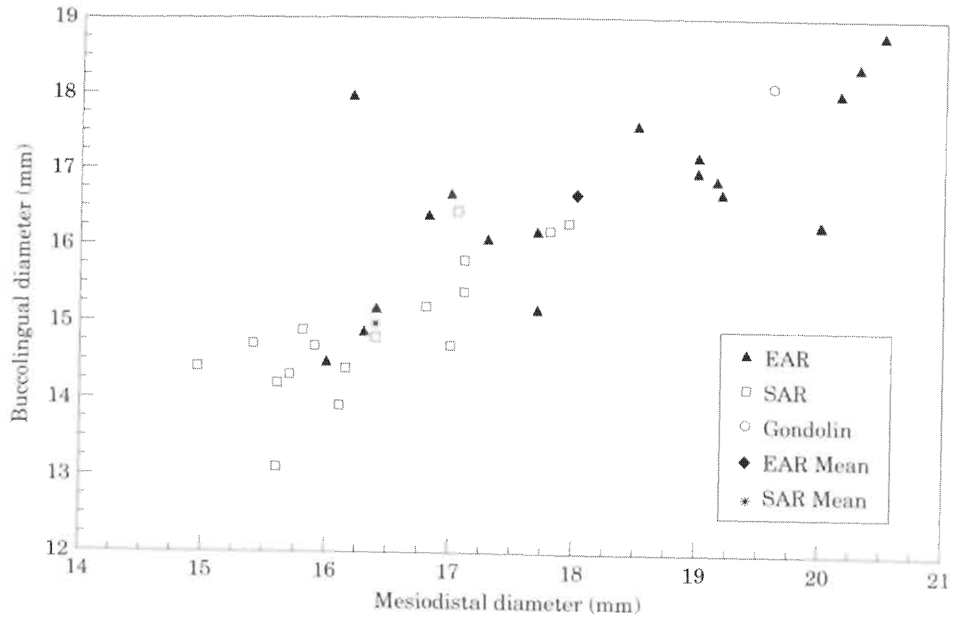

Figure 4. Mesiodistal diameter plotted against buccolingual diameter for lower second molars in "robust" australopithecines. Measurements of specimens were taken from Wood (1991) and Grine (1993) and are corrected mesiodistal diameters. The East African Robust sample (EAR) conforms to the Wood *et al.* (1994) *Paranthropus boisei sensu stricto* sample with the inclusion of lower second molar specimens which Suwa *et al.* (1996) list as *A. aethiopicus* and *A.* aff. *boisei* and Strait *et al.* (1997) include in their hypodigm of *Paranthropus aethiopicus*. The South African Robust sample (SAR) includes specimens from Swartkrans and one specimen, TM 1600, from Kromdraai.

Due to the geographic location of Gondolin (in South Africa instead of East Africa), it would probably be acceptable to attribute this tooth to *P.* cf. *robustus*, despite considerable controversy regarding robust australopithecine taxonomy and phylogeny (e.g., Skelton *et al.*, 1986; Wood & Chamberlain, 1987; Skelton & McHenry, 1992, 1998; Suwa *et al.*, 1996; Strait *et al.*, 1997; Strait & Grine, 1998), and the retention by some researchers of the taxon *P. crassidens* (e.g., Howell, 1978; Grine, 1985, 1998*a*, 1988*b*). For the present, however, we are content to conclude only that this tooth is a surprisingly large-sized specimen representing a population of South African robust hominids.

The unexpectedly large size of GDA-2 is extremely intriguing, but difficult to resolve with what we presently understand concerning "robust" australopithecine dental morphology, taxonomy and phylogeny in East and South Africa. Obviously, precise and reliable taxonomic designations require more information than that available from isolated dental specimens such as those described here. Recovery of additional hominid fossils from Gondolin and other South African sites (e.g., Drimolen), and particularly that of more complete specimens, will help to clarify the taxonomic position of the new material.

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References

Berger, L. R., Keyser, A. W. & Tobias, P. V. (1993). Brief communication: Gladysvale: first early hominid site discovered in South Africa since 1948. *Am. J. phys. Anthrop.* **92**, 107–111.

Brain, C. K. (1958). *The Transvaal Ape-Man-Bearing Cave Deposits*. Pretoria: Transvaal Museum Memoir, No. 11.

Brain, C. K. (1981). *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Chicago: University of Chicago Press.

Brain, C. K. (1993). Structure and stratigraphy of the Swartkrans Cave in the light of the new excavations. In (C. K. Brain, Ed.) *Swartkrans: A Cave's Chronicle of Early Man*, pp. 23–33. Pretoria: Transvaal Museum Monograph, No. 8.

Brink, A. B. A. & Partridge, T. C. (1965). Transvaal karst: some considerations of development and morphology, with special reference to sinkholes and subsidences on the far West Rand. *S. Afr. Geogr. J.* **47**, 11–34.

Clarke, R. J. (1985). *Australopithecus* and early *Homo* in southern Africa. In (E. Delson, Ed.) *Ancestors: The Hard Evidence*, pp. 171–177. New York: Alan R. Liss.

Clarke, R. J. (1994). Advances in understanding the craniofacial anatomy of South African early hominids. In (R. S. Corruccini & R. L. Ciochon, Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*, pp. 205–222. (Advances in Human Evolution Series, Volume 2). New Jersey: Prentice Hall.

Grine, F. E. (1981). Trophic differences between "gracile" and "robust" australopithecines: A scanning electron microscope analysis of occlusal events. *S. Afr. J. Sci.* **77**, 203–230.

Grine, F. E. (1984). The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene hominids. Ph.D. Dissertation, University of the Witwatersrand.

Grine, F. E. (1985). Australopithecine evolution: the deciduous dental evidence. In (E. Delson, Ed.) *Ancestors: the Hard Evidence*, pp. 153–167. New York: Alan R. Liss.

Grine, F. E. (1988*a*). Evolutionary history of the "robust" australopithecines: a summary and historical perspective. In (F. E. Grine, Ed.) *Evolutionary History of the "Robust" Australopithecines*, pp. 509–520. New York: Aldine de Gruyter.

Grine, F. E. (1988*b*). New craniodental fossils of *Paranthropus* from the Swartkrans Formation and their signficnce in "robust" australopithecine evolution. In (F. E. Grine, Ed.) *Evolutionary History of the "Robust" Australopithecines*, pp. 223–243. New York: Aldine de Gruyter.

Grine, F. E. (1993). Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans formation. In (C. K. Brain, Ed.) *Swartkrans: A Cave's Chronicle of Early Man*, pp. 75–116. Pretoria: Transvaal Museum Monograph, No. 8.

Howell, F. C. (1978). Hominidae. In (V. J. Maglio & H. B. S. Cooke, Eds) *Evolution of African Mammals*, pp. 154–248. Cambridge, MA: Harvard University Press.

Keyser, A. W. & Martini, J. E. J. (1990). Haasgat: A new Plio-Pleistocene fossil occurrence. *Palaeoecology Afr.* **21**, 119–129.

MacKenzie, K. (1994). History of events leading to palaeontological excavations of Gondolin, Alias "Mackenzie Cave". *Pal News*. **10**, 23–24.

Robinson, J. T. (1956). *The Dentition of the Australopithecinae*. Pretoria: Transvaal Museum Memoir, No. 9.

Skelton, R. R. & McHenry, H. M. (1992). Evolutionary relationships among early hominids. *J. hum. Evol.* **23**, 309–349.

Skelton, R. R. & McHenry, H. M. (1998). Trait list bias and a reappraisal of early hominid phylogeny. *J. hum. Evol.* **34**, 109–113.

Skelton, R. R., McHenry, H. M. & Drawhorn, G. M. (1986). Phylogenetic analysis of early hominids. *Curr. Anthrop.* **27**, 21–43.

South African Committee for Stratigraphy (1980). *Stratigraphy of South Africa, Part I: Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia and the Republics of Bophutatswana, Transkei and Venda*. Pretoria: Geological Survey of South Africa.

Strait, D. S. & Grine, F. E. (1998). Trait list bias? A reply to Skelton and McHenry. *J. hum. Evol.* **34**, 115–118.

Strait, D. S., Grine, F. E. & Moniz, M. A. (1997). A reappraisal of early hominid phylogeny. *J. hum. Evol.* **32**, 17–82.

Suwa, G., Wood, B. A. & White, T. D. (1994). Further analysis of mandibular molar crown areas in Pliocene and Early Pleistocene hominids. *Am. J. phys. Anthrop.* **93**, 407–426.

Suwa, G., White, T. D. & Howell, F. C. (1996). Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *Am. J. phys. Anthrop.* **101**, 247–282.

Tobias, P. V. (1967). *Olduvai Gorge: The Cranium and Maxillary Dentition of* Australopithecus (Zinjanthropus) boisei, Vol. 2. Cambridge: Cambridge University Press.

Tobias, P. V. (1991). *Olduvai Gorge: The Skulls, Endocasts and Teeth of* Homo habilis, Vol. 4. Cambridge: Cambridge University Press.

Vrba, E. S. (1982). Gondolin Site, Broederstroom, Progress Report. Progress Report to the National Monuments Council, Ref. #TM 3/6/9/1.

Watson, V. (1993). Glimpses from Gondolin: a faunal analysis of a fossil site near Broederstroom, Transvaal, South Africa. *Palaeont. Afr.* **30**, 35–42.

Wood, B. (1991). *Hominid Cranial Remains. Koobi Fora Research Project*, Vol. 4. Oxford: Clarendon Press.

Wood, B. A. & Abbott, S. A. (1983). Analysis of the dental morphology of Plio-Pleistocene hominids, I. Mandibular molars: crown area measurements and morphological traits. *J. Anat.* **136**, 197–219.

Wood, B. A. & Chamberlain, A. T. (1987). The nature and affinities of the "robust" australopithecines: a review. *J. hum. Evol.* **16**, 625–641.

Wood, B. A., Abbott, S. A. & Graham, S. H. (1983). Analysis of the dental morphology of Plio-Pleistocene hominids: II. Mandibular molars—study of cusp areas, fissure pattern and cross sectional shape of the crown. *J. Anat.* **137**, 287–314.

Wood, B., Wood, C. & Konigsberg, L. (1994). *Paranthropus boisei*: an example of evolutionary stasis. *Am. J. phys. Anthrop.* **95**, 117–136.