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PALAEONTOLOGY AND GEOLOGICAL CONTEXT OF A MIDDLE PLEISTOCENE FAUNAL ASSEMBLAGE FROM THE GLADYSVALE CAVE, SOUTH AFRICA.

by

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ABSTRACT

Palaeontological and geological research at the Gladysvale Cave during the last decade has concentrated on de-roofed deposits located outside the Main Chamber. This area has been termed the Gladysvale External Deposit (GVED) and consists of fossil-rich calcified and decalcified sediments. Here we report on the recent analysis of both the faunal material and the geological context of this deposit. The faunal assemblage, excavated from the decalcified sediments contains 29 mammal species including taxa rare or absent in the Witwatersrand Plio-Pleistocene fossil record (e.g. *Pelorovis* and *Kobus leche*). Carnivores and porcupines are identified as accumulating agents of the bones. No new hominin findings can be reported from this deposit, and no cultural remains have been recovered.

Geologically the calcified and decalcified breccias represent part of a large talus cone that is relatively unexposed. Uniquely for a cave fill in the Witwatersrand hominin-bearing sites, the sediments are horizontally stratified and form a number of flowstone bound sequences.

The dating of the *in situ* cemented sediments is based on electron spin resonance (ESR) and palaeomagnetism. Recent results indicate that the deposits are of Middle-Pleistocene age.

KEYWORDS: Middle-Pleistocene, Gladysvale, flowstone

INTRODUCTION

The Gladysvale cave is located ca. 13 km north east of Sterkfontein. This fossiliferous deposit was discovered in the mid-1930s, but it was not until 1991 that extensive surveying and excavations took place at the site. This new research led to the recovery of nearly 9000 identifiable macro-mammal fossils (Berger 1993; Berger & Tobias 1994).

Gladysvale is a large system of caves that in the roofed part is formed by an upper chamber and at least two large underground depositories (Figure 1). A de-roofed section located outside the upper chamber contains fossiliferous breccias which have been excavated since 1993. Part of these breccias form the Gladysvale External Deposit (GVED) (Lacruz 2002) and consist of fossil-rich calcified and decalcified sediments. The calcified breccias as presently exposed extend across an area of 20x5 m (Figure 2) and are horizontally stratified. The stratification of these sediments has previously been noted by Berger & Tobias (1994), who referred to the limited exposed breccias as the "pink breccia". The analysis presented here will further describe the stratigraphy of this sequence. The cemented breccias are surrounded by large pockets of soft decalcified matrix which cover an area of approximately 5x3 m that represent the current level of the excavation. No stratification is evident in these sediments.

Fossil collection in the early 1990s consisted of identification and preparation of material contained in *ex situ* breccia blocks. These blocks resulted from mining of the cave during the earlier part of the century (Berger & Tobias 1994). This search for fossils produced in 1992 an upper P^3 and M^2 attributed to *Australopithecus* cf. *africanus* (Berger 1992; Berger, *et al* 1993). Non-hominin material recovered from these unprovenanced blocks has been discussed in previous work by Berger (1993), Berger *et al*. (1993); Berger & Tobias (1994); Plug & Keyser (1994a); Avery (1995) and Mutter, *et al* (2001).

This study analyses only the provenanced fossil material excavated since 1999 from the decalcified sediments of the GVED, the geological context and the dating of this assemblage.

GEOLOGICAL CONTEXT AND STRATIGRAPHY

Berger & Tobias (1994) pointed out that the geology of the Gladysvale cave was more complex than had been previously interpreted by Martini & Keyser (1989). A provisional stratigraphy of the deposits located outside the upper chamber was described, assigning the various units informal names (Berger & Tobias 1994). At the time however only about 2m from the surface had been cleared, of which about 1m was mining rubble. The base of their stratigraphic section (pink breccia and stony breccia) therefore only just reached the top of the sequence now referred to as the GVED. As presently exposed, the GVED section is about 5 m thick, and is unique amongst the known cave deposits of this region in that it preserves a well-stratified sequence.

The stratigraphy of the GVED deposits is presented in Figure 3 and comprises nine sedimentologically distinguishable units, separated by flowstones of varying thickness and purity (Figure 3).

Each of the individual units has been identified on the basis of clast and matrix composition, sedimentary structure, and the presence or absence of micro- and macro faunal remains. Cores were drilled and petrographic thin sections cut of each of the major units. These aided in the description of the matrix and clast types, as well as in identifying various stages of bone diagenesis.

Although it is not the intention of this paper to provide a detailed description of each of the units, it is necessary to briefly discuss the nature of the fill inferred from the stratigraphic studies. Each of the units delineated for the GVED section are bound top and bottom by a flowstone layer (FS) and are termed flowstone bound units (FBUs; Units A-J on Figure 3). Packages of Flowstone Bound Units stack into thicker deposits here termed Flowstone Bound Intervals (FBIs) that are in turn capped by thicker accumulations of fairly uncontaminated flowstone. Utilising this technique three main cycles of sedimentation have been identified, each of which is bound at the base and top by a flowstone sequence. At places the tops of the individual flowstone units may show evidence of dissolution prior to the onset of the overlying period of sedimentation. The basal terminations of the overlying sedimentary unit tend to strongly downlap onto the top surface of the underlying flowstone, representing renewed fan sedimentation following a period of flowstone accumulation.

Following the interpretation of Moriaty, McCulloch, Wells & McDowell (2000) for similar deposits in the Pleistocene cave fills of the Naracoorte region of South Australia, such cyclic units are believed to represent the sedimentary responses of the system to changes in climate. Here we model the flowstones (particularly the thick, uncontaminated units F and J) to represent periods of above average rainfall, good vegetational cover outside the cave, and a fairly restricted cave entrance. Clastic depositional cycles on the other hand are interpreted as the sedimentary response to more arid climate, decreased vegetational cover and better run-off and sediment supply.

Therefore, the GVED sequence is interpreted as having been deposited on the distal reaches of a debris cone and the proximal reaches of the fan surface which drains off the cone (following the terminology of Moriarty *et al.* 2000), in response to changing climatic conditions and sediment supply through the Middle Pleistocene. A number of coarsening- and fining-upward packages represent proximal/distal shifts in the slope of the fan surface in response to increased or decreased sediment supply. The recognition of such flowstone bound sequences is thus important as such units approximate sequences in the temporal sense of the word. If, as we suspect, such sequences are climatically driven, then similar cycles should occur in all other cave fills in the Sterkfontein Valley hominin-bearing cave sites that were open to the surface during this time. Sequence boundaries marked by flowstone accumulations may be correlated to other caves and offer for the first time a methodology for direct correlation of Middle Pleistocene cave deposits in the entire region.

DATING OF THE GLADYSVALE DEPOSITS

Electron Spin Resonance

Fossil teeth are among the best materials for Electron Spin Resonance (ESR) dating, since the dating signal in enamel is extremely stable. This is one of the few techniques available for dating deposits like Gladysvale.

ESR quantifies total environmental radiation damage, and calculates ages by comparing this to the environmental radiation dose rate. After separating dentine and enamel, the enamel is powdered and divided into aliquots. These are then artificially irradiated with known doses, using a Cs-137 gamma source, to determine the specific radiation sensitivity of the sample and thence the total damage to crystals of hydroxyapatite (HAP) within the enamel. In HAP the damage results from creating carbonate radicals with an extra electron. Several summaries of the method are available (see, e.g., Aitken 1990; Ikeya 1993; Rink 1997; Skinner 2001).

The total dose rate has different components. Clearly, one is the dose contributed by radioisotopes in the sediments surrounding the tooth. These are measured by neutron activation analysis (NAA) on multiple sediments taken within a sphere of 30 cm around the tooth. In addition, dentine and enamel contain uranium and because uranium is absorbed by tooth enamel and dentine during burial, the internal dose rate in the tooth enamel varies with time. A mathematical function for this uptake is discussed in Blackwell, Blickstein & Skinner (2001), but given the complexities of the fossilization process, it is general practice to assume one of three simple models:

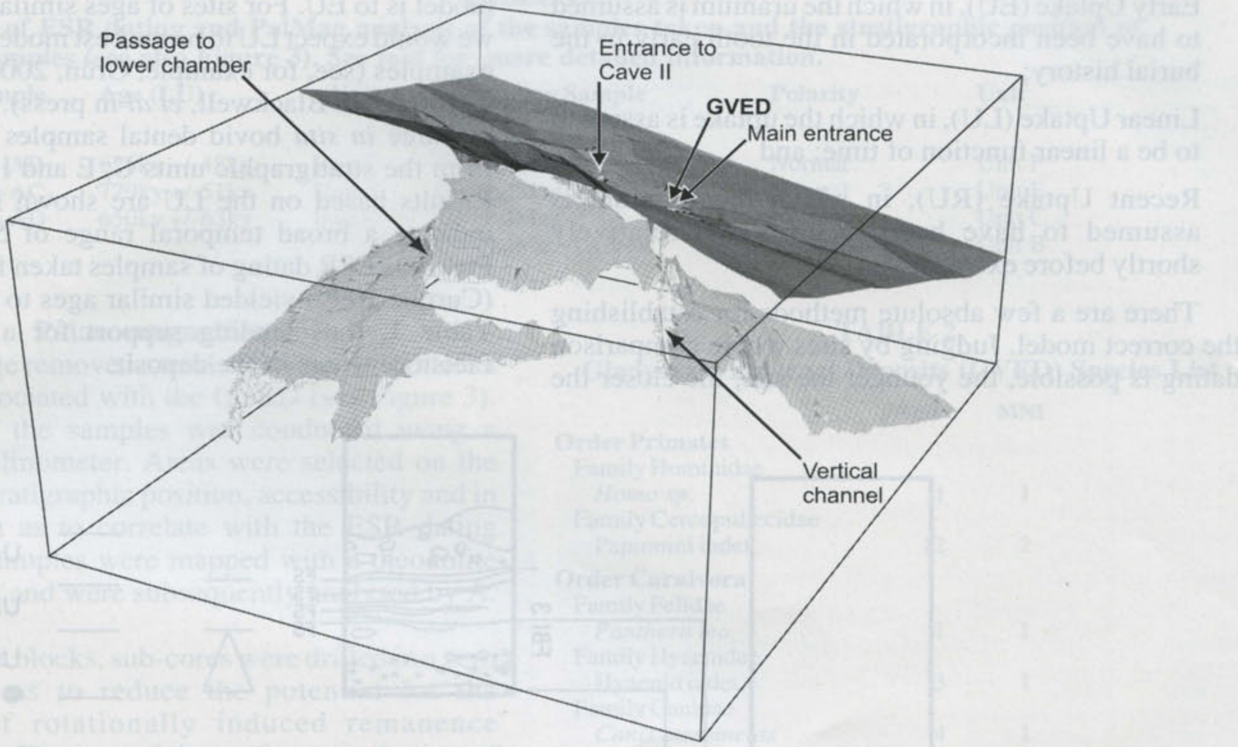

Figure 1. A 3-D image indicating the position of the GVED in relation to the underground deposits in the Gladysvale Cave. The GVED covers an area of 80 m². The lowermost sections of the Gladysvale system reach a depth of 65m.

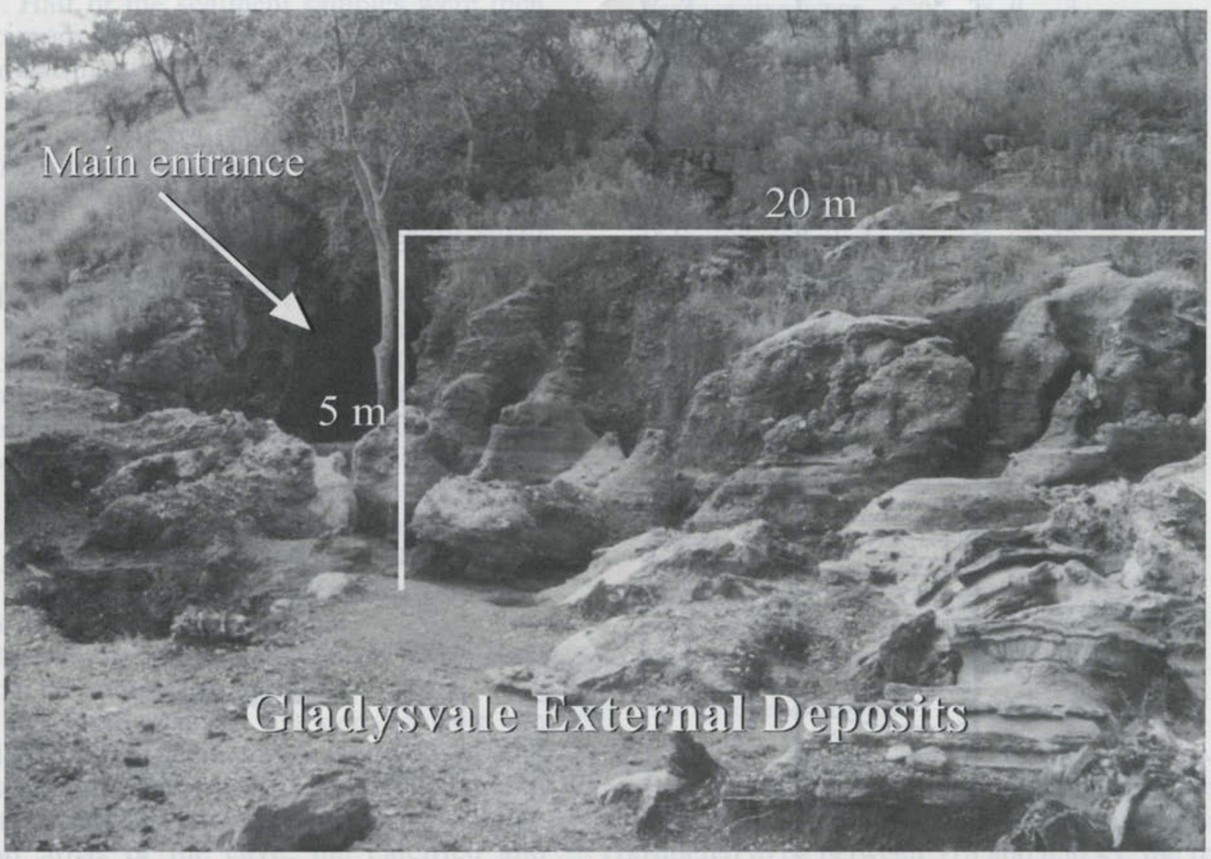

Figure 2. The Gladysvale External Deposits (GVED) are located outside the main upper chamber in the Gladysvale Cave System. The GVED consists of calcified and decalcified sections which have been the subject of study since 1993.

Early Uptake (EU), in which the uranium is assumed to have been incorporated in the tooth early in the burial history;

Linear Uptake (LU), in which the uptake is assumed to be a linear function of time; and

Recent Uptake (RU), in which the uranium is assumed to have been incorporated relatively shortly before excavation.

There are a few absolute methods for establishing the correct model. Judging by sites where comparison dating is possible, the younger the site, the closer the model is to EU. For sites of ages similar to Gladysvale we would expect LU to be the best model based on other examples (see, for example, Grün, 2000; Paddayya, *et al* 2002, and Blackwell, *et al* in press).

Three *in situ* bovid dental samples were collected from the stratigraphic units C, E and I (see Figure 3). Results based on the LU are shown in Table 1 and indicate a broad temporal range of 578 to 830 ky. Previous ESR dating of samples taken from the GVED (Curnoe 1999) yielded similar ages to those shown in Table 1, thus lending support for a broad Middle Pleistocene age of the deposit.

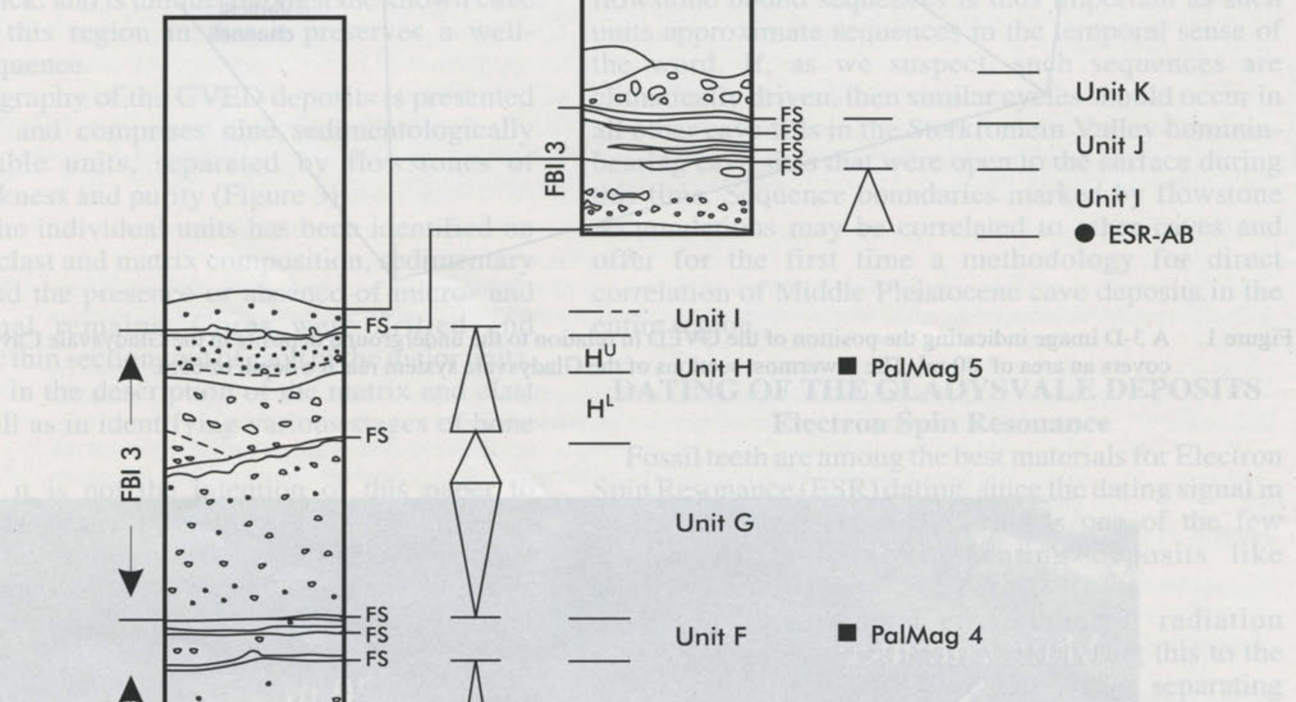

Figure 3. Stratigraphic section of the GVED. Each of the units delineated are bound top and bottom by flowstone layers (FS) which are termed Flowstone Bound Units (FBUs). These FBUs form thicker units termed Flowstone Bound Intervals (FBIs). Samples removed for ESR dating and palaeomagnetic analysis are shown in the stratigraphic unit from which these samples were removed (see also Table 1 for results).

TABLE 1.

Results of ESR dating and PalMag analysis of the samples taken and the stratigraphic position of these samples (see also Figure 3). See text for more detailed information.

ESR Sample	Age (LU)	Unit	Palaeomag Sample	Polarity	Unit
GV-ESR-AB	626ky +/-48ky	Unit I	GV-PalMag-4	Normal	Unit F
GV-ESR-AC	779ky +/-51ky	Unit E	GV-PalMag-3	Normal	Unit E
GV-ESR-AD	650ky +/-63ky	Unit C	GV-PalMag-2	Normal	Unit C
			GV-PalMag-1A&1B	Intermediate	Unit B

Palaeomagnetism

T.C. Partridge removed a total of five oriented blocks from strata associated with the GVED (see Figure 3). Orientation of the samples was conducted using a compass and clinometer. Areas were selected on the basis of their stratigraphic position, accessibility and in a manner such as to correlate with the ESR dating program. All samples were mapped with a theodolite before removal and were subsequently analysed by A. Herries.

From the five blocks, sub-cores were drilled in a zero field cage so as to reduce the potential for the acquisition of rotationally induced remanence magnetisations. Because of the surface weathering of some of the blocks, only the central portions of the sub-cores were used for this analysis.

The samples were first subjected to an Alternating Field cleansing of viscous remanence (VRM: remanence induced into the sample since its deposition). Half of the sediment samples were then subjected to more detailed thermal demagnetisation to try to isolate a primary remanence formed at the time of deposition. The other half and any calcite samples were subjected to comparative alternating field demagnetisation. Rock magnetic methods were undertaken on sub-samples and indicated fine-grained magnetite as the bulk magnetic mineral with small fractions of haematite.

Results from this pilot study (Table 1) show that three of the blocks (GV02-04) indicate normal primary directions of magnetisation, while block GV01 gave intermediate normal directions and block GV05 gave intermediate directions. Block GV05 gave directions consistent with highly brecciated samples where each individual clast has its own direction of magnetic remanence, causing an overall randomisation of the magnetic grains. Block GV01 may represent a transitional sample or may have experienced post-depositional effects such as slumping.

In conclusion, no polarity reversals have been detected from the samples analysed.

Because the fossil material has derived from the unstratified decalcified sediments, it is not possible to assign this assemblage to a specific geological horizon of the cemented breccias. It must be noted however, that unlike other areas of the cave, the calcified and decalcified sediments of the GVED have not been disturbed by mining. Thus, the fossil material from the decalcified breccias is believed to have formed by the *in situ* decalcification of the fossiliferous beds which form part of the cemented breccias. Therefore, the age estimates ascribed to the excavated assemblage is considered to be between 578 and 830 ky, the recently obtained ESR results (Table 1). However, in the absence of polarity reversals from the samples analysed, the age estimate for the fossil material from the GVED is considered to be younger than 780 ky, the

TABLE 2.

Gladysvale External Deposits (GVED) Species List

	NISP	MNI
Order Primates		
Family Hominidae		
Homo sp.	1	1
Family Cercopithecidae		
Papionini indet.	12	2
Order Carnivora		
Family Felidae		
Panthera leo	1	1
Family Hyaenidae		
Hyaenid indet.	3	1
Family Canidae		
Canis mesomelas	4	1
Order Artiodactyla		
Family Bovidae		
Tragelaphus strepsiceros	5	2
Taurotragus oryx	4	2
Pelorovis sp.	1	1
Syncerus sp.	1	1
Kobus leche	17	7
Redunca arundinum	8	3
Redunca fulvorufula	3	1
Hippotragus equinus	21	5
Hippotragus niger	2	1
cf. *Oryx gazella*	1	1
Megalotragus sp.	3	1
Connochaetes taurinus	4	3
Connochaetes sp. indet.	51	9
Damaliscus dorcas	12	2
Medium sized alcelaphines	119	13
cf. *Aepyceros* sp.	1	1
Raphicerus campestris	1	1
Oreotragus oreotragus	1	1
Antidorcas bondi	1	1
Makapania sp.	37	4
Family Suidae		
cf. Phacochoerus sp.	1	1
Family Giraffidae	1	1
Order Perissodactyla		
Family Equidae		
Equus capensis	9	3
Equus burchelli	4	2
Order Hyracoidea		
Procavia capensis	5	2
Procavia transvaalensis	8	2
Order Rodentia		
Hystrix africaeaustralis	4	1

TABLE 3.
Measurements of identified specimens from the GVED

Specimen Number	Taxonomy	Left=L Right=R	Tooth Mandible=m Maxilla=M	premolar=P molar=Ml	Length	Breadth
Artiodactyla						
GV 6988	*Tragelaphus strepsiceros*	L	M	Ml 2	25.44	20.44
GV4847	*T. strepsiceros*	R	m	P3	16.92	9.04
GV 8469	*T. strepsiceros*	L	m	P3	17.46	8.74
GV 5411	*T. strepsiceros*	R	m	P2	13.12	7.85
GV 8406	*Taurotragus oryx*	R	m	Ml 1	23.44	16.9
GV 4804	*T. oryx*	L	m	dP4	35.01	12.35*
GV 5393b	*T. oryx*	L	m	dP3	17.69	9.94
GV 5393	*T. oryx*	R	m	dP2	12.7	6.42
GV 5298	*Pelorovis sp.*	R	M	Frg	?	?
GV 5234	*Syncerus* cf. *caffer*	L	M	Ml 2	28.3	20.4
GV5246	*Kobus leche*	R	M	Ml 3	17.85	13.9
GV 8960	*K. leche*	L	M	Ml 3	17.4	13.86
GV 5079	*K. leche*	R	M	Ml 3	16.05	12.23
GV 6865	*K. leche*	R	M	Ml 3	17.72	12.74
GV 5132	*K. leche*	R	M	Ml 3	17.9	13.03
GV 8109	*K. leche*	R	M	Ml 3	15.81	*12.30
GV 7878	*K. leche*	L	M	Ml 3	16.53	12.59
GV 5114	*K. leche*	L	M	Ml 3	17.62	14.2
GV 5117	*K. leche*	R	M	Ml 3	18.12	14.4
GV 6219	*K. leche*	L	M	Ml 3	16.72	12.84
GV 5792	*K. leche*	L	M	Ml 2	15.93	13.61
GV 7209	*K. leche*	R	M	Ml 2	17.52	12.32
GV 5291	*K. leche*	R	M	Ml 3	16.99*	?
GV 5109	*K. leche*	L	m	P3	11.87	6.88
GV 8086	*K. leche*	L	m	Ml 1	14.62	9.83
GV 8081	*Redunca arundinum*	L	m	Ml 3	21.44	9.75
GV 4901	*R. arundinum*	R	m	Ml 3	21.11	9.54
GV 8586	*R. arundinum*	L	m	P4	10.4	6.63
GV 5313	*R.* cf. *arundinum*	R	m	dP4	?	?
GV 8325	*R.* cf. *arundinum*	L	m	P4	8.98	9.27
GV 5093	*R. arundinum*	R	M	P3	8.88	8.96
GV 5715	*R.* cf. *arundinum*	L	M	P4	9.4	9.43
GV 5829	*R. fulvorufula*	L	m	P3	7.47	4.36
GV 5320	*R. fulvorufula*	L	m	Ml 3	?	?
GV 5056	*Hippotragus equinus*	R	m	P4	18.88	12.97
GV 6913	*H. equinus*	R	m	P4	19.71	13.59
GV 7543	*H. equinus*	R	m	P4	19.96	13.52
GV 7848	*H. equinus*	R	m	P2	15.36	10.56
GV 7657	*H. equinus*	L	m	P2	13.86	10.57
GV 5367	*H. equinus*	L	m	Ml 3	31.99*	12.24*
GV 6947	*H. equinus*	R	m	Ml 3	32.35*	14.2
GV 7156	*H. equinus*	R	m	Ml 3	31.87	?
GV 4855	*H. equinus*	L	m	Ml 2	27.35	13.03
GV 8354	*H. equinus*	R	m	Ml 2	?	?
GV 5085*	*H. equinus*	L	m	Ml 2	?	?
GV 5146	same individual as 5085				?	?
GV 4804	*H. equinus*	L	m	Ml 2	25.31	13.19
GV 7165	*H. equinus*	R	m	dP4	?	?
GV 8182	*H. equinus*	L	m	dP4	29.74	11.87
GV 5226	*H. equinus*	L	m	dP4	30.1	12.25
GV 8607	*H.* cf. *equinus*	L	m	dP2	15.07	10.11
GV 8037	*H. niger*	R	M	Ml 2	24.15	18.68
GV 8956	*H. niger*	L	m	Ml 1	21.16	10.26
GV 8328	*Oryx* cf. *gazella*	R	m	Ml 2	18.12	13.07
GV 8250	*Antidorcas bondi*	L	mandible	Ml 2,3		
				Ml 2	14.38	6.88
				Ml 3	19.32	6.08
GV 8407	*Oreotragus oreotragus*	L	Maxilla	Ml 2,3		
				Ml 2	12.59	?
				Ml 3	11.94	?
GV 7541	*Raphicerus campestris*	L	M	Ml 1	7.28	6.71
GV 7670*	same individual as 7541		M	Ml 2	8.94	7.43
GV 5439	cf. *Aepyceros* sp.	L	M	Ml 1	14.59	11.17
Carnivora						
GV 4849	*Panthera leo*	L	m	Ml 1	30.06	16.2
Perissodactyla						
GV 5406	*Equus capensis*	L	m	P3	33.48	22.4
GV 7089	*Equus capensis*	L	m	P2	38.86	14.56
GV 4836	*Equus capensis*	R	m	P2	35.39	19.29
GV 4789b	*Equus capensis*	R	m	Ml 3	40.03	17.13
GV 8048	*Equus capensis*	R	m	P2	36.68	19.82
GV 7961	*Equus capensis*	L	m	?P3	38.25	18.51
GV 7248	*Equus capensis*	R	M	Inc 2	21.86	10.75
GV 4809	*Equus capensis*	R	M	Ml 3	33.98	?
GV 5871	*Equus capensis*	R	m	Inc 2	20.1	11.28
GV 5136	*Equus capensis*	R	M	Inc 3	22.51	13.14
GV7596	*E. burchelli*	R	M	Ml2	25.61	27.22
GV 8096	*E. burchelli*	R	m	P2	27.62	15.5
GV 5121	*E. burchelli*	R	m	ML1	25.09*	14.80*

* Estimated measurements

TABLE 4.

% MNI taxonomic groups from the GVED

Bovidae	78%
Carnivora	4%
Primates	4%
Equidae	6.7%
Others	7.3%

last palaeomagnetic reversal (Cande & Kent 1995). Therefore, the age of the GVED is established between 578 and 780 ky.

PALAEONTOLOGY OF THE GVED FOSSIL ASSEMBLAGE

The fossil assemblage from the GVED contains 29 mammal species, some of which are usually rare or absent in the Witwatersrand fossil accumulations (Tables 2, 3). Taxa like *Kobus leche* and *Pelorovis* are uncommon as fossils in the area. The genus *Makapania* is represented at the GVED, thus extending its temporal range into the late Middle-Pleistocene. The most abundant taxonomic group represented in the GVED is the Family Bovidae, with 18 species present (Tables 2, 4).

Previous analyses indicated that carnivores and porcupines were the main agents of accumulation of the faunal remains (Lacruz 2002). Punctate depressions, tooth scratches, gnawed epiphyses and characteristic porcupine gnawing are the main features of bone surface modification of fossils from the GVED. No tools (bone or stone) or cut-marked bones were recovered during the excavations (Lacruz 2002).

Order Artiodactyla
Family Bovidae

The GVED ungulate assemblage is dominated by the tribe Alcelaphini followed by Reduncini and Hippotragini (Figure 4). Other bovid tribes usually common in the fossil record of the Witwatersrand, like Antilopini (see e.g. Vrba 1980), are not well represented at the GVED. The taxonomic classification of the Bovidae used in this study follows that of Gentry (1992) with the exception of the genus *Aepyceros* which Vrba (1984) classifies in the tribe Aepycerotini.

Tribe Alcelaphini

The extant members of the alcelaphine tribe are among the most problematical to identify from teeth alone (Klein & Cruz-Uribe 1991). Morphological similarities, degree of size overlap between the species, and the stage of wear of the teeth are the main confounding factors (Vrba 1976; Klein & Cruz-Uribe 1991; de Ruiter 2001).

This situation is further complicated in the fossil record because of the great diversity of species known during the Pliocene and Pleistocene. Therefore, assigning dentitions to a meaningful taxonomic group has been a long-standing problem. The classification presented here is based on detailed comparative analysis with modern and fossil collections. A more detailed analysis of the GVED alcelaphine material is in preparation.

Genus *Megalotragus* van Hoepen, 1932

The genus *Megalotragus* is represented in southern Africa by two species, *M. eucornutus* and *M. priscus* (Gentry 1978; Brink *et al.* 1995). Horn core morphology is quite different in both species although identification based on isolated teeth is difficult. At least two individuals of this large extinct wildebeest are present in the GVED assemblage which have been assigned to *Megalotragus* sp.

Connochaetes taurinus (Burchell, 1823)

Two species of the genus *Connochaetes* are recognized in southern Africa during the Pleistocene (Gentry 1978) and both are extant. Horn core, dental

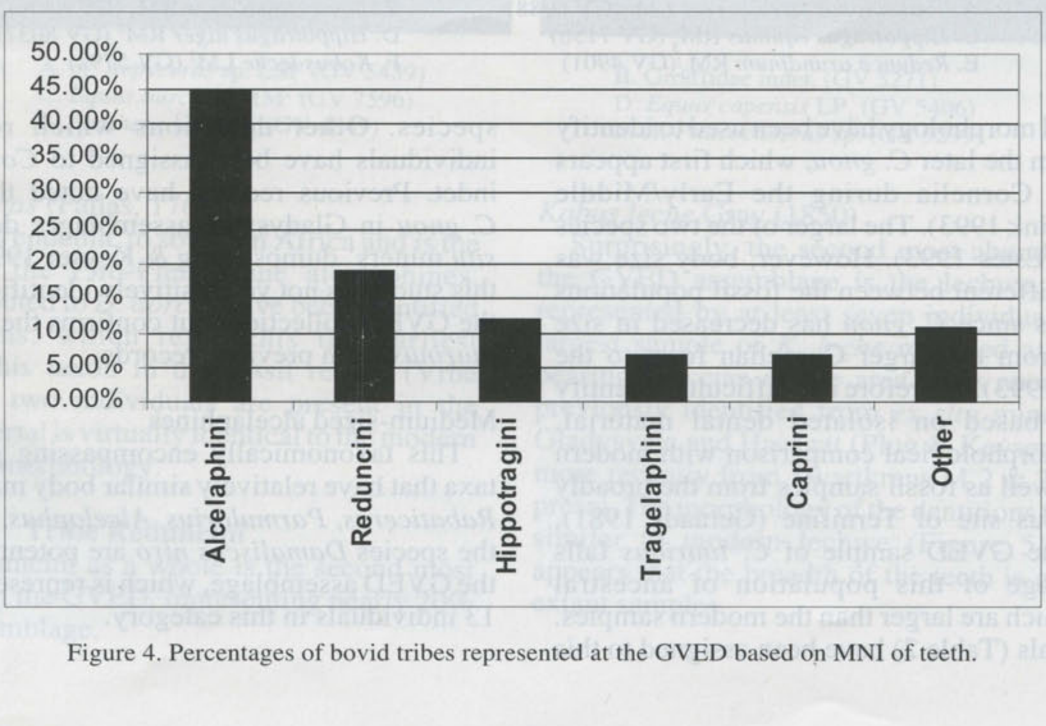

Figure 4. Percentages of bovid tribes represented at the GVED based on MNI of teeth.

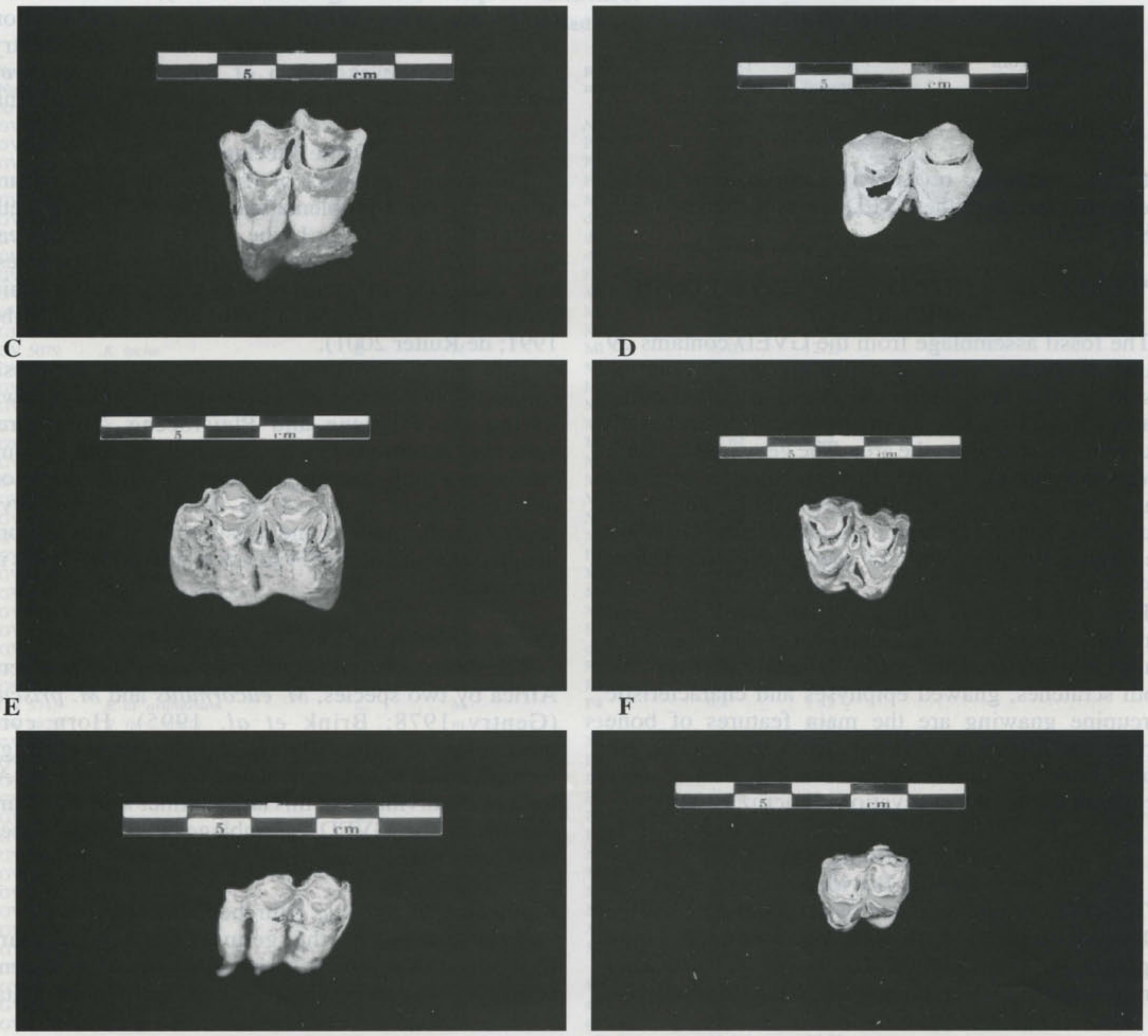

Figure 5. A. *Tragelaphus strepsiceros* LM^2 (GV 6988) B. *Taurotragus oryx* RM_1 (GV 8406)
C. *Hippotragus equinus* RM_3 (GV 7156) D. *Hippotragus niger* RM^2 (GV 8037)
E. *Redunca arundinum* RM_3 (GV 4901) F. *Kobus leche* LM^2 (GV 5792)

and post-cranial morphology have been used to identify *C. taurinus* from the later *C. gnou,* which first appears at the site of Cornelia during the Early/Middle Pleistocene (Brink 1993). The larger of the two species is *C. taurinus* (Estes 1993). However, body size was probably less different between the fossil populations of these species since *C. gnou* has decreased in size through time from the larger Cornelian form to the present (Brink 1993). Therefore it is difficult to identify these species based on isolated dental material. Metrical and morphological comparison with modern *C. taurinus* as well as fossil samples from the broadly contemporaneous site of Ternifine (Geraads 1981), indicate that the GVED sample of *C. taurinus* falls within the range of this population of ancestral *C. taurinus*, which are larger than the modern samples. Three individuals (Table 2) have been assigned to this species. Other dentitions which represent nine individuals have been assigned to *Connochaetes* sp. indet. Previous records have noted the presence of *C. gnou* in Gladysvale assemblages derived from *ex situ* miners' dumps (Plug & Keyser 1994a). However, this study has not yet positively identified this taxon in the GVED collection, but confirms the presence of *C. taurinus* from previous records.

Medium-sized alcelaphines

This taxonomically encompassing group includes taxa that have relatively similar body mass. The genera *Rabaticeras, Parmularius, Alcelaphus, Beatragus* and the species *Damaliscus niro* are potentially present in the GVED assemblage, which is represented by at least 13 individuals in this category.

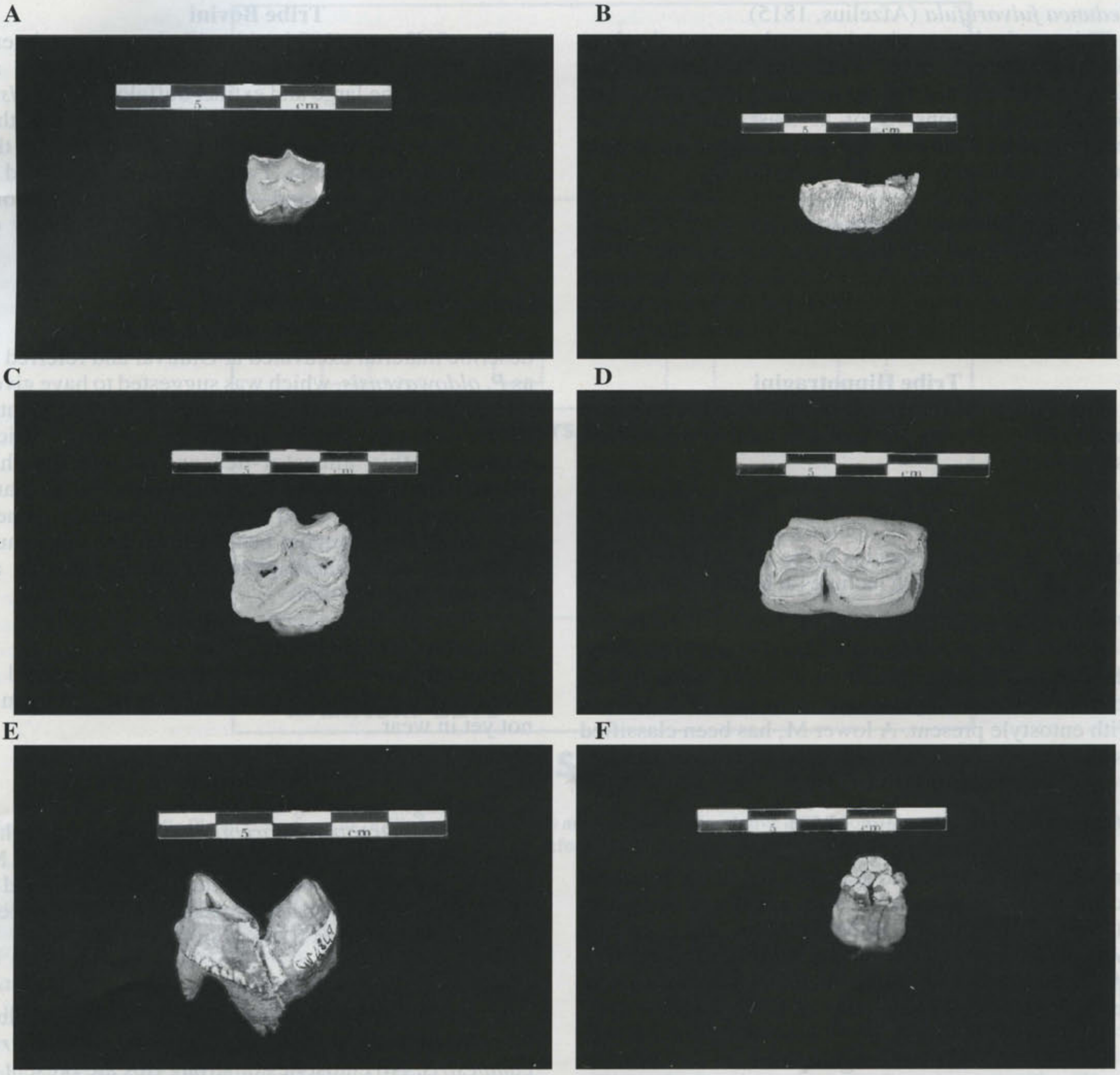

Figure 6. A. cf. *Aepyceros* sp. LM^1 (GV 5439) B. Giraffidae indet. (GV 5271)
C. *Equus burchelli* RM^2 (GV 7596) D. *Equus capensis* LP_3 (GV 5406)
E. *Panthera leo* LM_1 (GV 4849) F. cf. *Phacochoerus* sp. (GV 5299)

Damaliscus dorcas (Pallas, 1766)

This species is endemic to southern Africa and is the smallest of all the Plio-Pleistocene alcelaphines. Specimens attributed to *D. dorcas* have been identified from Swartkrans, which represents the earliest appearance of this taxon in the fossil record (Vrba 1995). At least two individuals are present in the GVED. The material is virtually identical to the modern form in size and morphology.

Tribe Reduncini

The tribe Reduncini as a whole is the second most abundant Tribe at the GVED, representing nearly 20% of the bovid assemblage.

Kobus leche Gray (1850)

Surprisingly, the second most abundant species in the GVED assemblage is the lechwe, *Kobus leche*, represented by at least seven individuals. This is the largest sample of *K. leche* recorded at the hominin-bearing breccias of the area. This species had been previously identified from *ex situ* miners' dumps at Gladysvale and Haasgat (Plug & Keyser 1994a,b) and more recently from Swartkrans M 2 & 3 (de Ruiter in press). The morphology of the dentitions from GVED is similar to modern lechwe (Figure 5), although it appears that the breadth of the teeth is greater than in extant samples.

Redunca fulvorufula (Afzelius, 1815)

This species has previously been documented only at Gladysvale (Berger *et al.* 1993) and Haasgat (Plug & Keyser, 1994b) in the Sterkfontein Valley sites. The GVED sample consists of at least one individual represented by a lower P_3 with no paraconid-metaconid fusion, and M_3 with unworn ectostylid.

Redunca arundinum (Boddaert, 1785)

At least five individuals are represented at the GVED assemblage (Figure 5), including two juvenile specimens. The Gladysvale dentitions appear to have a greater length and breadth than the modern forms.

Tribe Hippotragini

This tribe is the third most numerous of the bovids in the GVED, reaching 12% of the total GVED bovid assemblage.

Hippotragus equinus (Desmarest, 1804)

The roan antelope, *H. equinus*, (Figure 5) is one of the most represented species in the GVED assemblage with an MNI of 5, which includes at least two juveniles.

Hippotragus niger (Harris, 1838)

A right maxillary second molar (Figure 5) has been identified as *H. niger* based on its size (Table 3). The specimen is indistinguishable from the modern form with entostyle present. A lower M_2 has been classified as *H.* cf. *niger*. No confirmed records of this taxon exist from Gladysvale prior to this study.

cf. Oryx gazella (Linnaeus, 1758)

A single specimen, a right mandibular M_2, has been provisionally assigned to gemsbok based on its simple occlusal enamel pattern and size, as defined by Gentry (1978). No records of this taxon exist in the Witwatersrand sites during the Plio-Pleistocene. The specimen is worn and therefore cannot be assigned with certainty; it is thus assigned to *cf. Oryx gazella*.

Tribe Tragelaphini

This Tribe is well represented at the GVED with two species and a percentage close to 7% of the total bovid assemblage. The tragelaphine species present at the GVED have been previously recorded by Plug & Keyser (1994a) from the older Gladysvale deposits.

Taurotragus oryx (Pallas, 1766)

Eland is represented at the GVED (Figure 5) by at least two individuals, one of which is juvenile. All samples are isolated teeth very close in morphology to the modern eland.

Tragelaphus strepsiceros (Pallas, 1766)

The presence of kudu at the GVED is attested by at least two individuals that do not show any morphological differences from the modern form. An upper second molar (Figure 5) does not have entostyles or prominent ribs.

Tribe Bovini

Plug & Keyser (1994a) identified some specimens from the *ex situ* assemblages of Gladysvale as belonging to the large and extinct buffalo "*Pelorovis*", thus suggesting a wider geographic distribution of this taxon than had been previously considered in the southern African region. Two lineages are recorded at the GVED, *Syncerus* and "*Pelorovis*". The dentitions of these two genera differ in size and complexity of occlusal patterns (Vrba 1987).

Genus *Pelorovis* Reck, 1928

The genus *Pelorovis* was originally created to describe material excavated at Olduvai and referred to as *P. oldowayensis*, which was suggested to have given rise to the younger *"P". antiquus* (Gentry & Gentry 1978), the only known species in southern Africa. However, this ancestor-descendant relationship between the two species is not securely established, and hence the use of inverted commas in citing the name.

A single specimen has been attributed to this genus. It consists of an incomplete maxillary molar in an advanced stage of wear.

Genus *Syncerus* Hodgson, 1847

An unworn maxillary molar has been identified as *Syncerus* cf. *caffer*. The basal pillar in the specimen is not yet in wear.

Tribe Neotragini

Oreotragus oreotragus (Zimmerman, 1783)

At GVED *Oreotragus oreotragus* (klipspringer) has been identified from a left maxillary fragment with M^2 and M^3. A deciduous upper molar has been assigned to *O.* cf. *oreotragus*. A partial mandible with worn teeth has been classified as Neotragini indet.

Raphicerus campestris (Thunberg, 1811)

Two isolated maxillary molars of the same individual have been attributed to the steenbok, *Raphicerus campestris*. No entostyles or strong ribs are present in these specimens.

Tribe Antilopini

Antidorcas bondi (Cooks & Wells, 1951)

A left mandible with M_2 and M_3 has been identified as *Antidorcas bondi*. The specimen is slightly different from the known *A. bondi* recovered from fossil sites in the Witwatersrand area. The teeth are less hypsodont, have thinner enamel, and are generally larger than specimens from Swartkrans and Florisbad, but are very similar to the Cornelia forms.

Tribe Aepycerotini

Genus *Aepyceros* (Sundevall, 1847)

Aepyceros is rare in the Witwatersrand sites, with only one possible record from the earlier Gladysvale assemblages identified by H.B.S. Cooke (1978). Reed (1996) identified some material from the Makapansgat

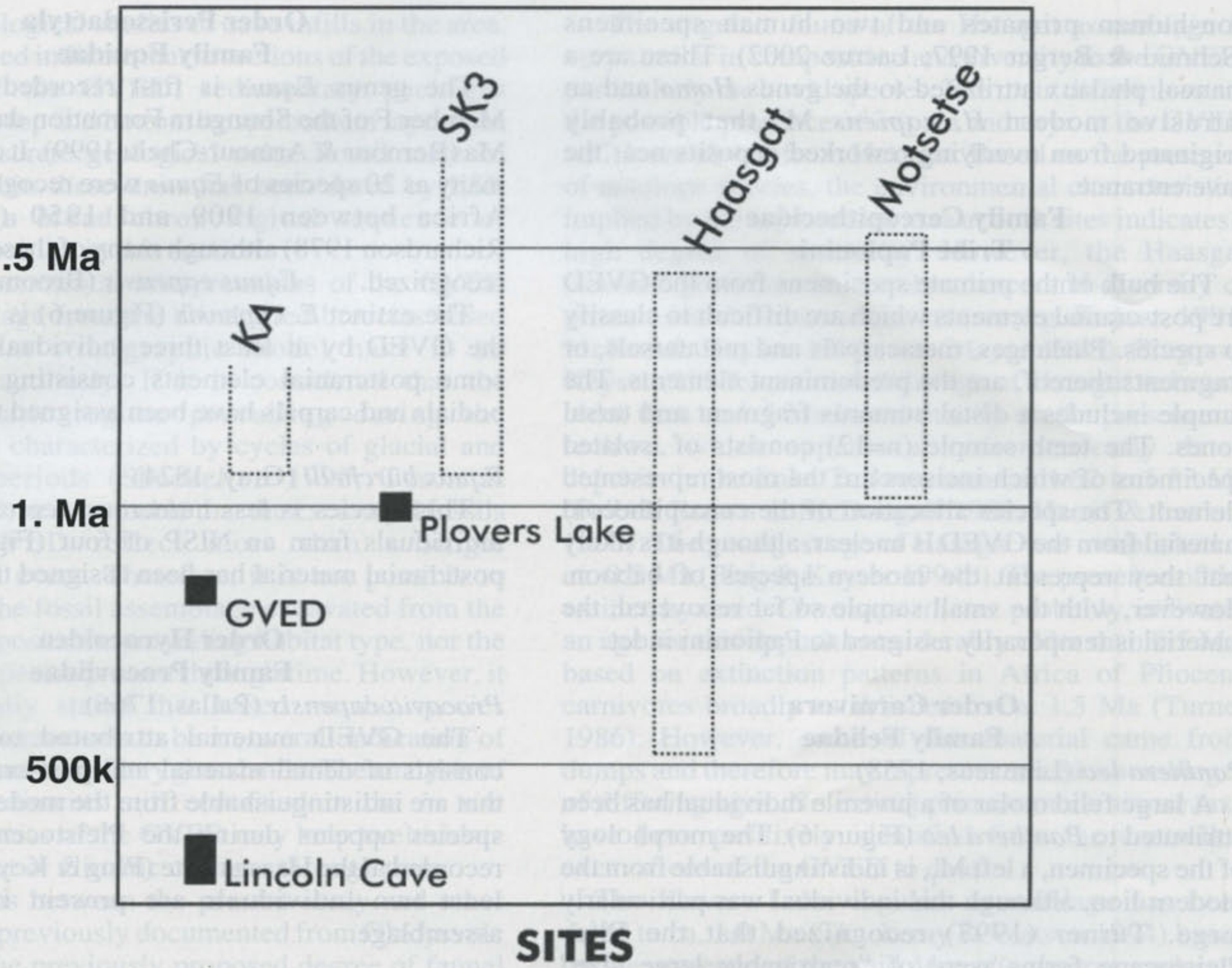

Figure 7. The Middle Pleistocene deposits of Gladysvale (GVED) are shown in their relative chronological position to other Pleistocene aged cave deposits in the Witwatersrand. See text for references and comments on the ages of these deposits.

Limeworks as cf. *Aepyceros* sp. At the GVED, a worn maxillary M^1 has been attributed to cf. *Aepyceros* sp. (Figure 6). The specimen is bigger than *Gazella vanhoepeni* and *G. gracilior* from the Makapansgat Limeworks and similar to the modern impala.

Subfamily Caprinae

Genus *Makapania* (Wells & Cooke, 1956)

Wells & Cooke (1956) originally described the genus *Makapania* from Makapansgat Limeworks and assigned this material to the tribe Alcelaphini. Gentry (1970) revised the material and re-classified it under the tribe Ovibovini.

Brink (1999) identified a new species of *Makapania* from fossil assemblages in the Cango Valley, Western Cape Province. The Cango Valley dentitions and associated postcranial elements are very similar in morphology and size to the Gladysvale specimens, indicating the possibility of a close taxonomic relationship. The GVED material is provisionally assigned to *Makapania* sp.

Previous records of *Makapania* are documented from Gladysvale. The only specimen is a right M^3 (Plug & Keyser 1994a) similar to the material from the GVED. A more detailed analysis of the GVED material is in preparation.

Family Giraffidae

Fossil giraffids are not abundant in the Witwatersrand accumulations. The single specimen recovered in the GVED (Figure 6), a mandibular premolar fragment, is likely to represent the modern giraffe, but this cannot be ascertained with certainty. The only previous record of modern giraffe, *Giraffa camelopardalis*, in the area is a phalanx from the site of Haasgat (Plug & Keyser 1994b).

Family Suidae

cf. *Phacochoerus* sp.

Only two specimens in the GVED assemblage represent the suids. A molar fragment which very likely belongs to the modern warthog shows closely packed oval columnar elements typical of this genus (Cooke & Wilkinson 1978) (Figure 6). However, the specimen is too incomplete for a precise taxonomic identification.

A fragment of an upper tusk 3cm long as well as the molar fragment have been assigned to cf. *Phacochoerus* sp.

Order Primates

In the GVED the Order Primates is represented by non-human primates and two human specimens (Schmid & Berger 1997; Lacruz 2002). These are a manual phalanx attributed to the genus *Homo* and an intrusive modern *H. sapiens* M^3 that probably originated from overlying reworked deposits near the cave entrance.

Family Cercopithecidae
Tribe Papionini

The bulk of the primate specimens from the GVED are post-cranial elements which are difficult to classify to species. Phalanges, metacarpals and metatarsals, or fragments thereof, are the predominant elements. The sample includes a distal humerus fragment and tarsal bones. The teeth sample (n=12) consists of isolated specimens of which incisors are the most represented element. The species allocation of the cercopithecoid material from the GVED is unclear, although it is likely that they represent the modern species of baboon. However, with the small sample so far recovered, the material is temporarily assigned to Papionini indet.

Order Carnivora
Family Felidae

Panthera leo (Linnaeus, 1758)

A large felid molar of a juvenile individual has been attributed to *Panthera leo* (Figure 6). The morphology of the specimen, a left M_1, is indistinguishable from the modern lion, although this individual was particularly large. Turner (1997) recognized that the Plio-Pleistocene forms were of "reasonably large size" which could explain the difference between the Gladysvale specimen and modern lion.

At the GVED there are a number of foot bones that have been attributed to Felidae indet. This material could belong to the lion represented by the M_1. The phalanges lack proximal epiphyseal fusion, indicating similarity in developmental stages and were recovered in close proximity to the tooth.

Family Hyaenidae

Three specimens have been identified as hyaenid indet. These are an upper lateral incisor, an incomplete lower premolar and a phalanx. No further taxonomic identification is possible with the available samples.

Family Canidae

The GVED material of the Family Canidae is represented by *Canis mesomelas* and a larger distal humerus of a size ranging between that of *Lycaon pictus* and *Canis mesomelas*.

Canis mesomelas (Schreber, 1778)

This species is one of the most common carnivores in the palaeontological record of the Witwatersrand sites. Only postcranial elements have been attributed to *C. mesomelas* from the GVED sample. These are two metacarpal bones, a proximal radius and a calcaneus, all of which are indistinguishable from the modern jackal.

Order Perissodactyla
Family Equidae

The genus *Equus* is first recorded in Africa in Member F of the Shungura Formation dated to ca. 2.36 Ma (Bernour & Armour-Chelu 1999). It appears that as many as 20 species of *Equus* were recognized in South Africa between 1909 and 1950 (Churcher & Richardson 1978) although many of these are no longer recognized.

Equus capensis (Broom, 1909)

The extinct *E. capensis* (Figure 6) is represented at the GVED by at least three individuals. In addition some postcranial elements consisting of accessory podials and carpals have been assigned to this taxon.

Equus burchelli (Gray, 1824)

This species is less numerous, represented by two individuals from an NISP of four (Figure 6). Some postcranial material has been assigned to this species.

Order Hyracoidea
Family Procaviidae

Procavia capensis (Pallas, 1766)

The GVED material attributed to this species consists of dental material and post-cranial elements that are indistinguishable from the modern hyrax. This species appears during the Pleistocene, being first recorded at the Haasgat site (Plug & Keyser 1994b). At least two individuals are present in the GVED assemblage.

Procavia transvaalensis Shaw, 1937

The extinct *P. transvaalensis* is the largest species of this genus, being about one and a half times the size of the living hyrax (Brain 1981). A maxillary fragment with teeth and three humeri have been assigned to this species. At least two individuals are represented in the GVED assemblage.

Order Rodentia
Family Hystricidae

Hystrix africaeaustralis (Peters, 1852)

The extant species represented in the southern African region is *H. africaeaustralis*. All specimens found at GVED have been assigned to this taxon on the basis of the morphological similarities between the material from GVED and the modern form.

Order Lagomorpha
Family Leporidae

All the material from the GVED was classified as Lagomorpha indet.

SUMMARY AND DISCUSSION

The complex nature of the sedimentary processes in the Plio-Pleistocene cave deposits of the Witwatersrand often results in the formation of indistinct sedimentary units which lack clear stratigraphy (Kuman & Clarke 2000). However, the case of Gladysvale is different in that the stratigraphy of this site has been a key feature in the modelling of stratigraphic profiles not commonly applied to geological studies of cave infills in the area. Results obtained indicate that in sections of the exposed sediments of the GVED, sedimentary packages bounded at the top and bottom by speleothem layers can be used as discrete geological units. Fossil material contained within these units has been dated by ESR establishing a broad chronological sequence of sediment deposition in this section.

Palaeoenvironmental interpretations of the GVED fossil assemblage from the decalcified breccias based on the present stratigraphic model have to be approached cautiously. If it is considered that the overall climatic regime prevailing during the Pleistocene is characterized by cycles of glacial and interglacial periods (Shackelton 1995; Tyson & Partridge 2000), it is probable that the excavated fossils from the GVED reflect more than a single environmental event. Therefore, it is not possible to discern from the fossil assemblage excavated from the decalcified deposits the prevailing habitat type, nor the predominant species present through time. However, it may be broadly stated that based on the species represented, there seems to be an overall indication of open edaphic and secondary grasslands. The analysis of fossils and sediments still contained in the *in situ* cemented breccias of the GVED may help to elucidate possible habitat or climatic changes through time.

Comparisons between the present study and other faunal studies previously documented from Gladysvale indicate that the previously proposed degree of faunal diversity (Berger & Tobias 1994), especially in the Family Bovidae, is supported by the recently excavated fossil material. New additions to previous faunal lists from Gladysvale include *Procavia capensis* and cf. *Oryx gazella*. In contrast to previous records from the site, no *Hipparion* material has been recovered from the GVED but, as previously documented (Berger *et al.* 1993), the giant cape zebra (*Equus capensis*) is widely represented. No further fossilized seeds have been identified and no Pliocene hominin, suids, monkeys or carnivore taxa previously recorded from the Gladysvale *ex situ* material (Berger *et al.* 1993) are associated with the GVED. This indicates faunal differences between the deposits and confirms Berger & Tobias (1994) and Schmid & Berger (1997) previous age estimates of younger infills in the Gladysvale Cave System.

The estimated age of the exposed sediments of the GVED ranges from 578 ky to 780 ky. Therefore, based on interpretations of the geology, fauna and dating, it seems clear that the fossiliferous deposits from the Gladysvale Cave System (not restricted to the GVED) represent temporal periods that range from the Late Pliocene through to the Middle Pleistocene and possibly younger.

A provisional chronological placing of the GVED faunal assemblage in relation to other Pleistocene aged deposits in the Witwatersrand is shown in Figure 7. No sites possibly older than 1.5 Ma are included in this Figure.

The ungulate fauna of the Haasgat assemblage is very similar in composition and diversity to the GVED, particularly the bovid species. The main differences are the possible presence of impala and oryx at the GVED which are absent from Haasgat. Based on the presence of antelope species, the environmental characteristics implied by the represented taxa at both sites indicates a high degree of similarity. However, the Haasgat assemblage differs in the abundance and diversity of primate and the hyaena species (see e.g. Keyser, 1991; McKee & Keyser 1994; von Mayer 1998). Plug and Keyser (1994b) estimated the age of Haasgat to be not older than ca.1.5 Ma based mainly on the presence of lechwe, which appears at radiometrically dated deposits in the Lake Turkana area ca. 1.62 to 1.33 Ma (Feibel, Brown & McDougall 1989; Harris & Leakey 1993). The youngest age of Haasgat was established at ca. 0.5 Ma (Plug & Keyser 1994b). The presence of the extinct hyaenid *Chasmaporthetes* probably indicates an age for this deposit considerably older than 0.5 Ma, based on extinction patterns in Africa of Pliocene carnivores broadly established to ca. 1.5 Ma (Turner 1986). However, some of this material came from dumps and therefore may represent mixed assemblages of differing ages. No extinct primate or carnivore taxa have been positively identified from the controlled excavations of the GVED to date.

The Plovers Lake ungulate assemblage has been dated to ca. 1.0 Ma (Thackeray & Watson 1994) based on the presence of the suid *Metridiochoerus andrewsi* and the rodent species *Mus minutoides*. The overall composition of the Plovers Lake assemblage is similar to that of the GVED, although it differs in the presence of *Metridiochoerus* in the former. The last appearance of *M. andreiusi* is recorded at Olduvai Beds III (Cooke & Williamson 1978), dated to ca. 800ky (Brown 1994), although other dates have been proposed (see e.g. Thackeray & Watson 1994). However, this locality within the Plovers Lake Farm remains fairly unexcavated.

The new site of Motsetse (Berger & Lacruz in press) has been provisionally dated to ca. 1.6 to 1.0 Ma because of the presence of *Dinofelis* cf. *piveteaui*. The last appearance of this taxon is dated to ca. 1.0 Ma (Ditchfield *et al.* 1999), which may indicate an older age of the Motsetse assemblage than the exposed breccias of the GVED. However, the available information on the faunas from Motsetse is fairly restricted.

The Lincoln Cave North (LCN) assemblage at Sterkfontein has been dated to ca. 253 ky to 115 ky (Reynolds 2000). With the exception of the possible presence of bushbuck and grey rhebok in this assemblage (Reynolds 2000), the reduced list of remaining taxa at LCN is similar to the GVED. However, it must be noted that the LCN deposit may have been reworked because of the presence of early stone-age tools in the assemblage. The nearby deposit of Lincoln Cave South (LCS) supports this idea based on the presence of *Australopithecus robustus*, *Homo ergaster* and middle stone-age tools in this assemblage (Reynolds 2000).

Other deposits in the Witwatersrand which have been dated to ca. 1.0 Ma are Swartkrans 3 (Brain 1995) and Kromdraai A (see e.g. Kuman *et al.* 1997). However, the occurrence of extinct primate, suid and carnivore taxa at KA, including *Homotherium* which is last recorded in Africa in the Kaitio Member of West Turkana (Turner *et al.* 1999) dated to ca. 1.6 Ma (Harris *et al.* 1988), may suggest an age for this deposit older than 1.0 Ma. Turner (1997) considers that the faunal age of SK3 is broadly similar to Members 1& 2, dated by Brain (1995) to ca. 1.5 Ma and older. Therefore it seems likely that these deposits are older than 1.0 Ma and not contemporaneous with the exposed sections of the GVED.

The faunal composition of the Gladysvale assemblage is essentially Florisian in character with no typically Cornelian taxa, such as hipparions or extinct suids. With the exception of the kudu, all the bovid taxa of the Gladysvale assemblage are represented in the Florisbad spring faunal list (Brink 1987; Brink & Henderson 2000).

Work at Gladysvale will continue, focusing on fossil deposits bordering the GVED which are believed to be exposed sections of the original talus cone. If the interpretations of the geology of this area are correct, it is likely that older sediments, possibly contemporaneous with early members of Sterkfontein and Swartkrans, will be uncovered.

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REFERENCES

AITKEN, M. 1990. *Science-based Dating in Archaeology*. London, Longmans, pp.274.

AVERY, M. 1995. A preliminary assessment of the micromammalian remains from Gladysvale cave, South Africa. *Palaeontologia africana* **32**, 1-10.

BERGER, L.R. 1992. Early hominid fossils discovered at Gladysvale Cave, South Africa. *South African Journal of Science* **88**, p.362

BERGER, L.R. 1993. A preliminary estimate of the age of the Gladysvale australopithecine site. *Palaeontologia africana* **30**, 51-55.

BERGER, L.R., KEYSER, A.W. & TOBIAS, P.V. 1993. Brief communication: Gladysvale: First early hominid site discovered in South Africa since 1948. *American Journal of Physical Anthropology* **92**, 107-111.

BERGER, L.R. & TOBIAS, P.V. 1994. New discoveries at the early hominid site of Gladysvale, South Africa. *South African Journal of Science* **90**, 223-226.

BERGER, L.R. & LACRUZ, R. (in press). Preliminary report of the first excavations at the new fossil site of Motsetse, Gauteng. *South African Journal of Science*.

BERNOR, R.L. & ARMOUR-CHELU, M. 1999. Towards an evolutionary history of African hipparionine horses. **In:** Bromage, T.G. & Schrenk, F. (eds), *African Biogeography, Climate Change and Human Evolution*, 189-215. New York, Oxford University Press.

BLACKWELL, B.A.B., SKINNER, A.R. & BLICKSTEIN, J.I.B. 2001. ESR isochron exercises: How accurately do modern dose rate measurements reflect paleodose rates? *Quaternary Science Reviews (Quaternary Geochronology)* **20:** 1031-1039.

BLACKWELL, B.A.B., ROSENWASSER, N.L., BLICKSTEIN, J.I.B & SKINNER, A.R. (in press). **In:** Doronichev, V.B. (ed), *The Excavations at Treugol'naya Cave, Northern Caucasus, Russia*. Laboratory of Prehistory, St Petersburg.

BRAIN, C.K. 1981. *The Hunters or the Hunted, an Introduction to African Cave Taphonomy*. Chicago, University of Chicago Press.

BRINK, J.S. 1987. The archaeozoology of Florisbad, Orange Free State. *Memoirs van die Nasionale Museum*. 24

BRINK, J.S. 1993. Postcranial evidence for the evolution of the black wildebeest, *Connochaetes gnou*: an exploratory study. *Palaeontologia africana* **30**, 61-69.

BRINK, J.S. 1999. Preliminary report on a caprine from the Cape mountains, South Africa. *Archaeozoologia* **X**, 11-26.

BRINK, J.S., de BRUIYN, H., RADEMEYER, L.R. & van der WESTHUIZEN, W.A. 1995. A new find of *Megalotragus priscus* (Alcelaphini, Bovidae) from the Central Karoo, South Africa. *Palaeontologia africana* **32**, 17-22

BRINK, J.S. & HENDERSON, Z.L. 2000. A high resolution Last Interglacial MSA Horizon at Florisbad in the context of open-air occurrences in the central interior of southern Africa: an interim statement. **In**: Conard, N (ed.) *Middle Palaeolithic and Middle Stone Age Settlement Sytems*. Kens Verslag, Tuebingen, 1-20.

BROWN, F.H. 1994. Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites **In:** Coruccini, R.S. & Ciochon, R.L (eds) *Integrative Paths to the Past*, Prentice Hall, New Jersey, 285-312.

CANDE, S. & KENT, D.V.J. 1995. Revised calibration of the geomagnetic polarity timescale for the late Cretaceous and Cenozoic. *Journal of Geophysical Research* **100**, 6093-6098.

CHURCHER, C.S. & RICHARDSON, M.L. 1978. Equidae. **In:** Maglio, V.J. & Cooke, H.B.S. (eds), *Evolution of African Mammals*. Cambridge, Harvard University Press.

COOKE, H.B.S. 1963. Pleistocene mammal faunas of Africa, with particular reference to S. Africa. **In:** Howell, F.C. & Bouliere, F.(eds), *African Ecology and Human Evolution*, 65-116. Chicago, Aldine.

COOKE, H.B.S. 1978. Faunal evidence for the biotic setting of early African hominids. **In:** Jolly, C. (ed.), *Early Hominids of Africa*, 267-284. New York, St. Martins.

COOKE, H.B.S. & WILKINSON, A.F. 1978. Suidae and Tayasuidae. **In:** Maglio, V.J & Cooke, H.B.S. (eds), *Evolution of African Mammals*. Cambridge, Harvard University Press.

DE RUITER, D.J. 2001. *A Methodological Analysis of the Relative Abundance of Hominids and Other Macromammals from the Site of Swartkrans, South Africa*. Unpublished PhD Thesis. University of the Witwatersrand, Johannesburg.

DE RUITER, D.J. in press. Revised faunal lists for Members 1-3 of Swartkrans, South Africa. *Annals of the Transvaal Museum*.

DITCHFIELD, P., HICKS, J., PLUMMER, T., BISHOP, L.C. & POTTS, R. 1999. Current research on the Late Pliocene deposits north of Homa Mountain, southwestern Kenya. *Journal of Human Evolution*, **36**:123-150.

ESTES, R.D. 1993. *The Safari Companion*. South Africa. Russel Friedman Books.

FEIBEL, C.S, BROWN, F.H. & McDOUGALL, I. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* **78,** 595-622.

GENTRY, AW. 1970. Revised classification for *Makapania broomi*, Wells & Cooke (Bovidae, Mammalia). *Palaeontologia africana* **13,** 63-67.

GENTRY, A.W. 1978. Bovidae. **In:** Maglio, V.J & Cooke, H.B.S.(eds), *Evolution of African Mammals*. Cambridge, Harvard University Press.

GENTRY, A.W. 1992. The Sub-Families and Tribes of the Family Bovidae. *Mammal Review* **22** (1),1-32.

GERAARDS, D. 1981. Bovidae et Giraffidae (Mammalia: Artyodactila) du Pleistocene du Ternifine (Algerie). *Bulletin Museum National d'Histoire Naturelle, Paris* **4**(3):47-86.

GRUN, R. (2000). An alternative model for open systems U- series/ESR age calculations: (closed system U-series)-ESR, CSUS-ESR. *Ancient TL* **18,** 1-4.

HARRIS, J.M., BROWN, F.H. & LEAKEY, M.G. 1988. Stratigraphy and palaeontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science*, Number 399. Natural History Museum of Los Angeles County.

HARRIS, J.M. & LEAKEY, M. 1993. The faunal context. **In:** Walker, A & Leakey, R.E.F. (eds) *The Nariokotome* Homo erectus *skeleton*. Cambridge, Harvard University Press, 54-62.

IKEYA, M. 1993. New applications of Electron Spin Resonance. *World Scientific*, Singapore. p. 500.

KEYSER, A.W. 1991. The palaeontology of Haasgat: a preliminary account. *Palaeontologia africana* **28,** 29-33.

KLEIN, R.G. & CRUZ-URIBE, K. 1991. The bovids from Elandsfontein, South Africa, and their implications for the age, palaeoenvironment and origins of the site. *African Archaeological Review* **9,** 21-79.

KUMAN, K., FIELD, A.S. & THACKERAY, J.F. (1997). Discovery of artefacts at Kromdraai. *South African Journal of Science* **93,** 187-193.

KUMAN, K. & CLARKE, R.J. 2000. Stratigraphy, artefacts industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution* **38,** 827-847.

LACRUZ, R.S. 2002. *Analysis of Stratified Fossil Deposits from the Gladysvale Cave, South Africa.* Unpublished M.Sc. Thesis. University of the Witwatersrand, Johannesburg.

MARTINI, J.E.J. & KEYSER, A.W. 1989. The caves of the John Nash Game Reserve. *Bulletin of the S. A. Speleological Association*. **30,** 39-46.

McKEE, J.F & KEYSER, A.W. 1994. Craniodental remains of *Papio angusticeps* from Haasgat Cave. *International Journal of Primatology* **15**(6),823-841.

MORIARTY, K.C., McCULLOCH, M.T, WELLS, R.T. & McDOWELL, M. C. 2000. Mid-Pleistocene cave fills, megafaunal remains and climate change at Naracoorte, South Australia: Towards predictive model using U-Th dating of speleothems. *Palaeogeography, Palaeoclimatology, Palaeoecology* **159,** 113-143.

MUTTER, R.J., BERGER, L.R. & SCHMID, P. 2001. New evidence of the giant hyaena, *Pachyocrocuta brevirostris* (Carnivora: Hyaenidae), from the Gladysvale Cave Deposit (Plio-Pleistocene, John Nash Nature Reserve, Gauteng, South Africa).
Palaeontologia africana **37,** 103-113.

PADDAYA, K., BLACKWELL, B.A.B., JHALDIYAL, R., PETRAGLIA, M.D., FEVRIER,S., CHADERTON, D.A., BLICKSTEIN, J.I.B. & SKINNER, A.R., 2002. Recent findings on the Acheulian of the Hungsi and Baichbal valleys, Karnataka, with special reference to the Isampur excavation and its dating. *Current Science* **83,** 641-647.

PLUG, I. & KEYSER, A.W. 1994a. A preliminary report on the bovid species from recent excavations at Gladysvale. *South African Journal of Science* **90,** 357-359.

PLUG, I. & KEYSER, A.W. 1994b. Haasgat cave, a Pleistocene site in the Central Transvaal: Geomorphological, faunal and taphonomic considerations. *Annals of the Transvaal Museum* **36** (9), 139-145.

REED, K.E. 1996. *The Palaeoecology of Makapansgat and other African Plio-Pleistocene Hominid Localities.* Unpublished PhD Dissertation. State University of New York at Stony Brook.

REYNOLDS, S.C. 2000. *Sterkfontein: Exploration of Some Lesser Known Archaeological and Fossil Deposits.* MSc Thesis, University of the Witwatersrand, Johannesburg.

RINK, W. J. 1997. Electron Spin Resonance (ESR) dating and ESR applications in Quaternary science and archaeometry. *Radiation Measurements* **27,** 975-1025.

SHACKELTON, N.J. 1995. New data on the evolution of Pliocene climatic variability. **In:** Vrba, E.S., Denton, G.H., Partridge, T.C. & Burckle, L.H. (eds) *Palaeoclimate and Evolution with Emphasis on Human Evolution,* 242-248. New Haven and London, Yale University Press.

SCHMID, P. & BERGER, L.R. 1997. Middle Pleistocene hominid carpal proximal phalanx from the Gladysvale site, South Africa. *South African Journal of Science* **93,** 430-411.

SKINNER, A. 2000. ESR dating: Is it still an "experimental" technique? *Applied Radiation and Isotopes,* **52,** 1311-1316.

THACKERAY, J.F & WATSON, V. 1994. A preliminary account of faunal remains from Plovers Lake. *South African Journal of Science* **90,** 231-232.

TURNER, A.1986. Some features of African larger carnivore historical biogeography. *Palaeoecology of Africa and the Surrounding Islands*, **17**,237-244.

TURNER, A. 1997. Further remains of Carnivora (Mammalia) from the Sterkfontein Hominid Site. *Palaeontologia africana* **34,** 115-126.

TURNER, A., BISHOP, A.C., DENYS, C. & McKEE, J.K. 1999. A locality-based listing of African Plio-Pleistocene Mammals. **In:** Bromage, T. & Schrenk, F. (eds), *African Biogeography, Climate Change and Human Evolution*. Appendix pp 369-399.

TYSON, P. D. & PARTRIDGE, T.C. 2000. Evolution of Cenozoic climates. **In:** Partridge, T.C.& Maud, R.R. (eds), *The Cenozoic in Southern Africa* 371-387. Oxforn, Oxford Press.

VON MAYER, A. 1998. *A Reassessment of Cercopithecoides in Southern Africa.* Unpublished MSc Dissertation, University of the Witwatersrand, Johannesburg.

VRBA, E.S. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoir* **21**.

VRBA, E.S. (1980). The significance of bovid remains as indicators of environment and predation patterns. **In:** Behrensmeyer, A.K. & Hill, A.P. (eds) *Fossils in the Making*, 247-271. Chicago, University of Chicago Press.

VRBA, E.S. 1984. Evolutionary Patterns and Processes in the Sister-Group Alcelaphini-Aepycerotini (Mammalia: Bovidae). **In:** Eldredge, N. (ed.) *Living Fossils*, pp.62-79. New York, Springer.

VRBA, E.S. 1987. A revision of the Bovini (Bovidae) and a preliminary revised checklist of the Bovidae from Makapansgat. *Palaeontologia africana* **26**(4), 33-46.

VRBA, E.S. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and palaeoclimate. **In:** Vrba, E.S., Denton, G. H., Partridge, T.C.& Burckle, L. H. (eds), *Palaeoclimate and Evolution with Emphasis on Human Origins*, 385-424. New Haven and London. Yale University Press.

WELLS, L.H. & COOKE, H.B.S. 1956. Fossil Bovidae from the Limeworks Quarry, Makapansgat, Potgietersrus. *Palaeontologia africana* **4**, 1-55.