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Journal Title: *Changing climates,
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within arid southern Africa and
adjoining regions /*

Volume: Issue:

Month/Year: 2015

Pages: 71-

Article Author: Brink, James

Article Title: A reconstruction of the skull of
Megalotragus priscus (Broom, 1909), based on a
find from Erfkroon, Modder River, South Africa,
with notes on the chro

ISSN: 9781138027046

OCLC #: 912377434

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CHAPTER 6

A reconstruction of the skull of *Megalotragus priscus* (Broom, 1909), based on a find from Erfkroon, Modder River, South Africa, with notes on the chronology and biogeography of the Species

James S. Brink

*Florisbad Quaternary Research Department, National Museum,
Bloemfontein, South Africa
Centre for Environmental Management, University of the Free State.
Bloemfontein, South Africa*

C. Britt Bousman

*Department of Anthropology, Texas State University, San Marcos,
Texas, USA
GAES, University of the Witwatersrand, Johannesburg, South Africa*

Rainer Grün

*Research School of Earth Sciences, The Australian National University,
Canberra, Australia*

ABSTRACT: A reconstruction of the skull of the giant aelaphine bovid, *Megalotragus priscus*, is provided based on a brain case and horn cores discovered and excavated at the late Florisian locality of Erfkroon on the Modder River, central Free State Province, South Africa. The sedimentary context of the *M. priscus* specimen can be correlated with fluvial deposits dated previously by luminescence to the Last Interglacial. Electron Spin Resonance (ESR) analyses of dental specimens from various localities at Erfkroon indicate a terminal Middle Pleistocene and Late Pleistocene age for these deposits. The skull reconstruction of *M. priscus* is aided by an upper jaw and mandible from the Late Pleistocene locality of Mahemspan. The *M. priscus* materials from Erfkroon, Mahemspan and other localities allow a re-evaluation of the morphological affinities of the species and it appears to be closer to wildebeest-like aelaphines (genus *Connochaetes*) than to hartebeest-like aelaphines (genera *Alcelaphus* and *Damaliscus*). Variability in the fossil horn cores suggests sexual dimorphism and some degree of territorial behaviour. It also suggests geographic variability in the populations of *M. priscus* in central southern Africa during the later part of the Middle Pleistocene and Late Pleistocene, before its extinction at the end of the Late Pleistocene and early Holocene.

6.1 INTRODUCTION

The terraces of the Vaal River are well-known for producing abundant vertebrate fossils that span the Plio-Pleistocene and younger geological ages (Helgren, 1977). The tributaries of the Vaal River, such as the Modder and Riet Rivers, are equally rich in Quaternary fossil vertebrates and archaeological materials. The Modder and the Riet Rivers have lower-gradient longitudinal profiles than the Vaal River (Tooth *et al.*, 2004), flowing over less-resistant bedrock and forming floodplain deposits controlled by igneous barriers, mostly dolerite. These floodplain deposits become eroded as the rivers incise, cutting through dolerite barriers, and in the process the fossil contents of the floodplain deposits are exposed in erosional areas, locally known as dongas. Such erosional areas can be extremely rich sources of vertebrate fossils and archaeological materials. On two adjacent farms on the Modder River, "Erfkroon" and "Orangia" (Figure 1; Churchill *et al.*, 2000; Lyons *et al.*, 2014), extensive fossil exposures were discovered in June 1996 during routine reconnaissance by the Florisbad Quaternary Research Department of the National Museum, Bloemfontein. One of the first major discoveries on the farm "Erfkroon" was a skull and horn cores of a giant aelaphine antelope, *Megalotragus priscus* (Broom, 1909). This find is unusually complete with a well-preserved braincase attached to the horn cores, which provides the opportunity of improved understanding of the skull morphology and affinities of the species. The aim of this contribution is to provide a description of this find, its sedimentary context and age estimates based on Electron Spin Resonance analyses (ESR). A reconstruction of the skull of *M. priscus* is proposed, which is based on the Erfkroon specimen and assisted by a complete mandible and a maxillary fragment from a pan site in the central Free State Province, known as "Mahemspan" (Figure 1). The fossil materials from Mahemspan were discovered and excavated in the late 1930's and 1940's by staff of the National Museum (Hoffman, 1953), and in this contribution we also provide a summary taxonomic list and ESR age estimates for this fossil occurrence.

Although the general awareness of the importance of the tributaries of the Vaal River as sources of Quaternary fossils became somewhat diminished in the second half of the 20th century (Cooke, 1964; Klein, 1984), the early development of the field of Quaternary Palaeontology in South Africa was closely linked to the Modder River. During the 19th and early 20th centuries the Modder River deposits produced the first recorded discoveries of Pleistocene fossils in South Africa. In 1839 a giant long-horned buffalo (*Synacerus antiquus*) was found in the banks of the Modder River and reported to the Geological Society of London (Seeley, 1891). A few years later Broom described the second major find of an extinct Pleistocene mammal from the Modder River sequence—a giant aelaphine, which he named *Bubalis priscus* (Broom, 1909), now referred to the genus *Megalotragus* Van Hoepen (Gentry and Gentry 1978). The stretch of the Modder River that produced these fossils is situated between the present-day Kruger's Drift Dam and the confluence of the Modder and the Riet Rivers (Figure 1), which is in the same general area where the Erfkroon fossil sites are situated. Thus, it is noteworthy that both the Erfkroon find reported here and the type specimen of *M. priscus* are from essentially the same stretch of fossil deposits of the Modder River and they are probably of comparable geological age. Broom's type specimen from the Modder River lacks much of the distal parts of the horn cores and the braincase is not complete. The Erfkroon specimen complements the type specimen and extends our understanding of the species.

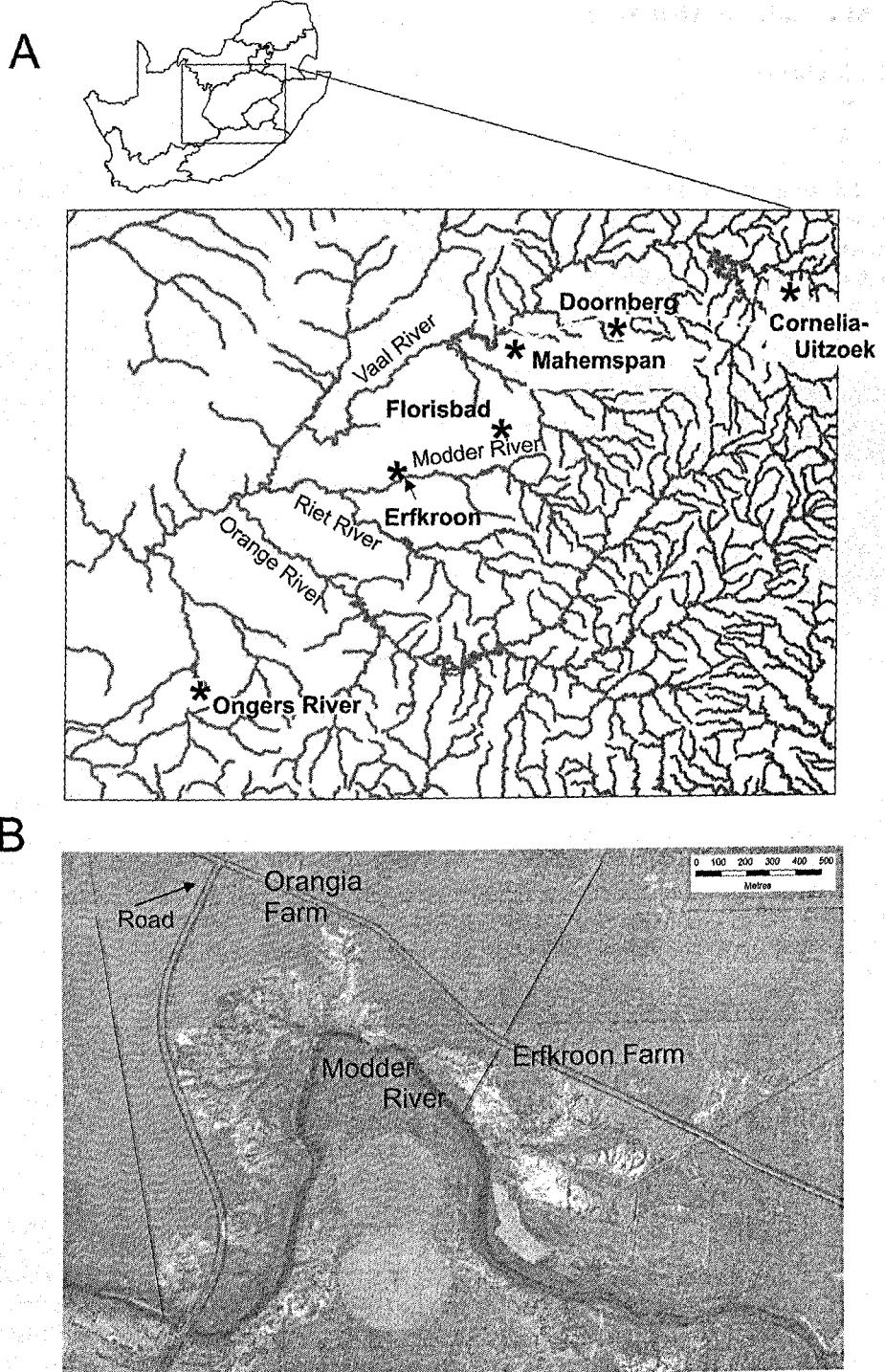


Figure 1. A map illustrating the geographic position of the localities with *Megalotragus*, as referred to in the text (A) and a plan view the fossil-bearing exposures on the farms Orangia and Erfkroon (B).

6.2 MATERIALS AND METHODS

6.2.1 Mahemspan

In the late 1930's and early 1940's E.C. Van Hoepen and A.C. Hoffman from the National Museum, Bloemfontein, excavated a large faunal sample from the lunette of Mahemspan ($27^{\circ}45'50''$ S; $26^{\circ}08'50''$ E; Figure 1), situated between Hoopstad and Wesselsbron, Free State Province (Unpublished reports in library of the National Museum). In 1994 one of us (JSB) visited the site and the approximate position of the excavation was relocated through the help of Mrs. De Villiers, the owner of the farm. She was present when Van Hoepen and Hoffman conducted their excavations. Fossil specimens in the same state of preservation as in the collections at Florisbad Quaternary Research Station were found on the surface. Unfortunately a trial excavation did not reveal any *in situ* materials. The site is now covered by aeolian sand, as was the case before the material was exposed by wind action during the intense droughts of the 1930's. The site is now part of a ploughed land.

The *in situ* fossil materials collected by Van Hoepen and Hoffman were found at the base of the lunette and the original death assemblage appears to have been deposited in a marsh-like area in the presence of calcium carbonate-rich groundwater. This is evident from the extensive presence of calcrete deposits in and on the fossils. The fossil matrix, which is still attached to many specimens in the old collection due to cementation by calcium carbonate, is a pale-brown, partly calcified sand. This was used to establish the background radiation for the ESR measurements.

6.2.2 Erfkroon

After the discovery of fossil-bearing deposits on the farms Erfkroon and Orangia (Figure 1), collectively referred to as "Erfkroon", luminescence dating and sediment analysis (Churchill *et al.*, 2000; Tooth *et al.*, 2013; Lyons *et al.*, 2014; Table 1) suggest that the bulk of the deposits on the farm Orangia represents a Late Pleistocene fluvial terrace. We have named it the "Orangia" Terrace (Figures 2 and 3), and it has both channel and overbank facies. The channel facies sit unconformably on Ecca Bedrock and make up the lower two horizons of the terrace, the Lower Gravel and the Green Sand. The Lower Gravel is composed of small-to-large subrounded to rounded shale and calcium carbonate gravels supported by a dark olive-brown clayey-sand matrix.

Table 1. A comparative list of OSL and IRSL dates (ka) from the Orangia Terrace, as given in previous studies.

	OSL (Lyons <i>et al.</i> , 2014)	OSL (Tooth <i>et al.</i> , 2013)	IRSL (Tooth <i>et al.</i> , 2013)	IRSL (Churchill <i>et al.</i> , 2000)
Brown	$0.83 \pm 0.09 - 6.32 \pm 0.67$			
Upper Grey	$11.3 \pm 0.98 - 19.5 \pm 1.04$			25 ± 1.2
Red	$20.0 \pm 1.19 - 32.2 \pm 1.74$	32 ± 2	29 ± 2	
Lower Grey	$40.1 \pm 2.30 - 43.5 \pm 3.18$	42 ± 2	42 ± 3	
Green Sand			118 ± 35	113 ± 6
Lower Gravel				163 ± 7

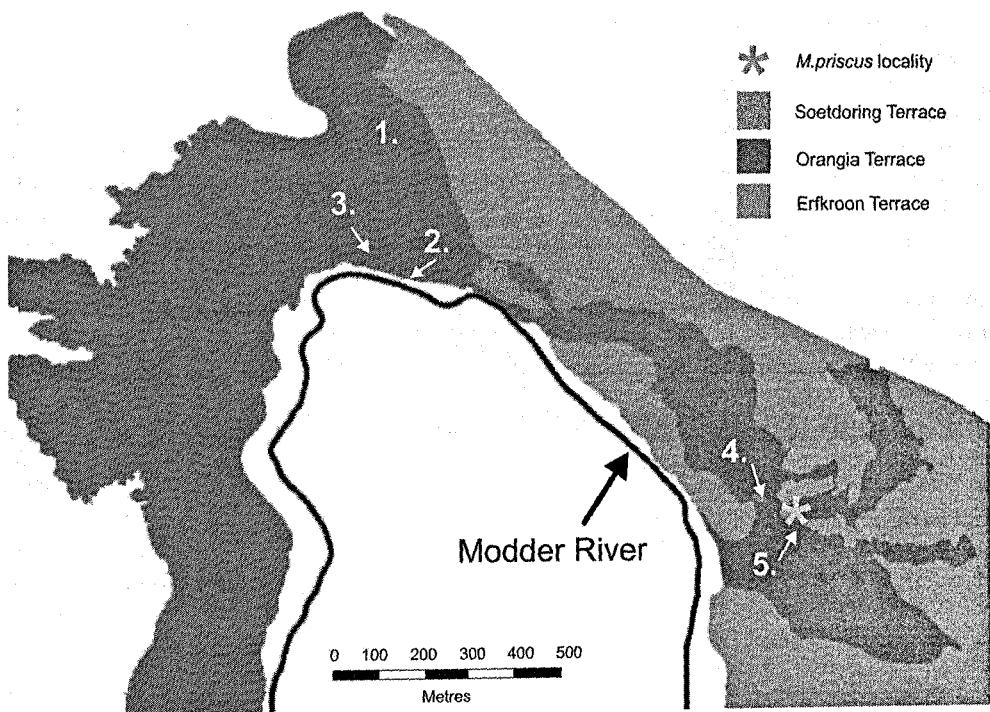


Figure 2. A plan view of the Erfkroon sedimentary deposits, showing the approximate lateral extent of the Erfkroon and Orangia Terraces, the ESR sampling localities and the find locality of the *Megalotragus priscus* specimen. The numbers of the ESR localities correspond to the numbers in Table 4 and in Figure 3.

It is truncated by erosion which forms an unconformity on its upper surface. The Lower Gravel is classified as a C soil horizon. Above this is the Green Sand, which is composed of small Ecca shale pebbles supported in a silty sand to very fine sand matrix. Iron staining is common and highlights tilted lamella and thin beds. Both of these layers reflect fluvial channel deposition. The top of the Green Sand also is truncated by erosion to form another unconformity. This is also a C soil horizon.

Above this unconformity are the overbank facies consisting of the Lower Grey, Red, Upper Grey, and Brown palaeosols. The Lower Grey sediments are yellowish brown to strong brown alternating sand and clay laminae grading up to a clay loam. Calcium carbonate nodules increase upwards in the profile in frequency and size. The Lower Grey grades into the lower part of the Red, which shifts to a yellowish red very firm sandy loam with coarse moderate subangular blocky structure and with no calcium carbonate nodules. It is bound by unconformities on the top and bottom.

The upper part of the Red is a yellowish red sandy loam with coarse, weak subangular blocky structure. It grades into the Upper Grey from a strong brown to light yellowish brown firm loams to sandy loams. Calcium carbonate nodules are absent in the bottom of the Upper Grey, slowly increase in density and size upwards in the profile and then decline at the top of the horizon. The Brown palaeosol overlies the Upper Grey and grades from a strong brown to dark brown loam with declining amounts of calcium carbonate nodules upwards in the profile.

The Orangia Terrace is covered by a thin (~25 cm) aeolian deposit, which corresponds with the "Sandy Cap" of Lyons *et al.* (2014) and we have named it the "Soetdoring Terrace". The Soetdoring Terrace has not been described in detail, but preliminary

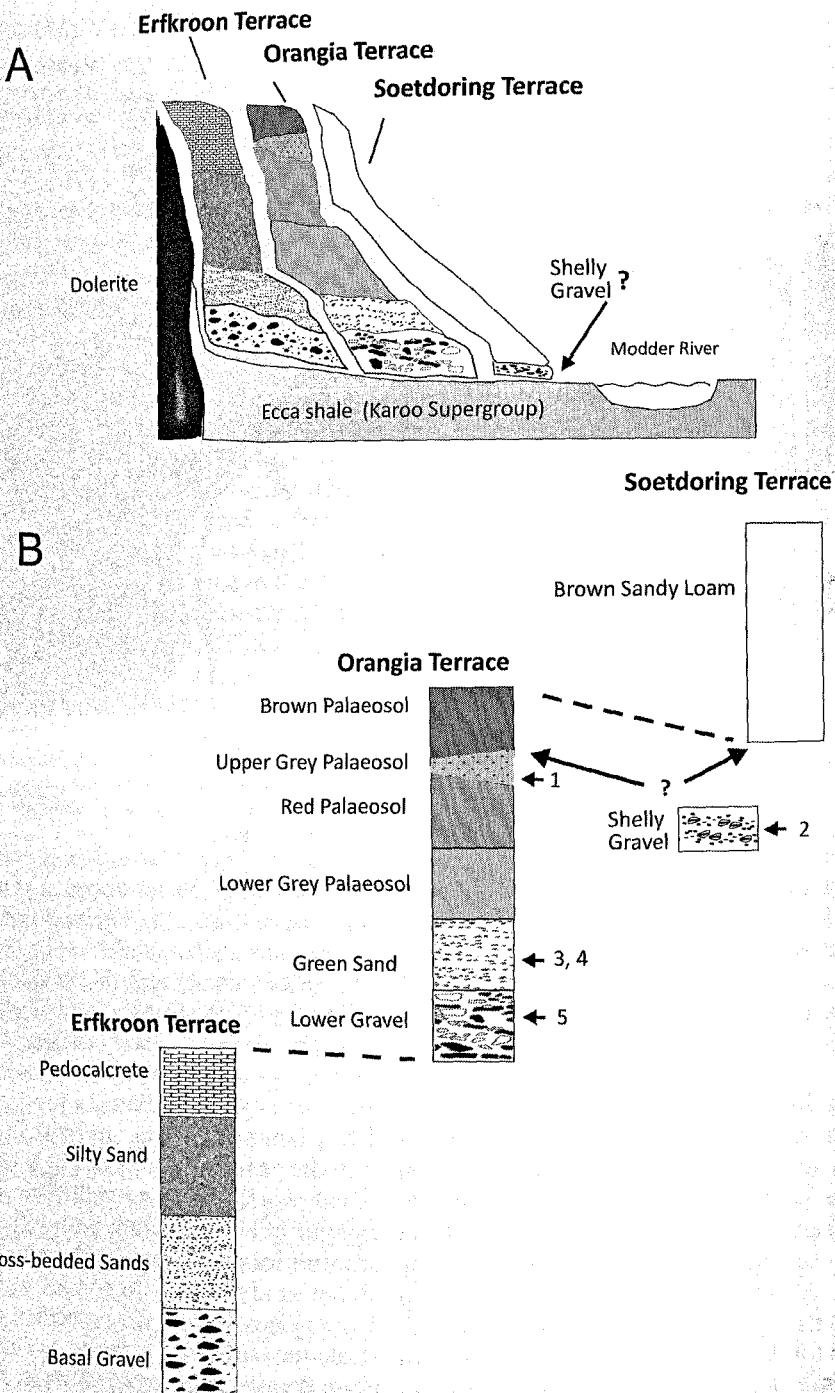


Figure 3. A diagram illustrating our current interpretation of the terrace deposits of the Modder River, as seen on the farms "Erfkroon" and "Orangia" (A). The Erfkroon, Orangia and Soetdoring terraces reflect sequential and possibly, marginally overlapping periods of deposition (B). We are at present uncertain of the correct stratigraphic position of the Shelly Gravel as either a lateral facies of the Upper Grey of the Orangia Terrace or the basal horizon of the Soetdoring Terrace. The numbers and arrows indicate ESR sampling points, as illustrated in Figure 2.

observations indicate that it is a light brown sandy loam with at least two buried soils that consist of dark brown to strong brown loams. This deposit becomes deeper towards the present-day channel of the Modder River, where it appears to be underlain by a shelly, fossil-rich gravel deposit, referred to as "Sandy gravel with bivalves" (Lyons *et al.*, 2014). The bivalves in this deposit occur articulated and, therefore, they are untransported and not redeposited and must post-date the depositional event that produced the gravel horizon. For the present purpose we refer to this horizon informally as the "Shelly Gravel" (Figure 3). We are uncertain whether it forms the basal horizon of the Soetdoring Terrace or whether it is a lateral facies of the Upper Grey of the Orangia Terrace.

Upstream from Orangia, on the farm of Erfkroon, the Late Pleistocene overbank component of the sedimentary package is less well developed, but numerous fluvial gravel outcrops proved to be highly fossiliferous. Some of these outcrops are thought to be older than the Orangia Terrace deposits and these are collectively referred to as the "Erfkroon Terrace". These can easily be distinguished by the lack of carbonate clasts so common in the Lower Gravel of the Orangia Terrace. The Erfkroon Terrace deposits include four lithostratigraphic units. From bottom to top these are the Basal Gravel, Cross-Bedded Sand, Silty Sand and Pedocalcrete (Figure 3). These deposits have not been described in detail, but it is important to note that the Basal Gravel completely lacks carbonate clasts, which are a significant component of the Orangia Terrace Lower Gravel. We believe that the overlying Pedocalcrete horizon of the Erfkroon Terrace is the source of the carbonate clasts in the Lower Gravel of the Orangia Terrace.

The *M. priscus* specimen was found embedded in the Lower Gravel at the contact with the overlying Green Sand (Figure 4). Its original orientation of deposition was

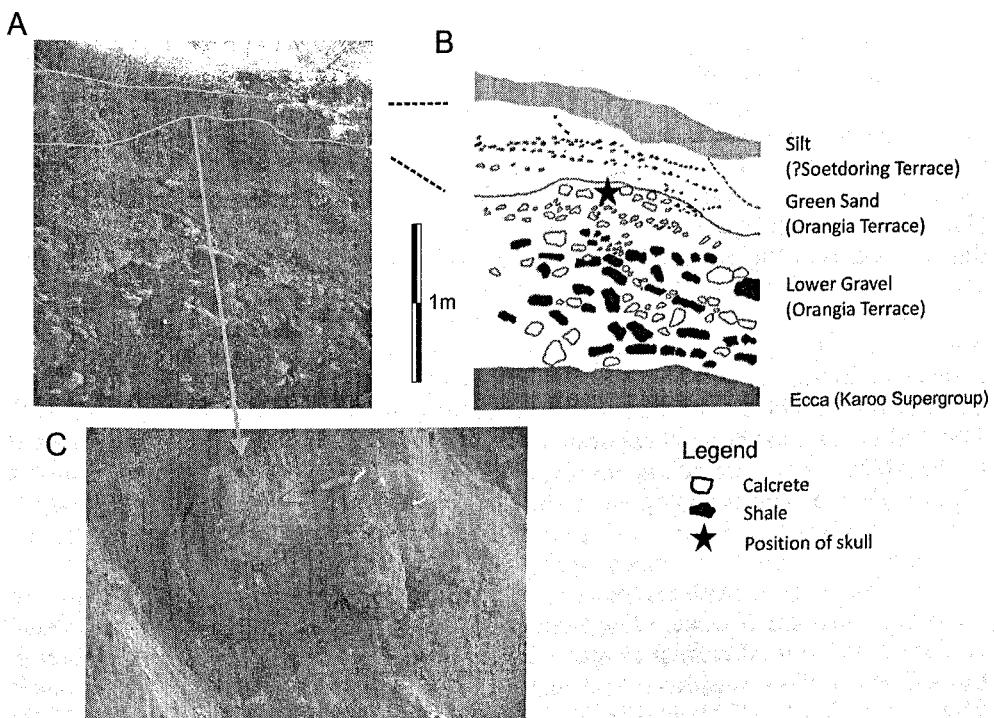


Figure 4. The exposed sedimentary profile of the outcrop, showing the *in situ* position of the skull of *M. priscus* (A), a diagram of the profile, illustrating the *in situ* position of the skull at the contact between the Lower Gravel and the Green Sand (B) and the skull being exposed during excavation (C).

with the horns down and the snout facing upwards. However, the upper dentitions and premaxillae were not preserved and their position would have coincided with the contact between the Lower Gravel and the overlying Green Sand, suggesting that these parts of the skull were eroded away some time after deposition or during the deposition of the Green Sands. The left horn core was broken off and was recovered first. The rest of the specimen was *in situ* and was excavated by first cutting away some of the deposit to create a step. The step was used as a platform from which to work and to allow excavation in plan view. In this way the whole specimen was exposed and consolidated. Wooden struts were used to maintain the connection between the horn cores and the braincase. Later, in the fossil laboratory at the Florisbad Quaternary Research Station the preparation was completed and the left horn core was glued back.

In 2002 and in 2010 we took ESR samples and measurements at various localities in the Orangia Terrace (Figures 2 and 3). In order to establish the gamma dose rate for the various localities, readings were taken with a portable gamma detector. Excavated dental samples of known provenance were used for ESR testing, with the exception of the dental specimens from the Upper Grey palaeosol, which were collected from the surface. From recent test excavations it is clear that these specimens originally derive from the Upper Grey palaeosol.

6.3 RESULTS

6.3.1 Mahemspan

Comparative taxonomic lists are given in Table 2 for the Last Interglacial fossil assemblages from Erfkroon, the fossil assemblage of Mahemspan and for the Florisbad Spring assemblage. The Mahemspan fossil materials are unusually complete. The giant aelaphine, *M. priscus*, is the predominant element in the collection and is represented by virtually all skeletal elements. The Mahemspan collection of *M. priscus* represents probably the largest and most complete sample of this species in southern Africa. The completeness of the material and the predominance of large-bodied taxa in the assemblage raise the question of selective recovery of the material. However, from the care that was taken in the preparation of the fossils before excavation and the meticulous accessioning of the material it is evident that the excavators took considerable trouble to recover the material as completely as possible and it appears unlikely that recovery was selective. The presence of sun cracks and porcupine gnawing on specimens, the absence of hyaena coprolites and the paucity of carnivores in the fossil assemblage argue against the likelihood that it represents the contents of ancient hyaena burrows. This and the fact the bones were originally deposited in marshy conditions, may point to the Mahemspan assemblage representing natural deaths or carnivore kills on the edge of the pan. This is analogous to the taphonomic reconstruction of the Florisbad Spring assemblage, which is considered to represent the remains of carnivore hunting and scavenging around the ancient spring pools (Brink, 1987, 1988; Grün *et al.*, 1996).

Various authors made reference to the Mahemspan material and formed opinions on its geological age (Cooke, 1974; Gentry and Gentry, 1978). Van Hoepen (1947) and Hoffman (1953) used cranial elements from this assemblage for taxonomic descriptions. Cooke (1974) considered Mahemspan material to be Florisian in age, but somewhat older than the Florisbad spring material. However, based on the shape of the black wildebeest horn cores Gentry and Gentry (1978) suggested an age younger than the Florisbad spring material. The ESR results for an early uranium uptake model (EU) suggest an age of around 12,000 years BP and for a linear uranium uptake model

Table 2. Taxonomic list of Florisian faunas: a comparison between Erfkroon Last Interglacial levels (L/I), Mahemspan and Florisbad Spring*.

	Florisbad spring	Erfkroon L/I	Mahemspan
Primates			
<i>Homo helmei</i>	1		—
Lagomorpha			
<i>Lepus</i> sp.	6	4	—
Rodentia			
<i>Hystrix africæ-australis</i>	1	—	—
<i>Pedetes</i> sp. cf. <i>P. capensis</i>	8	—	—
Carnivora			
<i>Aonyx capensis</i>	3	—	—
<i>Cynictis penicillata</i>	—	2	—
<i>Galerella sanguinea</i>	1	—	—
<i>Atilax paludinosus</i>	3	—	—
<i>Canis mesomelas</i>	6	2	—
<i>Vulpes chama</i>	—	2	—
<i>Lycaon pictus</i>	3	1	—
<i>Crocuta crocuta</i>	7	—	7
<i>Panthera leo</i>	1	1	1
Perissodactyla			
<i>Equus capensis</i> ††	73	6	80
<i>Equus lylei</i> ††	61	1	cf.
<i>Equus quagga</i> subsp.	97	2	48
<i>Ceratotherium simum</i>	3	—	—
Artiodactyla			
<i>Hippopotamus amphibius</i>	333	2	4
<i>Phacochoerus africanus/aethiopicus</i>	33	2	17
<i>Taurotragus oryx</i>	24	1	21
<i>Syncerus antiquus</i> ††	25	1	28
<i>Kobus leche</i> †	60	2	21
<i>Kobus</i> sp.†	4	—	—
<i>Hippotragus</i> sp.†	16	—	2
<i>Damaliscus niro</i> ††	111	11	11
<i>Damaliscus pygargus</i>	9	12	19
<i>Alcelaphus buselaphus</i>	8	—	10
<i>Connochaetes gnou</i>	284	10	24
<i>Connochaetes taurinus</i>	—	—	9
<i>Megalotragus priscus</i> ††	30	2	241
<i>Antidorcas bondi</i> ††	889	34	1
<i>A. marsupialis</i>	107	2	6
<i>Raphicerus campestris</i>	4	—	—

††Extinct.

†Regionally extinct.

*Faunal lists modified and adapted from Brink (1987, 1994; in press).

Table 3. Electron Spin Resonance results on dental specimens from Makemspan.

Sample	Dose	De error	U (EN)	U (DE)	TT	U (SED)	Th	K (SED)	EU Age (ka)	EU- error	LU Age (ka)	LU error
1411												
1412 AM	24.9	0.9	1.86	88.2	1230	5.5	1.75	0.45	13.6	0.8	17.6	1
1412 AS1	24.3	0.4	2.04						13.3	0.7	17.2	0.8
1412 BS1	23.7	0.4							14	0.7	7.6	0.9
1413 AS1	16.7	0.7	0.89	24.5	700				13.1	0.6	16.5	0.8
1413 BS1	19	0.2	1.08	32.4	730				11.6	0.7	13.3	0.8
1413 CS1	19.5	0.2	1.36	54.8	830				12.5	0.6	14.7	0.7
1414 AS1	18.7	0.2	0.98	26.9	730				11.4	0.5	14.2	0.7
1414 BS1	19.2	0.3	1.33	40.1	700				12.8	0.6	14.8	0.7
1415 AM	16.7	0.3	0.7	20.94	930				11.7	0.6	14.2	0.7
1415 AS1	16.8	0.3		21					12.8	0.6	14.3	0.7
1415 BS1	15.5	0.3	0.6	25.8	830				12.9	0.6	14.4	0.7
1415 CS1	15.6	0.2	0.58	28.4	1130				11.4	0.6	12.9	0.7
									12.1	0.6	13.6	0.7

(LU) of around 13–17,000 years BP (Table 3). These age estimates support the suggestion of Gentry and Gentry (1978) that the Mahemspan assemblage postdates that of the Florisbad Spring (Grün *et al.*, 1996).

6.3.2 Erfkroon

In Table 2 the taxonomic list for Erfkroon represents the fossil assemblages from the Last Interglacial levels. These are the Lower Gravel and Green Sand from the Orangia Terrace, as recovered on the farms Erfkroon and Orangia (see Table 1). The ESR age estimates for the various horizons of the Orangia Terrace are given in Table 4 and are based on the testing of the dental specimens recovered from the farms Erfkroon and Orangia. The numbers of the sample batches in Table 4 correspond to the sampling localities given in Figures 2 and 3. The EU age estimates from the Upper Grey (Orangia Terrace) seem to correspond fairly well with the luminescence estimates, as referred to above, but there is some disagreement between the luminescence and the ESR estimates from the Green Sand of the Orangia Terrace. The ESR estimates for the Shelly Gravel suggest a terminal Late Pleistocene age. We are at present uncertain whether the Shelly Gravel is a lateral facies of the Upper Gray of the Orangia Terrace or the basal horizon of the Soetdoring Terrace. The ESR estimates accord well with either stratigraphic interpretation (Figure 3).

The *M. priscus* skull and horn cores were found in an outcrop which we correlate with the Lower Gravels and Green Sands of the Orangia Terrace (Figure 4). Based on the luminescence dating of the Orangia Terrace this would imply a Last Interglacial age for the *M. priscus* outcrop. We were not able to recover dental specimens from the *M. priscus* outcrop for ESR testing, but the presence of abundant rolled calcareous blocks together with clasts of shale gives confidence to the correlation of this deposit with the Lower Gravel of the Orangia Terrace.

6.3.3 Horns and braincase of *M. priscus*

6.3.3.1 The Erfkroon specimen

The Erfkroon specimen consists of a braincase and both horn cores (Figure 5; Table 5). The left horn core tip is not preserved. The horns are dorso-ventrally compressed near the bases and in mid-course, but become rounded towards the last third of their course. Near the base of the horn on the anterior surface there is a slight swelling, also present in the Florisbad specimen FLO 2274. Horn pedicels are fused and overhang the occipital surface. Horns are bent down sharply and diverge with a mutual angle of around 150°. In mid-course they are sub-horizontal before they curve up and forward and there is clockwise torsion on the right. The horns have faint transverse ridges near the bases, an indication of nodes on the horn sheath. The frontals' suture appears less extremely fused than in *C. gnou*. There is no postcornual fossa. The braincase appears antero-posteriorly shortened in lateral view. This is due mainly to the reduction in the parietals, which are visible only in lateral view so that the occipital makes contact with the frontal. The combined effect of the reduction in the braincase and the posterior projection of the fused pedicels is that the braincase appears partly hidden beneath the horn bases. This configuration of the braincase appears to have caused the nuchal crest to have become inverted to form a concave structure in order to allow sufficient

Table 4. Electron Spin Resonance results on dental specimens from Erfkroon.

Sample	Dose	DE error	U (EN)	U (DE)	TT	SI	S2	U (SED)	Th (SED)	K (SED)	gamma	EU Age (ka)	EU-error	LU Age (ka)	LU error	
1. Upper Grey, Orangia Terrace																
1920 AS1	56.7	2.1			1470	50	450					42	4	50	6	
1920 BS1	33	1.1			1440	40	470	3.8	4.5	0.81	744.5	25.2	2.6	29.5	3.5	
1923 AS1	45.5	1.1			1130	70	340	1.45	6.5	1.29	695.9	24.9	2.1	32	3	
1923 BS1	49	1.3			1110	90	270					27.2	2.3	35	3	
1926 AS1	49.7	0.7			1000	90	330	3	8.5	1	873.8	22.4	1.8	31	2	
1926 BS1	44.2	1.4			1130	90	160					22	1.8	29.4	2.8	
2. Duke 8, Shelly Gravel, Incertae sedis																
1929 AS1	43.4	1.3	3.7	99	960	50	50					696.7	18	1.2	25.2	1.6
1929 BS1	48.5	1.3	3.8	115	1090	50	50					843.5	19.7	1.2	27.8	1.7
1930A	54.4	0.8	0.88	112	800	40	70					770.1	23.6	1.5	32	2
1930B	41.1	0.6	0.51	112	970	70	160					20.3	1.3	27.1	1.7	
1931A	40.6	0.5		181	710	50	70					11.5	0.8	17.6	1.1	
1931B	43.9	0.6	5.5	168	820	90	60					13.6	0.9	20.4	1.2	
1932A	54.7	0.6	10	144	1040	70	300					14.7	1.1	23.2	1.5	
1932B	63.3	1	4.5	147	1010	30	190					20.8	1.4	31	1	
1932C	41.6	0.5	1.5	169	1000	160	190					17.1	1.1	24.2	1.5	
3. Hippo Site, Green Sand, Orangia Terrace																
1939A	733	17	8	102	1180	90	90					713	158	13	261	19
1939B	825	20	9.1	109	1090	70	70					698	153	12	253	19
1940A	661	13	9.3	91	690	20	20					127	10	209	15	
1940B	0		11	90	530	20	20									
1941A	0		2	82	2510	290	290	2.6	6.6	1.07	724.8					
1941B	0		2.3	82	2620	225	225									
1941C	0		2.8	82	2550	290	290									
4. W Site, Green Sand, Orangia Terrace																
1948A	580	13	3.7	65	760	50	50					135	12	201	18	
1948B	796	16	13	71	730	20	20					124	11	199	17	
1949A	568	10	8	23	900	90	90					135	12	201	18	
1949B	522	9	4.5	21	890	110	70					161	14	223	22	
1950A	587	11	5	26	730	50	50					164	15	232	22	
1950B	407	6	2.3	26	860	100	90					157	14	204	21	
5. Duke 13, Lower Gravel, Orangia Terrace																
1953A	1582	65	36	90	650	35	35					123	13	218	23	
1953B	1697	30	27	86	580	40	40					154	15	270	25	
1954A	601	10	3.5	72	1020	60	150					183	13	277	18	
1954B	613	7	4.8	77	1230	100	180					173	12	268	18	

area for the attachment of the neck muscles. Although the specimen is somewhat damaged in this region, it appears that the nuchal furrow extends into a very pronounced supramastoid crest anteriorly, while posteriorly it links with the petrosal part of the temporal to form a very strong structure for neck muscle attachment. The occipital condyles are very wide. The basioccipital is short, wide, approaches being rectangular, has no median ridge and has large anterior tuberosities (tubercula muscularia). The basioccipital and the sphenoid are not on the same plane, but have an angle of around 140°.

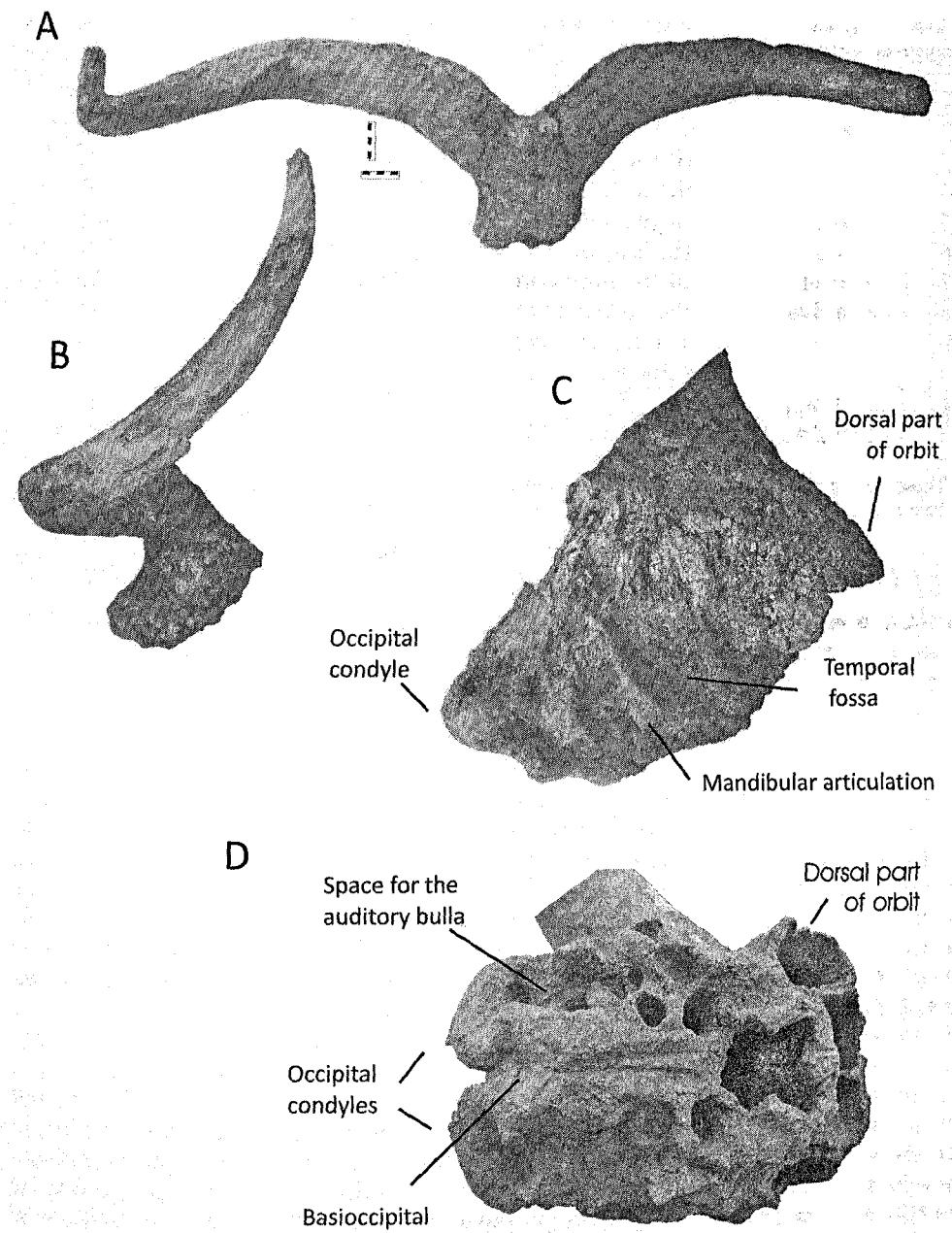


Figure 5. The complete braincase and horn cores of *Megalotragus priscus* from Erfkroon: Frontal view (A), right lateral view (B), enlarged right lateral view of the brain case (C) and a basal view (D). The scale is in centimetres.

The bullae tympanicae are not preserved, but the spaces in which they were situated are preserved and it can be deduced that they were moderately large and rounded. The foramina ovalia are quite large. From the remaining part of the frontal it is evident that the angle of the braincase to the face is small, approaching 90°. There is enough of the posterior margin of the orbits preserved to suggest that they would have been at least moderately projecting.

Table 5. Measurements (in mm) of the *Megalotragus priscus* skull and horn cores from Erfkroon. The equivalent measurements given in Von den Driesch (1976) for cattle (*Bos taurus*) are indicated in brackets

1	Least frontal breadth (32)	143.5
2	Greatest breadth across the orbits (33)	172.8 ⁺
3	Greatest diameter of the pedicel	107.7
4	Least diameter of the pedicel	83
5	Greatest diameter of the base of the horn core (45)	108.5
6	Least diameter of the base of the horn core (46)	83
7	Greatest diameter of the horn core at mid-section	90.5
8	Least diameter of the horn core at mid-section	65.1
9	Greatest breadth of occipital condyles (26)	144*
10	Greatest breadth of the foramen magnum (28)	40.5*
11	Least breadth between the bases of the horn cores (31)	57 ⁺
12	Least breadth of the braincase (30)	142.2

+ These measurements are estimates due to incomplete preservation of the relevant parts.

* These measurements are minimum values, because of damage to the specimen.

6.3.3.2 Comparisons

It is a commonly held view that all very large-bodied acelaphine antelope in Africa belong to one genus, *Megalotragus* Van Hoepen, 1932, and that the various fossil species of this genus are closely related (Gentry, 1978, 2010; Gentry and Gentry, 1978; Gentry et al., 1995; Vrba, 1979, 1997). Previously a smaller-bodied species from Rusinga Island, Kenya, *Rusingoryx atopocranion* Pickford and Thomas, 1984, was referred to the genus *Megalotragus* (Vrba, 1997), but more recently in a revision of the morphological and phylogenetic relationships of this species it was re-assigned to *Rusingoryx* as a genus distinct from *Megalotragus*, although closely related (Pickford and Thomas, 1984; Faith et al., 2011). Previously it was suggested that an East African species, *M. kattwinkelii*, is ancestral to the southern African *M. priscus*, which is considered to include two temporal forms, *M. priscus eucornutus* and *M. priscus priscus* (Gentry and Gentry, 1978). However, this hypothesis seems no longer to be supported (Gentry, 2010). There is no fossil evidence yet for the species *M. eucornutus* and *M. priscus* outside of southern Africa, although Faith et al. (2011) mentions the presence of large wildebeest-like acelaphine from the Wasiriya Beds on Rusinga Island, which they refer to the genus *Megalotragus*. *M. eucornutus* is known only from Cornelius-Uitzoek, the type locality of the Cornelian Land Mammal Age (LMA) and from Cornelius-Mara, a nearby locality of similar age (Brink et al., 2012; Brink, in press). It has been noted that there are grounds for maintaining the specific distinction between *M. priscus* and *M. eucornutus*, based on horn core morphology (Bender and Brink, 1992), but also on dental proportions (Brink, 2005). Thus, for the sake of clarity the distinction between names *M. eucornutus* Van Hoepen, 1932 and *M. priscus* (Broom, 1909) is maintained here.

Originally the Florisbad giant acelaphine material was named *Bubalis helmei* by Dreyer and Lyle (1931). Van Hoepen (1932) described an isolated find of an incomplete horn core pair with intact pedicels from the farm Doornberg, on the Sand River near Kroonstad, Free State Province, as *Pelorocerus elegans*. Van Hoepen (1947) described the Mahemspan material initially as *Pelorocerus mirum*. He also redescribed the Florisbad *B. helmei* as *Lumatoceras mirum* (Van Hoepen, 1947), which was later referred to *Alcelaphus helmei* by Cooke (1952) and again to *Pelorocerus helmei* by Hoffman (1953). Subsequently Cooke (1964) referred the Florisbad material to both

Pelorocerus helmei and to *Lunatoceras mirum*. Eventually Gentry and Gentry (1978) included the Florisbad material and all other Florisian giant alcelaphine materials in *M. priscus*. This was followed by Vrba (1979, 1997), Klein (1984) and Brink (1987).

The synonymy of the genus *Megalotragus* and the species *Megalotragus priscus* is as follows:

Genus *MEGALOTRAGUS* Van Hoepen 1932
1932 *Megalotragus* Van Hoepen
1932 *Pelorocerus* Van Hoepen
1953 *Lunatoceras* Hoffman
1965 *Xenocephalus* Leakey

Type species. *Megalotragus priscus* (Broom 1909)

The type specimen (SAM 1741) is a cranial fragment with part of the left horn core preserved and it is housed in the Iziko South African Museum in Cape Town.

1909 *Bubalis priscus* Broom
1931 *Bubalis helmei* Dreyer & Lyle
1932 *Pelorocerus elegans* Van Hoepen
1947 *Lunatoceras mirum* Van Hoepen
1951 *Connochaetes grandis* Cooke & Wells

The Erfkroon specimen is very similar to the type specimen, but more complete. An almost complete set of horn cores from Florisbad, FLO 2274, is virtually identical to the Erfkroon specimen in terms of size, horn shape and horn curvature, but lacking the braincase. In FLO 2274 the frontals' suture is partially fused, as in the Erfkroon specimen and similar to the Barbary sheep, *Ammotragus lervia*. In another Florisbad specimen, FLO 2273, the horns tend to be more sharply curved, they extend further backwards at their bases before curving sideways and forwards. The bases of the horn cores lack the protuberance on the cranial surface, as seen in the Erfkroon specimen and in FLO 2274. The mutual angle between the horn bases is somewhat smaller, while the specimen is generally more gracile. This specimen is probably a female, while the Erfkroon specimen, the type specimen and FLO 2274 appear to be of males.

In addition to the above the horn core of *M. priscus* from the Ongers River near Britstown, central Karoo (Brink *et al.*, 1995), has a base that is not antero-posteriorly extended and appears to be somewhat rounded in cross section. There is no basal protuberance and, while it is difficult to estimate the degree of pedicel fusion in this specimen, it appears to have had a reasonably wide mutual angle between the horn cores. The specimen is very gracile and in size comparable to the specimen from Doornberg, C. 1711. Of all the specimens assigned to *M. priscus* the Doornberg specimen have the smallest mutual angle between the horn core bases, a condition that is considered to be plesiomorphic for *Megalotragus* (Gentry and Gentry, 1978). For this reason it is probable that the Doornberg specimen is geologically older than the other specimens of *M. priscus* under consideration here. The Ongers specimen resembles the Doornberg specimens in gracility, but has a wider mutual angle between the horn bases. The horn core bases of the Doornberg specimen are also less expanded antero-posteriorly than the Ongers River specimen and have no basal protuberances, which is also a plesiomorphic condition for *M. priscus*. Both these specimens are likely to be female.

In the type specimen of *P. mirum* (C. 2013) from Mahemspan the horn pedicels are not as extremely fused as in the Erfkroon and Florisbad specimens and the area of pedicel fusion is less elevated above the frontals (Van Hoepen, 1947). The mutual angle between the horn bases is reduced, resembling the Doornberg specimen. The basal parts of the horn cores are not as robust as in the large specimens from

Erfkroon and Florisbad. The cranial sides of the horn bases are not preserved and it cannot be established whether there were protuberances. This specimen appears to be male.

In specimen C. 2537 from Mahemspan, a frontal fragment with the basal parts of the horn cores preserved, there is a marked posterior projection of the horn bases and the horn bases are much thinner. There is a reduced mutual angle between the horn core bases, a reduced degree of pedicel fusion, while the frontals' suture appears less fused than in the Erfkroon and Florisbad specimens. C. 2537 is also more gracile than Mahemspan specimen C. 2013 and very similar to the Doornberg specimen and, consequently, is likely to be female.

Mahemspan specimen C. 2246 has an equally narrow mutual angle between the horn core bases. In contrast with the Erfkroon specimen the nuchal crest forms a convex relief, and is not inverted, and it is not as wide as in the Erfkroon specimen. In the co-type of *P. mirum* from Mahemspan, C. 2292, the horn base appears not to have a protuberance and it is not antero-posteriorly extended. The curvature of the horns is intermediate between the large forms from Florisbad and Erfkroon and the small specimens from Doornberg and Mahemspan. These specimens are probably female.

6.3.3.3 Sexual dimorphism and geographic variability in the horn cores of *M. priscus*

The more complete and dated materials available now for *M. priscus* allow an appreciation of sexual dimorphism and geographic variability. Although there is considerable variability in size, the horn core specimens of *M. priscus* can be separated into categories of male and female. Females are those with more gracile horn cores, with less dorso-ventral extended basal parts and with slightly shorter horn curvature. Males, on the other hand, have generally larger horn cores, with dorso-ventral expanded horn bases and with a thickening, or protuberance on the dorsal side. Male horns tend to be more horizontally positioned, as seen in the Erfkroon specimen, and to be less sharply curved. This supports the observation that the mutual angle in *M. priscus* horn cores is a sexually dimorphic character with males tending to have more downward pointing horns than females and that a greater mutual angle is associated with greater robusticity (Brink et al., 1995).

The type specimen and the specimens from Florisbad and Erfkroon are considerably larger than those from Mahemspan, Doornberg and the Ongers River. In the Mahemspan specimens there is a lesser degree of horn pedicel fusion, the fused pedicels are less elevated above the frontals and the horn cores are generally more vertically inserted. Previously it has been suggested that morphological variability in *M. priscus* horns represent a temporal cline in that horns become more downward and forward pointing in the course of geological time (Cooke, 1974). This statement was based on the assumption that Mahemspan predates the Florisbad spring assemblage. However, on the evidence presented here it appears now that Mahemspan is of terminal Late Pleistocene age and that a more likely explanation for horn core variability may be that it reflects sexual dimorphism and geographic variability in populations. Although undated, the Doornberg specimen, C. 1711, named *P. elegans* by Van Hoepen (1947), is probably an early and very gracile female version of *M. priscus*. Similarly, the two forms of giant alcelaphine from Florisbad, "*P. helmet*" and "*L. mirum*", probably reflects sexual dimorphism in *M. priscus*, with the former being male and the latter female.

On the available fossil evidence *M. priscus* can be divided into two morphological entities, which may have represented two geographic variants. This is a very tentative observation and will need further testing. If the variability observed truly reflects geographic variability, it would be in parallel with the variation seen in extant populations

of hartebeest, *Alcelaphus buselaphus* subsp., and tsessebe, *Damaliscus lunatus* subsp. (Kingdon, 1997).

6.4 RECONSTRUCTING THE SKULL OF *M. PRISCUS*

The horn core pair and braincase from Erfkroon, an upper jaw fragment (C. 1804) and a lower jaw (C. 2472), both from Mahemspan (Figure 5), form the basis of the reconstruction of the skull of *M. priscus* (Figures 6 and 7). Because it is possible to establish the position of the jaw articulation on the Erfkroon braincase, the Mahemspan lower jaw allows the estimation of the length of the face. Also, in conjunction with the remnant of the frontal, the mandible allows the angle of the braincase to the face to be estimated. The extreme posterior position of the horn bases and the position of the occipital condyles suggest a hanging, ox-like head position. Even if the Mahemspan materials may represent a different geographic population from the Erfkroon and Florisbad materials, this will result in only marginal distortion in the skull proportions, since the dentitions from Florisbad and Mahemspan seem to be identical in morphology and size (Brink, 2005). Because the Erfkroon specimen is used as the basis for the reconstruction, the reconstructed skull represents a male of the geographic population to which the type specimen and the Florisbad spring specimens belonged. At present nasal bones of *M. priscus* are not known in the fossil record and this reconstruction suggests only moderately inflated nasals. The nasals represent the most speculative aspect of the reconstruction.

The lower jaw of *M. priscus* is unusually elongated compared to other alcelaphines. Mesially, the diastema is enlarged to balance the increase in the posterior extension of the ramus, while the angle between the ramus and the corpus is widened to around 135°. These features are modifications to allow the mandible to fit the extremely elongated skull. A similar, but less extreme widening of the angle between the ramus and the corpus is seen in the mandible of *Rusingoryx atopocranion* (Faith *et al.*, 2011). Another parallel to this extreme morphology of the lower jaw can be found in the hartebeest and in the Barbary sheep, *Ammotragus lervia*. In both the latter species there is some degree of fusion of the horn pedicels and the horn bases are positioned posteriorly on the skull, which is reflected in the widened angle between the ramus and corpus of the mandible. In *C. taurinus* the lower jaw is also somewhat elongated, but less so than in the hartebeest, while the angle of lower jaw is not as wide. In *C. gnou* and blesbok the ramus is sub-vertical and the corpus relatively short and stout.

6.5 DISCUSSION

6.5.1 Morphological relationships of *M. priscus*

Broom emphasised the hartebeest-like horn bases of the animal (Broom, 1909), which is reflected by his choice of genus name for the specimen ("Bubalis"). Although the skull of *M. priscus* is characterised by extreme elongation and by the fusion and posterior extension of the horn pedicels, reminiscent of some of the geographic variants of *Alcelaphus buselaphus*, there are a number of characters more typical of the genus *Connochaetes*. These are the tendency for the horns to curve sideways, downward and then forward and the reduction in the prominence of nodes on the horns. The simplicity of the occlusal enamel patterns of the dentitions and the morphology of the postcrania, discussed elsewhere (Brink, 2005), are also characteristic of wildebeest.

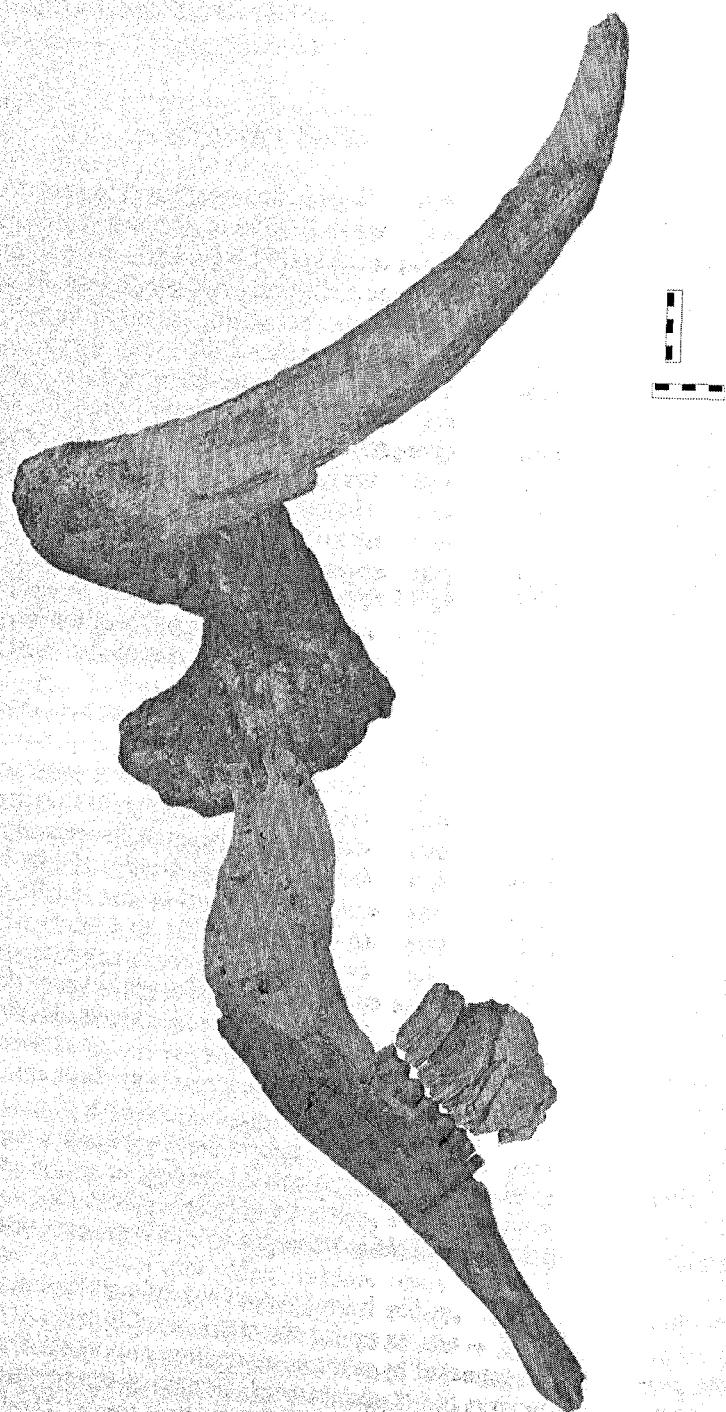


Figure 6. An arrangement in approximate natural position of the Erfkroon braincase and skull (A), a lower jaw from Mahemspan (B) and an upper jaw fragment from Mahemspan (C). This arrangement is the basis of the reconstruction of the skull of *M. priscus*, as given in Figure 7. The scale is in centimetres.

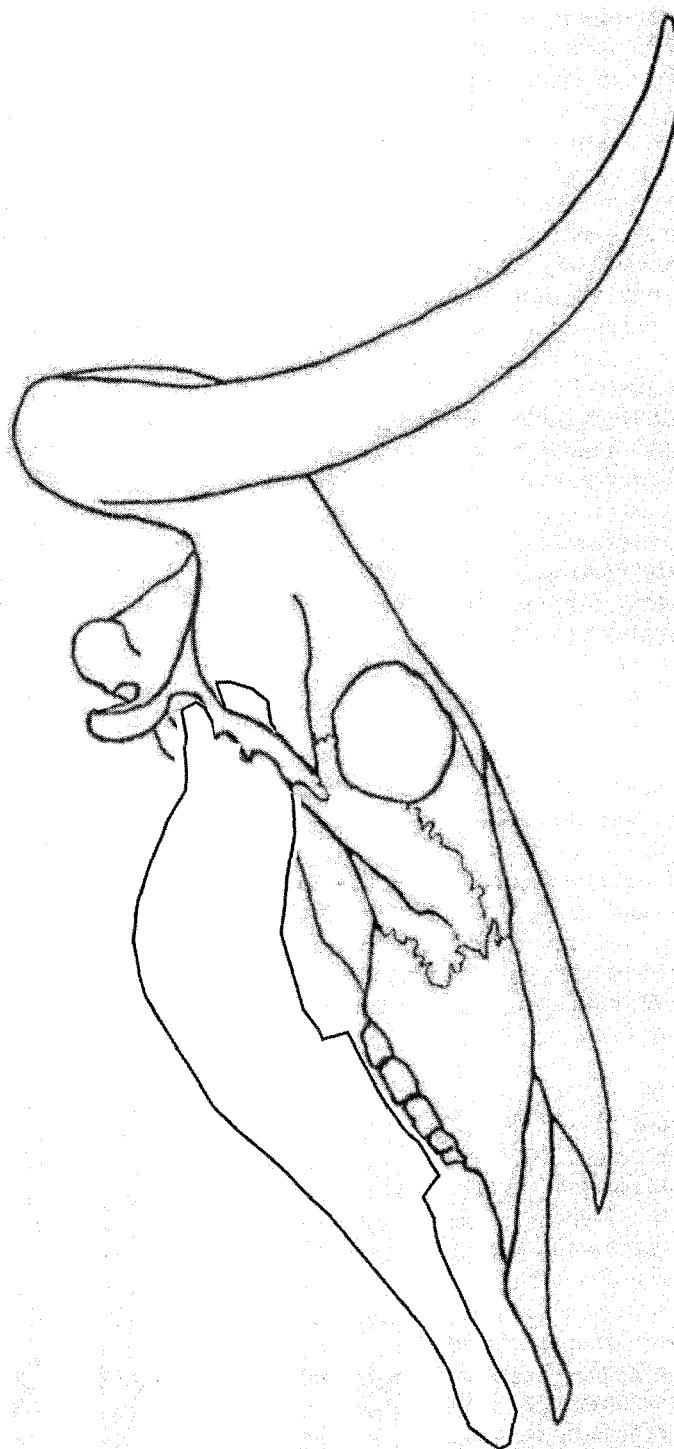


Figure 7. A reconstruction of the skull of *M. priscus*. The scale is as in Figures 6.

Previously the position of *M. priscus* within the wildebeest clade has not been apparent due to the erroneous assumption that facial lengthening, clockwise torsion in the right horn and related changes in horn base morphology are uniquely derived characters shared with the genus *Alcelaphus* (Hoffman, 1953; Wells, 1959, 1964; Klein, 1984; Vrba, 1979). It now appears that these characters reflect parallel adaptation with the hartebeest and that *M. priscus* was in fact a very large and derived form of wildebeest. It should be noted further that Vrba's phylogenetic re-analysis (Vrba, 1997) and the phylogenetic analysis of Faith *et al.* (2011) support the interpretation of the genus *Megalotragus* being closely related to the genus *Connochaetes*.

There are obvious similarities between *M. priscus* and *M. kattwinkelii*, and a number of shared derived characters unite the two species. These are elongated skulls, horns with some degree of transverse ridge development, horns inserted far behind the orbits, projecting orbits and an occipital surface that faces mainly backwards with a median vertical ridge (Gentry and Gentry, 1978; Vrba, 1997). It may be predicted that inflated nasals could be added to these characters and it will be of interest to find sufficiently well preserved nasals of *M. priscus* to test this assumption. However, there are some derived characters in *M. priscus*, which are not shared by *M. kattwinkelii*, but there are also some characters in which *M. priscus* is more plesiomorphic. Uniquely derived characters in *M. priscus* in relation to *M. kattwinkelii* are the more posterior position of the horn core insertions, the extreme state of fusion of the pedicels, very large horn size, the almost horizontal angle at which the horns curve outwards from the pedicels before they curve forward (more extreme in the Erfkroon and Florisbad specimens), the fact that the fused pedicels of the horn cores overhang the occipital and possibly large bullae tympanicae. The plesiomorphic characters of *M. priscus* in relation to *M. kattwinkelii* include a less reduced premolar row, in which the P³ and possibly the P² were still present, while in *M. kattwinkelii* only the P⁴ was present (Gentry and Gentry, 1978). This mosaic of characters suggests that *M. kattwinkelii* was probably not an ancestor of *M. priscus*, in spite of being closely related. *M. kattwinkelii* occurs in the fossil record until the end of the Early Pleistocene and possibly later (Faith *et al.*, 2011). *M. priscus*, first appeared in the Elandsfontein Main assemblage, which is thought to date to the end of the Early Pleistocene (Brink, in press), but it became extinct at the end of the Late Pleistocene/early Holocene (Klein, 1984). Therefore, in temporal range *M. kattwinkelii* overlaps with *M. priscus* and this temporal overlap adds to the doubt regarding the suggested ancestor-descendant relationship between *M. kattwinkelii* and *M. priscus*.

The possible ancestor-descendant relationship between *M. eucornutus* and *M. priscus*, initially mentioned by Gentry and Gentry (1978) and Vrba (1979, 1997), is not discussed further in Gentry (2010). However, this question can be further considered on the available evidence. The closely positioned horn bases, the orientation of the horn bases, the clockwise curvature and the lesser degree of fusion of the pedicels accord with *M. eucornutus* being an ancestor of *M. priscus*. However, the absence of any indication of nodes on the horns of *M. eucornutus* would be unexpected if it were ancestral to *M. priscus*. Nodes are not found on the horns of early alcelaphines, such as *Damalacra neanica* and *D. acalla* from Langebaanweg, nor in extant members of the genus *Connochaetes*, but they are present in the genera *Beatragus*, *Alcelaphus* and *Damaliscus*, which represent a different, 'non-wildebeest' branch of alcelaphine evolution. Thus, in wildebeest-like alcelaphines nodes on horns indicate a plesiomorphic condition and their presence on the horns of *M. priscus*, even though in reduced state, would have to be interpreted as an evolutionary reversal to accommodate *M. eucornutus* as the ancestor of *M. priscus*. The paucity of fossil material of *M. eucornutus* hampers proper evaluation. Apart from the horn core specimens and a few dental and

postcranial elements from Cornelia-Uitzoek, very little of the body of *M. eucornutus* is known. Other than Cornelia-Uitzoek and Cornelia-Mara (Butzer, 1974; Cooke, 1974; Brink *et al.*, 2012) the only fossil locality in the interior of southern Africa that may have produced material of *M. eucornutus* is Gladysvale (Lacruz *et al.*, 2002), but so far no horn material of *M. eucornutus* has been found there. At Elandsfontein, which has produced a substantial collection of Cornelian large mammals, only *M. priscus*, and not *M. eucornutus* is recorded (Klein *et al.*, 2007). Therefore, on the existing evidence it appears unlikely that *M. eucornutus* was ancestral to *M. priscus*.

6.5.2 Behavioural implications of the skull morphology of *M. priscus*

Kingdon (1982) ascribes the increased profile of the head of the hartebeest to the importance of head signals in these animals, usually executed in slow movements. This contrasts with blue wildebeest, in which a very small proportion of the horns is visible in profile, but which has very energetic body and head movements during intraspecific encounters. Kingdon further notes that such behaviour in wildebeest may be associated with high densities when large herds form. The horn profile and the morphological characters suggesting the aggressive use of the horns in *M. priscus* are wildebeest-like. Also, the evidence for a specialised grazing niche is in accordance with the aggregation of large herds in open, Highveld-type grasslands (Brink and Lee-Thorp, 1992; Codron *et al.*, 2008), which is in contrast to the hartebeest and the genus *Damaliscus*. Hartebeest do not form herds in such large numbers as blue wildebeest. They tend to occupy ecotonal habitats rather than the more homogeneous short grass plains, favoured by *Connochaetes taurinus* in East Africa and *C. gnou* in southern Africa. The niche of the hartebeest as a roughage grazer is different from the short grass grazer niche of *C. taurinus* and *C. gnou* (Hofmann and Stewart, 1972; Codron and Brink, 2007; Brink and Lee-Thorp, 1992). In *M. priscus* the hanging head position and the forward curvature of the horns resemble *C. gnou* and the wild ancestor of cattle, *Bos primigenius*.

The picture that emerges is of a large-bodied wildebeest with some degree of territorial behaviour, where large herds formed, occupying a highly specialised grazing niche in the open grasslands of southern Africa. This niche disappeared at the end of the Late Pleistocene, evidently due to a reduction in the productivity levels of grasslands, which may be linked to increased aridity and reduced availability of soil moisture on a large geographic scale, as suggested by Brink and Lee-Thorp (1992) and supported by new evidence from the Erfkroon sedimentary record (Lyons *et al.*, 2014). The extinction of *M. priscus* coincided with the extinction of five other specialised grazing ungulates and the local extinction of a wetland faunal component in central southern Africa (Brink, in press). This coincidence reinforces the impression that aridity was a key driving factor in the end-Pleistocene extinction process.

6.6 CONCLUSION

The Erfkroon specimen and the new age estimates from Erfkroon and Mahemspan allow a revised and more detailed view of the morphological relationships of *Megalotragus priscus* and of its behaviour. It is evident that the animal was a large form of wildebeest, and not closely related to hartebeest, that it showed sexual dimorphism and probably some degree of territorial behaviour. The Erfkroon specimen allows a reconstruction of the skull of *M. priscus*, which suggests an extremely elongated skull that was held in life in a hanging, ox-like position. The head position, the forward curvature

of the horns and the degree of sexual dimorphism are in accordance with the suggested territorial behaviour and add to our understanding of *M. priscus* as a large-bodied specialised grazer in the Florisian grasslands of southern Africa. Its extinction towards the end of the Pleistocene and early Holocene formed part of a southern African extinction event that included five other specialised grazers and the regional extinction of a wetland faunal component, suggesting widespread and increasing aridity in this time in the southern African subregion.

ACKNOWLEDGEMENTS

The authors thank the owners of the farms Erfkroon, Hein Bezuidenhoudt, and Orangia, Johan van der Berg, for their interest and for allowing access to their properties. We thank Lloyd Rossouw and Kris Carlson for field assistance and the Florisbad crew, Abel Dichakane, Ernest Maine, Willem Nduma, Bonny Nduma, Peter Mdala and Adam Thibeletsa for assistance in the excavation and preparation of the Erfkroon *M. priscus*. Maria Brink is thanked for reading an earlier draft of the manuscript. JSB would like to thank the French Embassy in Pretoria, South Africa, and the National Research Foundation of South Africa for financial support. The Council and Director of the National Museum are thanked for supporting research on fossil mammal evolution in the central interior of southern Africa.

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