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A NEW FIND OF *MEGALOTRAGUS PRISCUS* (ALCELAPHINI, BOVIDAE) FROM THE CENTRAL KAROO, SOUTH AFRICA

by

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ABSTRACT

We document the occurrence of the Florisian, or late Quaternary, form of the giant alcelaphine, *Megalotragus priscus*, from dongas on the Ongers River, near Britstown in the central Karoo. This is significant as it confirms the occurrence of the species in the Karoo and it suggests significantly wetter environments and productive grasslands in the central Karoo in pre-Holocene times. The present-day Karoo environment did not maintain populations of large ruminant grazers similar to *M. priscus*, and other specialized Florisian grazers, prior to the advent of agriculture and pasture management. Aridification in recent times is the likely cause of changes in grassland quality and the local dissappearance of these animals, if not their extinction.

KEY WORDS: Alcelaphine evolution, Florisian mammals, Late Pleistocene extinction

INTRODUCTION

The giant alcelaphine antelope, *M. priscus*, is one of six extinct species which define the Florisian Land Mammal Age (Brink 1994; Hendey 1974). The species is known from a variety of late Quaternary sites in the interior of southern Africa as well as from the Cape Ecozone in pre-Holocene times (Brink 1987; Bender & Brink 1992; Klein 1980, 1984; Klein & Cruz-Uribe 1991). Ecologically the Florisian *M. priscus* is a specialised grazer on the basis of its dental morphology and its association with grassland faunal elements (Brink 1987, 1988; Brink & Lee-Thorp 1992; Klein 1980). The fossil record of *M. priscus* is best documented in the Orange Free State, the North-Western Cape, Transvaal and in the Cape Ecozone (Klein 1980). Apart from the identification of metapodial remains from Blydefontein, Northern Karoo (Bousman *et al.* 1988), the giant alcelaphine is unknown from fossil localities in the Karoo region (Klein 1980). In this paper we report on fossil mammal material from the Britstown district which includes remains of the Florisian species *M. priscus*. This find confirms the presence of the giant alcelaphine in the Karoo during the late Quaternary and suggests a much wetter palaeoenvironment compared to the modern semi-arid conditions of the Karoo.

In Africa the spread of grasslands was a key factor in the evolution and dispersal of open-habitat taxa such as alcelaphine bovids and equids (Churcher & Richardson 1978; Gentry 1978). A feature which seems to characterize bovid evolution in the Plio-Pleistocene of sub-Saharan Africa is the tendency towards regional differentiation through time. In southern Africa this is evidenced by an increase in endemism towards the late Quaternary, of which the modern bovid fauna is the product (Vrba 1976, 1979; Bigalke 1978; Gentry 1978; Gentry & Gentry 1978). One example of this increase in endemism is the evolution of *M. priscus*. An ancestral form, *M. katwinkeli*, is known from East Africa and possibly some southern African Plio-Pleistocene sites, but in the Middle and Late Pleistocene the genus *Megalotragus* is only found in southern African fossil assemblages (Gentry & Gentry 1978; Klein 1984; Marean 1992). Within the genus *Megalotragus* there also appears to be an evolutionary development from the Middle Pleistocene to the Late Pleistocene, in accordance with a general trend towards increased regional differentiation as also seen in other alcelaphine bovids, such as the black wildebeest *Connochaetes gnou* (Brink 1993). In contrast to the view of Gentry (1978), who recognises only one species, i.e. *M. priscus,* in southern African fossil assemblages, we consider the earlier Cornelian specimens to be sufficiently distinct from the later Florisian ones to warrant specific distinction. The earlier Cornelian species, *M. eucornutus,* tends to have horns which are more vertically inserted and horn bases with unfused pedicels, while the later Florisian forms show a tendency towards greater horn divergence and well developed fused horn pedicels, which is considered to be an advanced feature in bovids (Gentry & Gentry 1978, Vrba 1979; Bender & Brink 1992). Ecologically this development is mirrored by an increased grassland component of the large mammal faunas from the Middle to the Late Pleistocene (Cooke 1974; Klein 1984; Brink 1987). This trend reached its climax in the interior of southern Africa during the late Quaternary and it appears that the Florisian Land Mammal Age was characterised by a complex grazing system, reminiscent of the

Serengeti grazing succession (Brink 1987; Brink & Lee-Thorp 1992).

LOCALITY AND GEOLOGY

The fossil material was found in one locality in erosional gullies ("dongas") in the bank of the Ongers River, approximately 70 km north of Britstown in the Northern Cape Province. The area is known as the T'Kuip Hills and forms an elevated landscape (Figure 1). The Ongers River, which forms the border between the districts of Britstown and Prieska, follows a fault east of the high ground that forms the T'Kuip hills. Denudations of the river bank exposed the fossil material. The exposed sediments, from which the fossil material was collected, consist of fine grained silts in which calcrete occurs. The fossil material was collected during a student excursion of the Department of Geology, University of the Orange Free State, in 1993.

FOSSIL MATERIAL

The fossil material is accessioned in the collections of the Florisbad Quaternary Research Department of the National Museum, Bloemfontein and is numbered as follows; ONG-1 horncore, ONG-2 dentary, ONG-3 distal tibia.

Bovidae
Alcelaphini
Megalotragus priscus (Broom, 1913)

The material consists of the lower part of a right horncore (Figure 2) and a partial right dentary of a sub-adult individual (Figure 3). Although the horn base is only partially preserved, it is clear that the horn pedicels were fused at the midline, as in *M. priscus* from Florisbad. The pedicels of Cornelian specimens are incompletely fused, which is considered a primitive feature (Vrba 1979; Bender & Brink 1992). However, it is likely that the horns were less laterally orientated (Figure 2) than in the Florisbad specimens. Gentry & Gentry (1978) noted that horncores from Cornelia appear to be more vertically inserted and speculated that this may be a primitive feature or that it may reflect ontogenetic age, where younger individuals have less divergent horncores. Another possible explanation for the variability in horncore diversion in Florisian specimens is that it reflects sexual dimorphism. A plot of basal dimensions of Florisian horncores in the collections of the Florisbad Quaternary Research Department of the National Museum shows that the smaller specimens had less compressed bases (Figure 4). Apart from two complete specimens from Florisbad (FLO 2273 and FLO 2899), we were able to measure

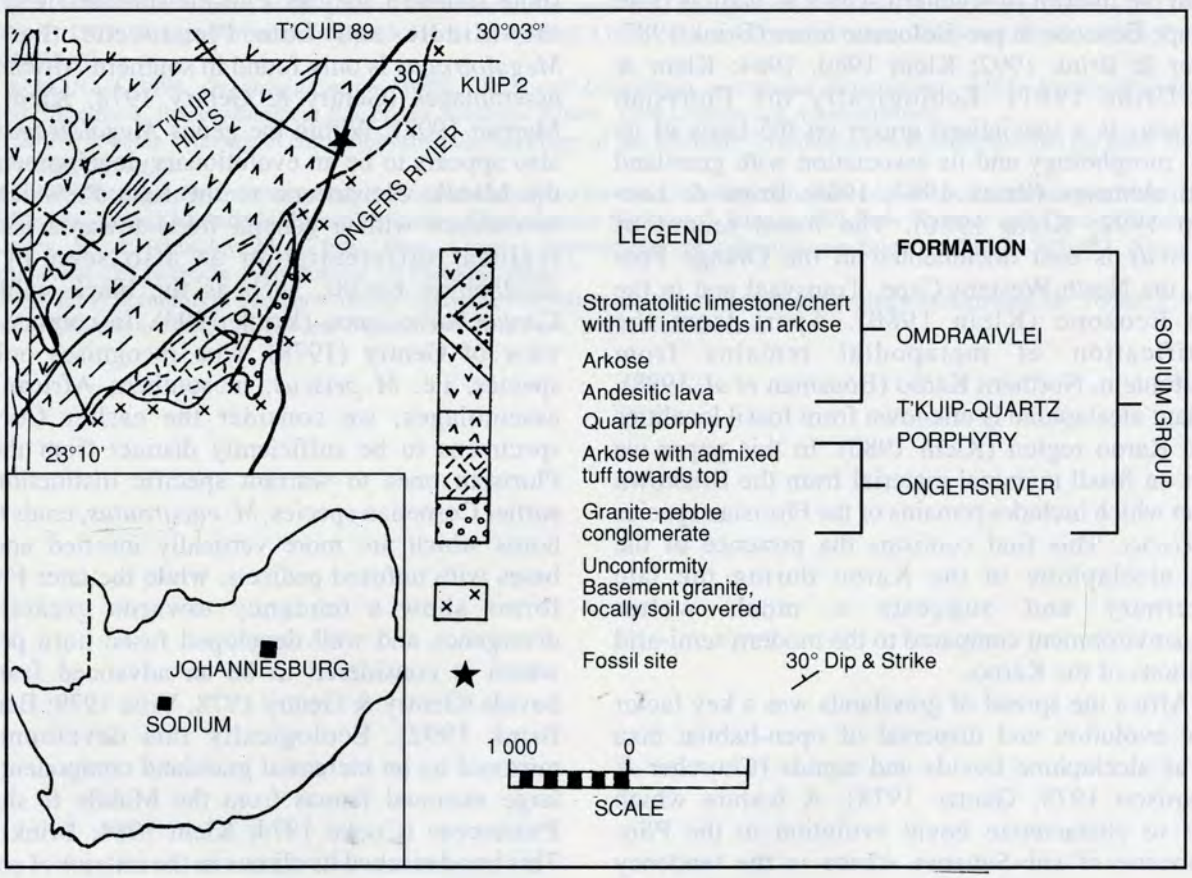


Figure 1. Maps showing the locality of the fossil material and surrounding bedrock geology where the Ongers River flows across an elevated landscape to the north of Britstown, Northern Cape Province.

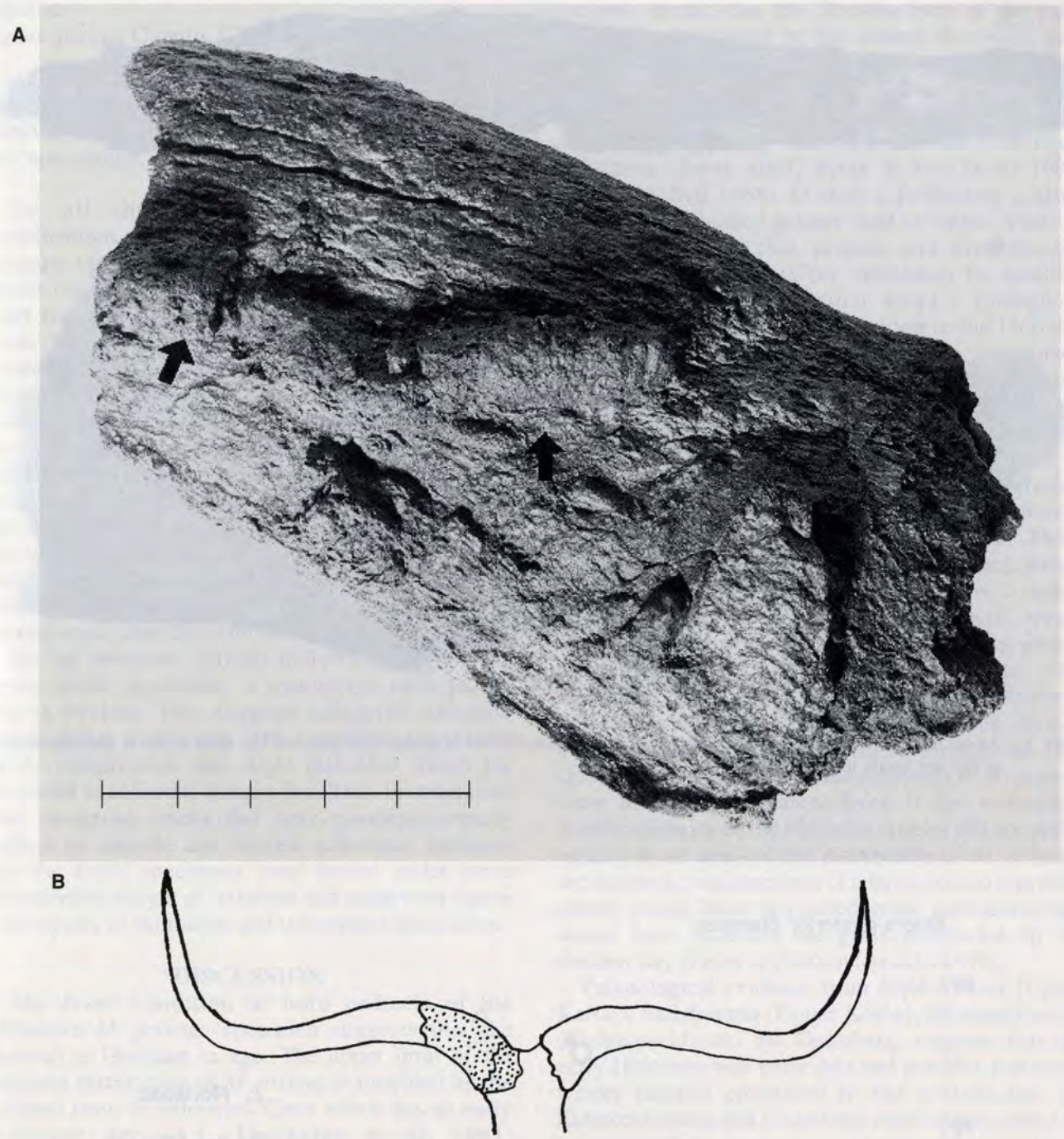


Figure 2. (A) Right horncore fragment of *Megalotragus priscus* (scale in centimetres). The illustration (B) shows the approximate natural position of the fragment .

additional specimens from the Sand River (catalogue number C. 1711) and from the Modder River (catalogue number C. 1607). The specimen from the the Sand River is a virtually complete horncore pair which shows well-developed fused pedicels, but more vertically inserted horncores than the much larger Florisbad specimens. If the small size of the Sand River specimen is taken as an indication that it is female, then pronounced basal compression and wide diversion in Florisian *Megalotragus* horncores could be taken as male characteristics. It is likely that the Sand River specimen is adult, since the horncores are virtually complete and show fully developed curvatures. In this context the Britstown specimen was probably a female.

The partial right dentary comprises only the horizontal ramus that contained milk premolars and developing molars. It is broken between M_2 and M_3, and lacks the symphysial region and the ascending ramus; dP_3 and most of dP_4 are missing. The hypoconid of dP_4 shows a stage of late wear, M_1 is in mid-wear, M_2 in early wear and M_3 is about to erupt, but is within the crypt. The short premolar row and the absence of P_2 are both apomorphic features characteristic of *Megalotragus priscus* (Gentry & Gentry 1978).

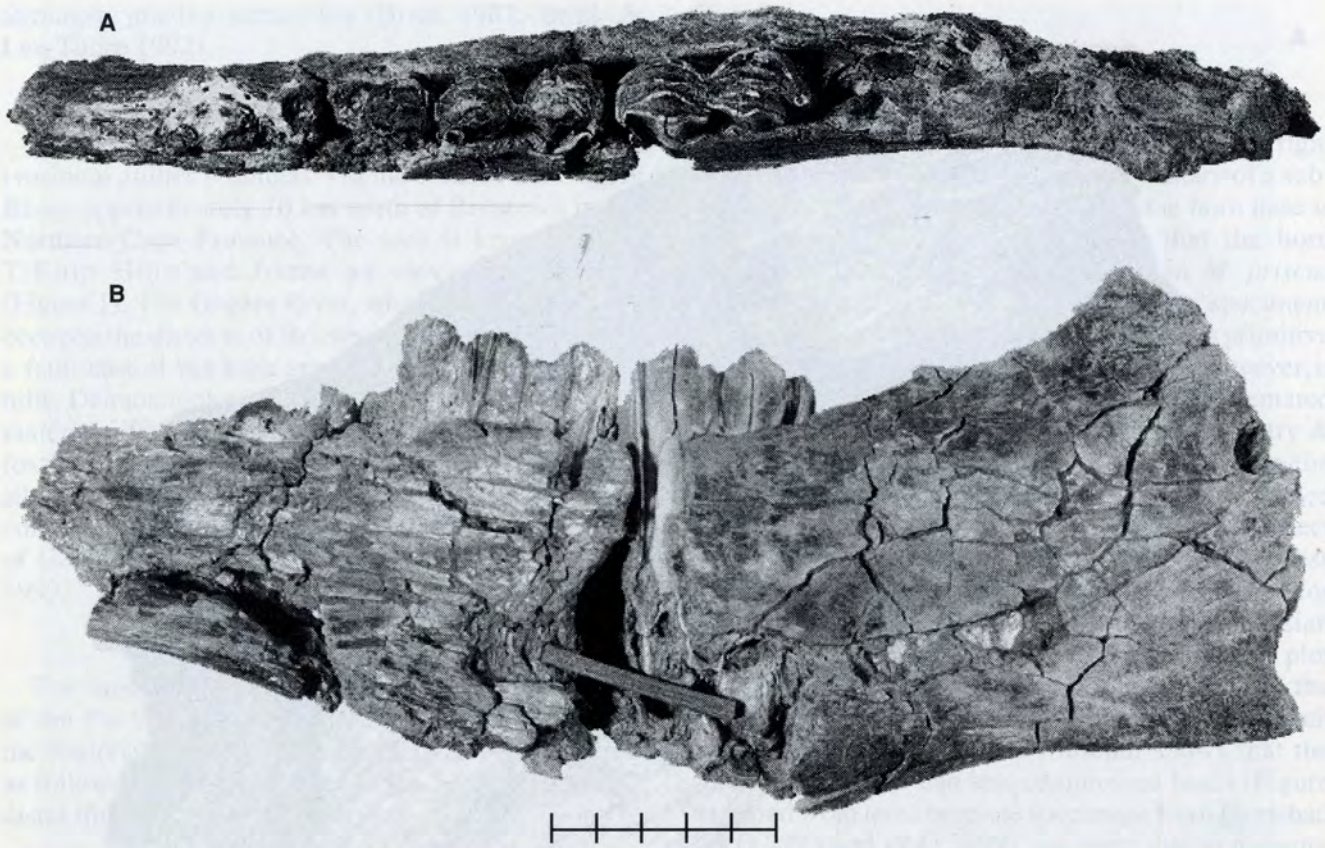


Figure 3. An occlusal view (A) and lingual view (B) of a right mandible of *Megalotragus priscus*. The third molar is still embedded in the jaw (scale in centimetres).

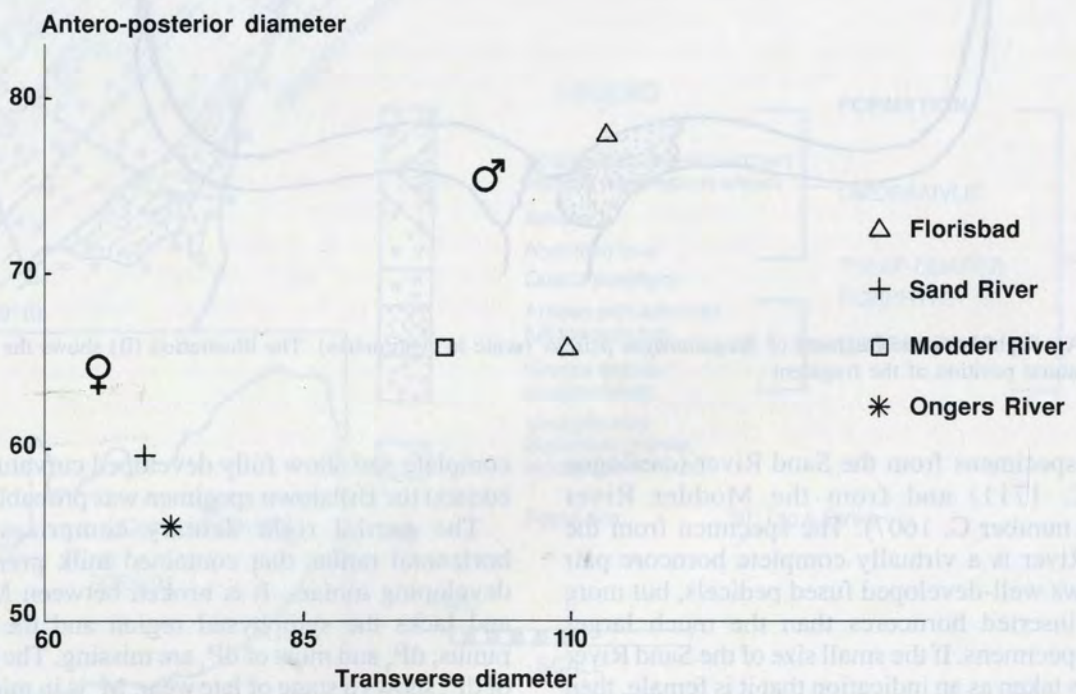


Figure 4. A scatter plot of *Megalotragus* horncore measurements. The two clusters are interpreted as representing sexual dimorphism.

Equidae
Equus quagga Gmelin, 1788

A distal fragment of an equid tibia, although large (distal maximum breadth: 73.8 mm; distal maximum depth: 54.0), is tentatively assigned to the plains zebra or Cape quagga.

TAPHONOMY

On all three specimens postdepositional modifications virtually obliterate possible traces of primary taphonomic agents. Only the equid tibia shows evidence of pre-depositional breakage, as the shaft was clearly shattered when the bone was still fresh. This may have been the result of the bone-crushing activities of either humans or carnivores. However, the extent of postdepositional alteration to the specimen precludes the identification of stone tool cutmarks or carnivore toothmarks. Unfortunately not much is known about the sedimentary context of the specimens and therefore, the primary agents of accumulation cannot be established. However, the typical reddish-brown colour of the specimens and calcrete adhesions suggest a matrix of aeolian soil which had become saturated by calciumcarbonate-rich ground water after deposition.

On the horncore, infilled hollows caused by the larvae of the horn moth, *Ceratophaga vastella*, are clearly evident. This suggests sub-aerial exposure before burial took place. The mandible specifically shows compression and slight distortion which are attributed to sediment compaction. This, in conjuction with numerous cracks that were postdepositionally infilled by calcrete and calcrete adhesions, indicates that the fossil specimens were buried under some considerable weight of sediment and underwent one or more cycles of saturation and subsequent dessication.

DISCUSSION

The fused condition of horn pedicels of the Britstown *M. priscus* specimen suggests that the material is Florisian in age. The upper limit of the temporal distribution of *M. priscus* is provided by the material from Wonderwerk Cave which has an early Holocene age (A.I. Thackeray et al. 1981; J.F. Thackeray 1983). From the Cape coastal zone giant alcelaphine material from Nelson Bay Cave dates to ca. 12 000 years ago (Klein 1984). The lower age limit of the Florisian Land Mammal Age is not firmly established, but a reasonable consensus is an age of not much older than end Middle Pleistocene, which is the assumed age for the Florisbad Spring assemblage (Klein 1984; Brink 1987). Although it is not possible to give a more precise age estimate of the fossil material than to suggest that it is of pre-Holocene late Quaternary age, it is likely, judging from its relatively unmineralised state, that the material is not old and probably not much older than terminal Pleistocene.

Even if the precise age of the specimens is not known, the value of the material lies in the fact that we are now certain that the Florisian form of the giant alcelaphine occurred in the central Karoo in pre-Holocene times. Ecologically this is significant, since the species has been associated with a range of other Florisian grazers in a grazing system resembling the present-day grazing succession of the Serengeti grasslands (Brink 1987; Brink & Lee-Thorp 1992; Gwynn & Bell 1968). In such a facilitating grazing system larger-bodied grazers feed at higher levels in the grassland and thus prepare and stimulate the individual grass plants for utilisation by smaller-bodied grazers. The extinct Bond's springbok, *Antidorcas bondi*, has a key position in the Florisian grazing system as the smallest of the specialized grazers and can be seen as a reliable indicator of highly productive grasslands (Brink & Lee-Thorp 1992). As the smallest of the specialised grazers, the presence of *A. bondi* in the fossil record may well be used to predict the geographical limits of the Florisian grazing system, which probably included at least the present highveld and most of the Karoo (Brink & Lee-Thorp 1992). *M. priscus*, as a large grazing ruminant, would have acted as one of the coarse grass feeders in such a grazing system. Grazing by larger animals would cause regeneration of nutrient-rich grass plants necessary for smaller-bodied ruminants. The hypothesis that virtually the entire interior of southern Africa, including the Karoo, accomodated such a grazing system at certain times during the late Quaternary is supported by the discovery of *M. priscus* from the Britstown area. Even if the ecological interdependance of the Florisian species did not apply equally in all areas of the distribution of *M. priscus*, the metabolic requirements of a large-bodied ruminant grazer would have demanded grass production that would have exceeded the grass production in the modern-day Karoo vegetation (Acocks 1975).

Palynological evidence from Blydefontein (Upper Karoo), Badsfontein (Upper Karoo), Eksteensfontein (Richtersveld) and the Cedarberg, suggests that the early Holocene was more arid and possibly had more winter rainfall compared to the present-day. At Eksteensfontein and Cedarberg aridification seems to be indicated by an increase of "succulent" pollens. Modern patterns of seasonality and rainfall were probably only established from the middle Holocene (Bousman et al. 1988; Scott 1992; Scott 1994; Scott in press). The existence of *M. priscus* in the Karoo could be seen as additional evidence for wetter conditions in pre-Holocene times and it is probable that its dissappearance from this area and elsewhere in central southern Africa at the end of the Late Pleistocene reflects early Holocene aridification on a wide-scale.

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