Preliminary investigation of Matjhabeng, a Pliocene fossil locality in the Free State of South Africa

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The early Pliocene is a relatively poorly understood period in southern Africa. Fossil deposits such as Langebaanweg (*c.* 5.0 Ma) and Makapansgat (*c.* 2.5 Ma) have each produced large and well-documented faunal assemblages, and it is clear that a significant turnover of fauna occurred between the early and late Pliocene respectively. However, the temporal separation between Langebaanweg and Makapansgat represents a significant gap in our knowledge of faunal composition and evolution in the Pliocene of southern Africa. In 2007 we began a programme of excavation at an early Pliocene locality referred to as Matjhabeng (formerly Virginia) in the Free State of South Africa. With an estimated age of 4.0–3.5 Ma, this site represents a temporal and geographic intermediate between the better known sites to the north and south. It also represents the only well-documented, river-deposited Pliocene locality in the central interior of southern Africa. After three years of excavation, we have recovered a diverse fauna that includes fish, amphibians, reptiles, birds and mammals. Mammals range in size from rodents to mammoths, including an array of proboscideans, perissodactyls and artiodactyls, alongside rare carnivores. We report here on the macromammalian assemblage recovered to date. In total, we have recognized 29 taxa, including the oldest *Ancylotherium* and the oldest *Megalotragus* fossils in southern Africa. Some of the taxa from Matjhabeng are shared with Langebaanweg, and others with Makapansgat, confirming the intermediate status of this locality. Isotopic analysis reveals the earliest indication of extensive grasslands in South Africa, though these grasslands were part of an environmental mosaic that included significant woodland, and probable wetland, components.

Keywords: *Megalotragus, Mammuthus subplanifrons,* faunal assemblage, isotopes, earliest grasslands.

INTRODUCTION

The early Pliocene of Africa represents a crucial period in the evolutionary history of the Hominidae, and in East Africa, numerous fossil localities in Ethiopia, Kenya and Tanzania sample this time frame (Brunet *et al.* 2002; Haile-Selassie *et al.* 2004; Leakey *et al.* 1995, 1998; White *et al.* 1994, 1995, 2009). However, the same period in South Africa is relatively poorly known. The site of Langebaanweg in the Western Cape has produced a particularly rich, well-documented faunal assemblage dating to approximately 5.0 Ma (Hendey 1981a,b, 1982). However, the chronologically closest sites to Langebaanweg with significant faunal samples are the hominin-bearing caves of the former Transvaal, such as Makapansgat and Sterkfontein, both of which fall into the late Pliocene. With dates of less than 2.5 Ma for these latter sites (Berger *et al.* 2002; Latham *et al.* 2007; Pickering & Kramers 2010; Walker *et al.* 2006), the temporal separation between Langebaanweg and Makapansgat/Sterkfontein represents a significant gap in our knowledge of faunal composition and evolution in the earlier Pliocene of South Africa. What is therefore needed is a faunal sample from a locality within this time range.

In 1955, during the course of digging operations to open a new railway cutting near the town of Virginia in the Free State, workers uncovered several fossils of an extinct proboscidean, including a tusk, a molar, and a proximal ulnar fragment. The site is located on Farm Virginia 448 (reference map 2826BB; 28°06′39′S, 26°54′56′E), and was originally referred to as the Virginia Railway Cut Site, though to avoid confusion with sites outside of South Africa we have renamed the locality Matjhabeng in honor of the Municipality in which it resides (Fig. 1). Originally attributed to a new species, *Mammuthus scotti* (Meiring 1955), these first fossils were later referred to *M. subplanifrons* (Maglio 1973; Maglio & Hendey 1970). Although *M. subplanifrons* is currently poorly defined (Cooke & Maglio 1972; Maglio & Hendey 1970), there are nonetheless several cranio-dental features that can diagnose the taxon (Kalb & Mebrate 1993; Maglio 1973). In particular, the presence of a characteristically curved tusk in the Matjhabeng specimen renders it one of the most securely identified *Mammuthus* individuals in Africa (Coppens *et al.* 1978; Maglio 1973). Within the Free State, in fact within the central interior of southern Africa, the site of Matjhabeng affords the unique opportunity to examine the composition of an early Pliocene faunal assemblage recovered from a horizontally stratified, riverine deposit.

PLIOCENE FAUNAS OF SOUTHERN AFRICA

The remarkable fauna recovered from the site of Langebaanweg stands in stark contrast to the faunas recovered from such late Pliocene South African localities as Makapansgat and Sterkfontein. Langebaanweg is generally considered to be earliest Pliocene in age at *c.* 5.0 Ma (Hendey 1981a,b, 1982), though some have suggested an even older date of 6.0 Ma (Gentry 1980). The

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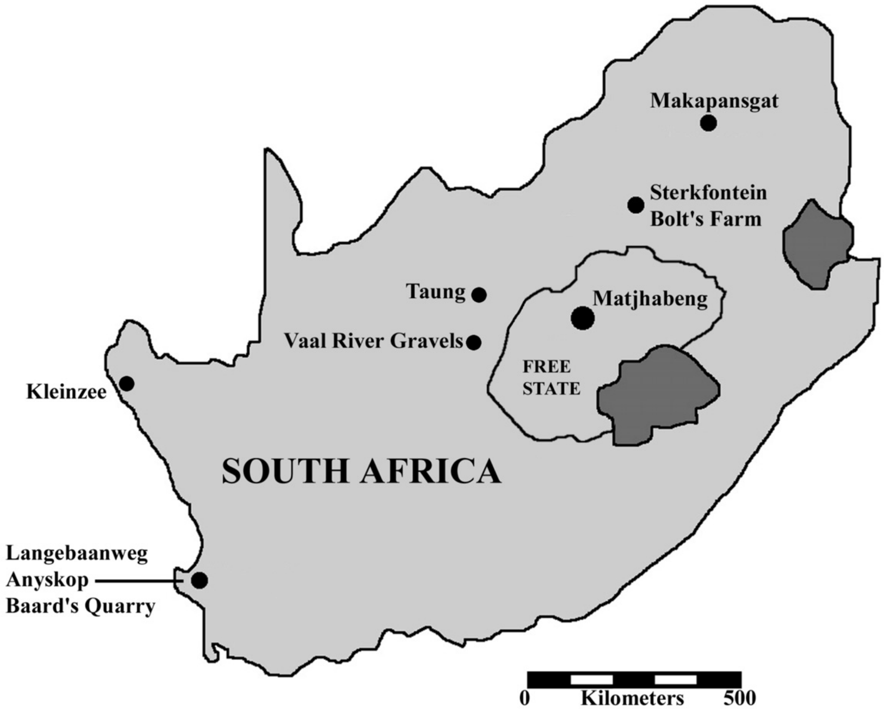

Figure 1. Map of South Africa showing the main fossil localities mentioned in the text.

faunal assemblage itself exhibits a number of taxa not known from elsewhere in southern Africa (Hendey 1976a,b, 1982), and represents a particularly rich and diverse animal community (Bone & Singer 1965; Gentry 1974, 1980; Hendey 1970, 1972, 1973, 1976a,b, 1978a,b, 1981a). The majority of Langebaanweg species are extinct, and include such exceptional taxa as the only ursid (*Agriotherium africanum*), okapi (Palaeotragine) and peccary (*Pecarichoerus africanus*) known in southern Africa (Hendey 1976a,b, 1982). Approximately 2 km east of Langebaanweg is the fossiliferous Bredasdorp Formation, which includes two separate deposits, Anyskop and Baard's Quarry (Hendey, 1978c, 1982). Anyskop appears to be later Pliocene in age, and comprises mainly land snail and tortoise shells with rare mammalian fossils (Hendey 1982). Baard's Quarry contains highly fragmented terrestrial vertebrate fossils that are considered to be either late Pliocene or early Pleistocene (Gentry 1980; Hendey 1978c). The first fossil specimen recovered from Baard's Quarry was a proboscidean molar fragment that was referred to *M. subplanifrons* (Hendey 1978c; Maglio & Hendey, 1970; Singer & Hooijer 1958). Unfortunately the specimen has since gone missing, and its identification as *M. subplanifrons* is inconclusive (e.g. Maglio 1973). Hendey (1978c) documented some level of mixing in the Baard's Quarry fauna, further complicating age estimation of the deposit.

The 'Older Gravels' of the Vaal River Gravels have produced a series of haphazardly collected fossils, some of which possibly exceed 4.0 Ma in age (Butzer *et al.* 1973; Helgren 1977, 1979). The majority of the fossils were collected in the early half of the last century by amateurs thus only minimal provenance information is available. Today virtually all of the Vaal River Gravels have been disturbed or destroyed by more than a century of active diamond mining. Although there is no clear relationship between fossils attributed to the 'Older Gravels', several important specimens have been described in the past, including the type specimen of *M. subplanifrons* (Osborn 1928). On the west coast of South Africa, Kleinzee is a little known fossil locality located approximately 400 km north of Langebaanweg in Namaqualand, at the mouth of the Buffels River. Originally thought to be 'middle Pliocene' (Stromer 1931), the site is now considered to be late Pliocene or early Pleistocene (Hendey 1970).

The site of Taung in the Northwest Province revealed the first ever recovered australopith fossil (Dart 1925). Although the initial consignment of breccia sent to Dart in 1924 included a selection of non-hominin fossils, the association between these fossils and the Taung Child itself is uncertain owing to the blasting operations that originally revealed the hominin skull (de Ruiter *et al.* 2010). Subsequent exploration in the 1920s (Hrdlička 1925) and again in the 1980s and 1990s (McKee & Tobias 1990) failed to recover additional hominin remains and the composition of the animal paleocommunity to which the Taung fossil belonged remains unknown. The age of the site is estimated at 2.8–2.4 Ma (McKee 1993), though uncertainty over the actual make-up of the Taung faunal assemblage makes an accurate age estimate difficult.

Bolt's Farm is located approximately 2 km southwest of Sterkfontein, and consists of a series of irregularly excavated gravel pits that have been unsystematically sampled over the past several decades. The majority of the fossil deposits have been destroyed by gravel mining activities, and the relationship between recovered fossils is uncertain. Age estimates range from 4.0–2.0 Ma for different components of the site, and it is clear that the Bolt's Farm complex does not represent a single depositional unit (Cooke 1991; Senegas & Avery 1998).

Sterkfontein was intermittently excavated between the 1930s and the 1950s (Broom 1951). Beginning in 1966, excavations that continue to this day have revealed an extensive collection of hominin fossils (Clarke 1998; Lockwood & Tobias 1999, 2002; Moggi-Cecchi *et al.* 2006). In addition, large and diverse faunal assemblages have been recovered from the various members of Sterkfontein (Brain 1981; Kibii 2007; Pickering 1999; Pickering *et al.* 2004; Turner 1987, 1997; Vrba 1976). Member 2 has been dated to approximately 3.3 Ma using magnetostratigraphy (Partridge *et al.* 1999, 2000) and 4.1 Ma using cosmogenic nuclides (Partridge *et al.* 2003). However, more recent estimates based on U-Pb indicate an age of 2.2 Ma (Pickering & Kramers 2010; Walker *et al.* 2006), a date that is more consistent with the fauna recovered from the site (Berger *et al.* 2002). Member 4 is estimated to be between 2.0–2.5 Ma (Berger *et al.* 2002; Delson, 1984, 1988; White & Harris 1977), with an ESR date of 2.1 Ma falling well within this temporal range (Schwarcz *et al.* 1994). The most recent U-Pb age estimate of 2.6–2.0 Ma for Member 4, with a probable rapid accumulation of most fossils around 2.2 Ma, supports these latter dates (Pickering & Kramers 2010). A series of infills once collectively referred to as Member 5, but now separated into 3 discrete deposits within this Member, are considered Plio-Pleistocene, aged between approximately 1.4–2.0 Ma respectively (Kuman & Clarke 2000).

Makapansgat has produced a very large and well-documented faunal assemblage (Ewer 1956, 1958; Reed 1996; Vrba 1987; Wells & Cooke 1956). Of the four fossil-bearing Members, only two have produced hominins (Members 3 and 4). With the exception of the younger and less completely excavated Member 5, the Makapansgat deposits can be dated to approximately 2.5 Ma (Delson 1984, 1988; Latham *et al.* 2007; White & Harris 1977). Although Makapansgat and Sterkfontein have themselves produced several extinct taxa (Reed 1996; Wells & Cooke 1956), it is clear that a significant turnover of fauna occurred between the early and the late Pliocene. At the same time, while primates tend to be relatively abundant in the Transvaal caves, to date only a single individual primate has been recovered from Langebaanweg (Grine & Hendey 1981).

THE MATJHABENG FAUNAL ASSEMBLAGE

In 2007 we began the first systematic excavations at the site of Matjhabeng, and have now conducted three excavation seasons. We have concentrated our activities in two principal areas: a 14 ×14 m pit on the Farm Virginia 448, and the erosional faces of the railway cutting itself. To date we have recovered 903 individually numbered specimens, representing a diverse assemblage that includes 14 orders, 21 families, and at least 29 discrete taxa (Table 1). At present the majority of taxa are not identifiable to the level of the species, though additional materials recovered continue to refine our taxonomic diagnoses. In this paper we describe the macromammalian assemblage, while the micromammalian and non-mammalian assemblages will be described elsewhere.

Excavations at Matjhabeng follow a complete collection strategy, as every bone, tooth, or fragment encountered is retained. Excavation proceeds in 1 × 1 metre squares along 10–20 cm depths depending on the sediment being excavated. Trowels are employed in softer sediments, while the more heavily cemented gravels require hammers and small probes to remove matrix. All fossils are point-provenanced when recognized *in situ,* and are provenanced to grid squares during sieving. Apart from overburden sediments, all materials are sieved using ¼-inch screens. A sample of these sieved sediments is rescreened using 0.4 mm fine-mesh screens to search for microfossils. Fossils are cleaned with small brushes, accessioned, and stored at the National Museum, Bloemfontein. Dental measurements are recorded for complete dental specimens using digital callipers, to the nearest 0.1 cm.

Order **PROBOSCIDEA** Illiger, 1811

Family **ELEPHANTIDAE** Gray, 1821

Mammuthus subplanifrons (Osborn), 1928

The original fossils recovered from Matjhabeng in 1955 were attributed to *M. subplanifrons* (Maglio 1973; Meiring 1955). The majority of mammoth fossils that we have recovered are isolated enamel fragments, though a complete molar tooth was retrieved in 2007 (MRC 138, Fig. 2). Although individual mammoth teeth are difficult to identify, the small size of this specimen suggests it represents a deciduous tooth, and several features of this tooth align it with *M. subplanifrons.* The tooth is broad, with 6 plates. The plates are relatively thick, with wide intervening cementum intervals. The enamel averages 3.2 cm thick, and is relatively unfolded. Each crown is divided into 6–9 apical digitations, with a prominent median cleft on the first plate. Additional mammoth tooth fragments, including several relatively complete enamel plates, support this diagnosis. The recovery of additional *M. subplanifrons* material is important in that it confirms we are indeed sampling the same area from which the original Matjhabeng (= Virginia Railway Cut) fossils were recovered.

Order **CARNIVORA** Bowdich, 1821

Family **HYAENIDAE** Gray, 1869

Three tooth fragments were recovered that are similar to hyaenid specimens from Langebaanweg, including half of a mandibular incisor (MRC 152), a canine enamel fragment (MRC 137) and a partial P^4 (MRC 210). These remains are too fragmentary to identify beyond the family level, nonetheless demonstrate the existence of at least one form of hyaenid at the site.

Family **CANIDAE** Gray, 1821

cf. *Vulpes* (A. Smith, 1833)

Two mandible fragments are identifiable as belonging to a small canid. One fragment is edentulous (MRC 734), while the other retains a slightly eroded premolar tooth

Table 1. List of taxa recovered during systematic excavations at Matjhabeng between 2007 and 2009.

Class	Order	Family	Tribe	Genus and species
Actinopterygii	Order indet.			
Amphibia	Anura	Family indet.		
Reptilia	Squamata	Agamidae		Gen. indet.
		Varanidae		*Varanus* sp.
		Gerrhosauridae		*Gerrhosaurus* sp.
		Elapidae		Gen. indet.
	Testudinata	Testudinidae		Gen. indet.
	Crocodylia	Crocodylidae		Gen. indet.
Aves	Podicipediformes	Podicipedidae		Gen. indet.
	Ciconiiformes	Threskiornithidae		Gen. indet.
Mammalia	Rodentia	Bathyergidae		cf. *Cryptomys*
		Muridae		Gen. indet.
		Gerbillinae		cf. *Tatera*
		Murinae		cf. *Aethomys*
				cf. *Euryotomys*
		Pedetidae		*Pedetes* sp.
	Insectivora	Soricidae		Gen. indet.
	Lagomorpha	Leporidae		Gen. indet.
	Proboscidea	Elephantidae		*Mammuthus subplanifrons*
	Carnivora	Hyaenidae		Gen. indet.
		Canidae		Gen. indet.
	Perissodactyla	Equidae		*Eurygnathohippus* sp.
		Chalicotheriidae		*Ancylotherium* sp.
	Artiodactyla	Giraffidae		*Sivatherium* sp.
		Hippopotamidae		*Hippopotamus* sp.
		Bovidae	Alcelaphini	*Megalotragus* sp.
				cf. *Damalacra* sp.
			Reduncini	Gen. indet.
			Antilopini	Gen. indet.
			Neotragini	Gen. indet.

(MRC 390, Fig. 3). Although the small size of the mandibles and tooth overlap with some larger viverrids, the premolar root is robust, rounded, and straight like that seen in canids. MRC 390 also compares favourably with the small canids from Langebaanweg that are equivalent in size to *Vulpes* (Hendey 1974).

Order **PERISSODACTYLA** Owen, 1848

Family **EQUIDAE** Gray, 1821

Eurygnathohippus van Hoepen, 1930

Numerous equid tooth fragments have been recovered, alongside a complete LP_4 (MRC 1), a complete RM_1 (MRC 845) and an isolated incisor (MRC 496) (Fig. 4). The premolars are hypsodont, with clearly delineated ectostylids, and both arms of the preflexids are short and directed perpendicular to the mesiodistal axes of the teeth. The incisor is large and cement filled, with an open infundibulum. Based on these characters, all three of these teeth can be attributed to the genus *Eurygnathohippus,* though a specific diagnosis is not yet possible.

Family **CHALICOTHERIIDAE** Andrews, 1923

Ancylotherium (Dietrich, 1942)

Two specimens have been attributed to the Chalicotheriidae, a right calcaneum (MRC 613) and an isolated tooth cusp (MRC 619). The only chalicothere taxon recognized in the Pliocene of Africa is *Ancylotherium hennigi* (Butler 1978). However, given the fragmentary nature of most African chalicothere fossils, and our imperfect grasp of morphological variability in this taxon, we refrain from assigning our fossils to the species level at present. That being said, the calcaneum does appear particularly diagnostic, as it compares favourably with calcanei assigned to *A. hennigi* from Makapansgat (Butler 1978; Webb 1965). Although it is approximately the same overall size as other large perissodactyls, such as white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceroses, it is less robustly built with a relatively slender neck (Fig. 5). Chalicothere fossils are quite rare in Africa, and Matjhabeng represents the earliest record of this taxon in South Africa.

Order **ARTIODACTYLA** Owen, 1848

Family **GIRAFFIDAE** Gray, 1821

Sivatherium Falconer & Cautley, 1835

Exploration of the eroding banks of the railway cutting revealed two giraffid specimens, a large ossicone fragment (MRC 650, found by J.S. Brink) and a partial tibia (MRC 3). Given their close proximity it is possible that they are derived from the same individual. The large ossicone fragment is well preserved (Fig. 6), and can be attributed to the extinct short-necked giraffe *Sivatherium.* Since ossicones are generally absent in *Sivatherium* females this is likely to be a male individual. Furthermore,

Figure 2. *Mammuthus subplanifrons* deciduous molar tooth (MRC 138). Scale bar = 50 mm.

given the relative lack of adornment of the ossicone, it is probable that this was a relatively young individual (see Churcher 1978: 525). The tibia is highly fragmented but appears relatively stout and long.

Family **HIPPOPOTAMIDAE** Gray, 1821

A single hippopotamus tooth fragment was recovered (MRC 647), likely representing a premolar. Given the fragmentary nature of the find, identifying the genus to which this tooth belongs is difficult. The genus *Hippopotamus* has been recognized at Langebaanweg (Hendey 1976a), while *Hexaprotodon* is unknown in the earlier Pliocene of South Africa. On this limited evidence we anticipate that future, more complete discoveries will confirm a diagnosis of *Hippopotamus* sp., though at present we assign this specimen only to the family Hippopotamidae.

Family **BOVIDAE** Gray, 1821

Tribe **Alcelaphini** Rochebrune, 1883

Megalotragus van Hoepen, 1932.

Bovid fossils in the form of isolated teeth are relatively common, though they tend to be badly fragmented and eroded from water rolling, rendering identification difficult. However, one specimen in particular is well preserved, a hemi-mandible with RM_{1-3} attributable to

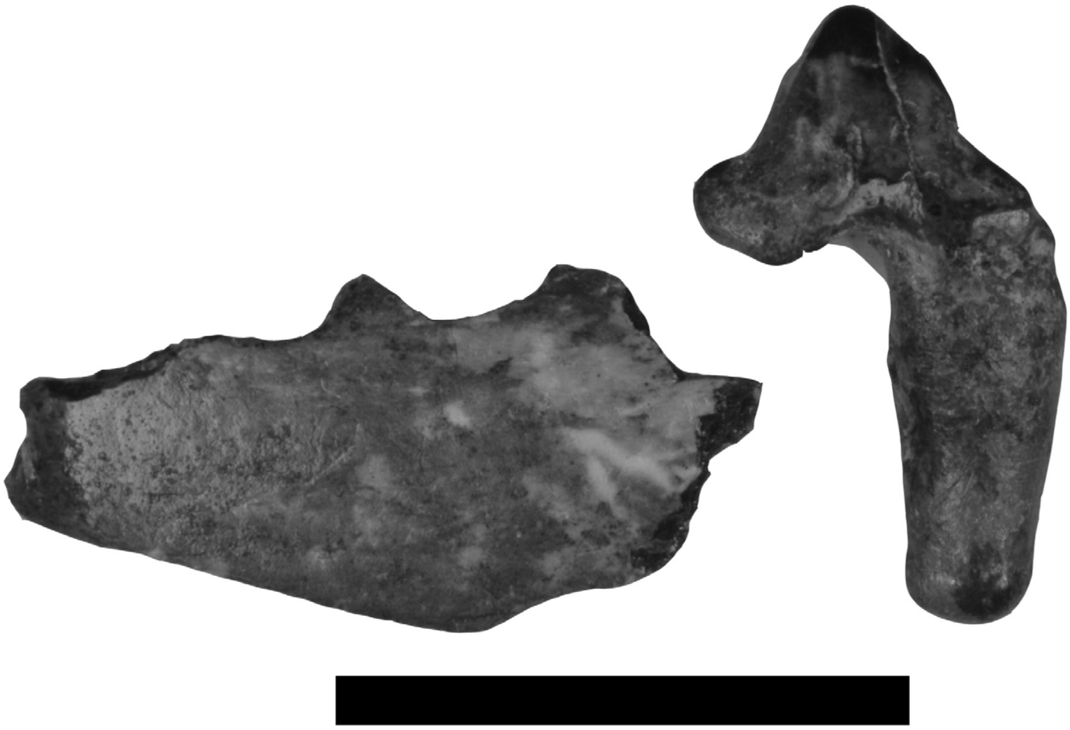

Figure 3. Mandible fragment and associated tooth of a small canid, probably *Vulpes* (MRC 390). Scale bar = 10 mm.

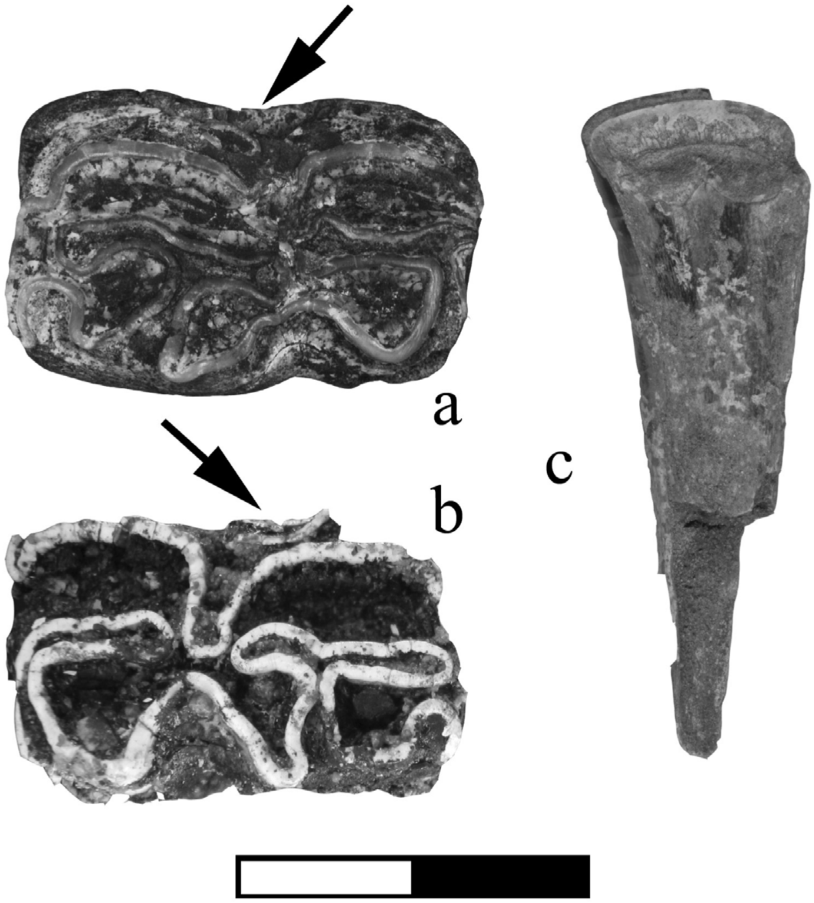

Figure 4. Isolated teeth of *Hipparion* sp.: **a**, LP_4 (MRC 1); **b**, RM_1 (MRC 845); **c**, isolated incisor (MRC 496). Arrows point to clearly separated ectostylids. Scale bar = 20 mm.

Megalotragus (MRC 605; Fig. 7). The lobes of the mandibular teeth of alcelaphines from Langebaanweg are more pointed, with more pronounced styles, confirming that this Matjhabeng specimen is not a late representative of the Langebaanweg fauna. Although small relative to later Pleistocene specimens from the Free State (Fig. 8), the teeth of MRC 605 nonetheless fall within the range of *Megalotragus* molar measurements recorded elsewhere in Africa. In addition, the corpus of the mandible is notably elongated and the angle of the ramus relative

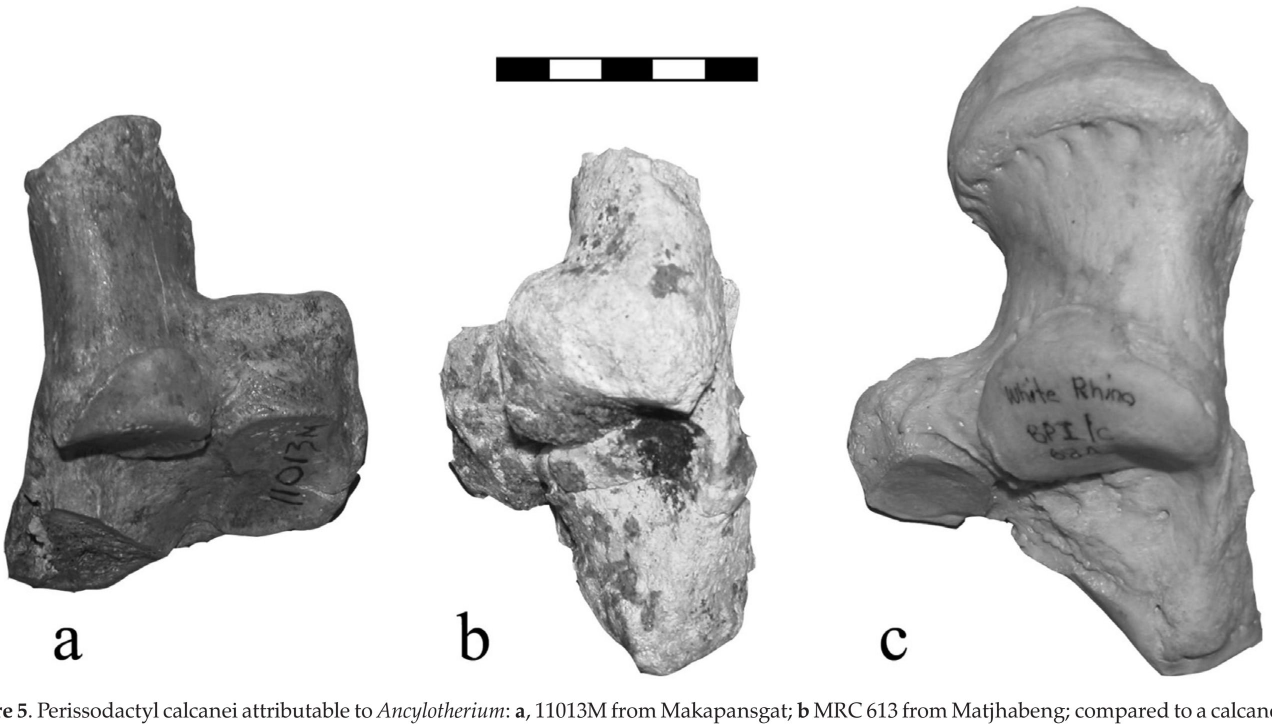

Figure 5. Perissodactyl calcanei attributable to *Ancylotherium*: **a**, 11013M from Makapansgat; **b** MRC 613 from Matjhabeng; compared to a calcaneum of *Ceratotherium simum*: **c**, BPI/C 684. Scale bar = 50 mm.

Figure 6. Large ossicone fragment of a probable young male *Sivatherium* (MRC 650). Scale bar = 50 mm.

to the corpus approaches 135°, similar to Mahemspan specimens (Brink 2005). Alongside the relatively uncomplicated occlusal pattern of the molars this posteriorly inclined ramus implies an elongated cranium such as that characterizing *Megalotragus.* Most species described in the genus *Megalotragus* are diagnosed on horn cores making comparison of MRC 605 difficult. As a result, until additional cranial material is recovered, we can only identify this specimen to the genus level. Notwithstanding, this mandible likely represents the oldest recorded appearance of *Megalotragus* in South Africa (see below).

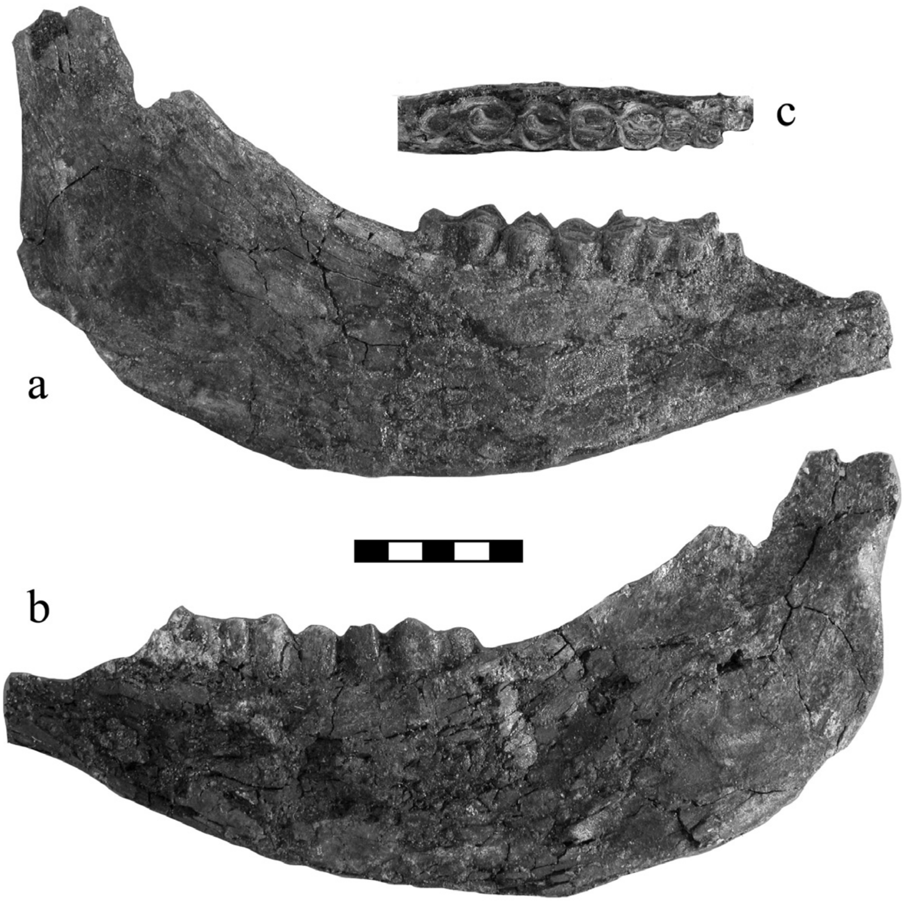

Figure 7. Relatively complete hemi-mandible of *Megalotragus* sp. (MRC 605) in (**a**) lateral, (**b**) medial and (**c**) occlusal views. Scale bar = 50 mm.

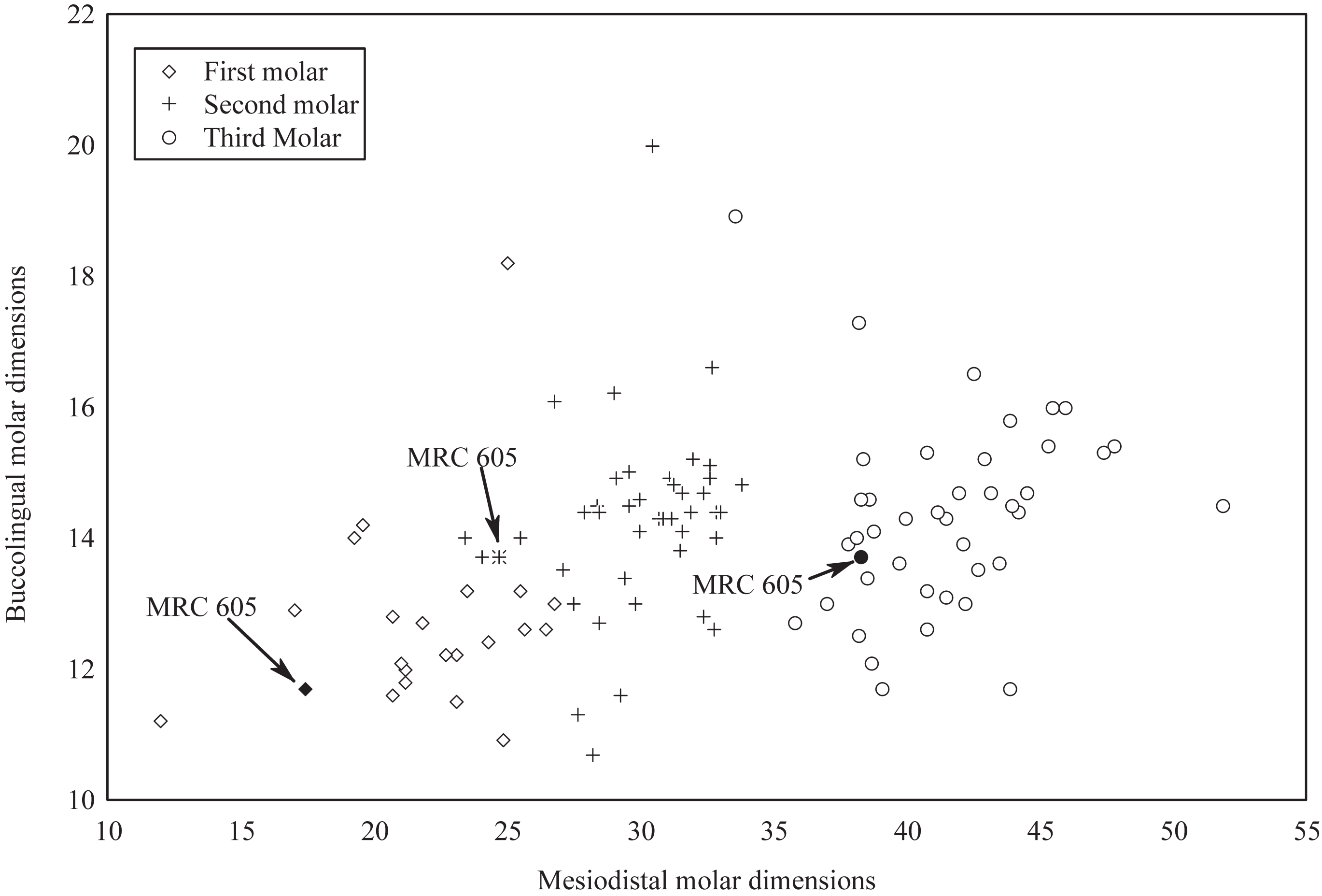

Figure 8. Scatter plot of mandibular molar measures of *Megalotragus* from Matjhabeng (MRC 605) compared to a selection of specimens from East and South Africa (measurements by D.J.D. for South African specimens, and from Harris (1991) for East African specimens). Although the Matjhabeng specimen is small, it falls within the ranges of molar teeth of *Megalotragus* from elsewhere in Africa.

cf. *Damalacra* Gentry, 1980

Several tooth fragments and a badly fragmented mandible (MRC 96) of alcelaphines were recovered, all of which compare favourably in size and morphology with *Damalacra* specimens from Langebaanweg. However, given that none of these fragments preserve complete teeth, the identification of *Damalacra* is only tentative at present.

Additional Bovidae specimens

A single tooth of a small Reduncini was recovered (MRC 795) and although little detail beyond a tribal level diagnosis is available we nonetheless record the presence of this tribe at Matjhabeng. The Antilopini are represented by a single tooth fragment (MRC 820) that is approximately the same size as a modern springbok. The Neotragini are represented by two post-cranial elements, an external cuneiform (MRC 804) and a magnum (MRC 824), both of which are consistent with being from a single individual. These neotragine fossils are considerably smaller than springbok (Antilopini) and are approximately similar in size to steenbok (*Raphicerus*) though they do not conform to this latter taxon. In fact their closest comparison is *Ourebia*, a taxon with a poorly documented fossil record. Post-cranial remains attributable to the Bovidae are also known with several relatively complete elements such as radii and cervical vertebrae present. These relatively rare post-cranial elements illustrate the potential for good preservation since the cervical vertebra, for instance, is almost complete including much of the otherwise delicate zygapophyses.

STRATIGRAPHIC ANALYSIS OF MATJHABENG

In addition to fossil recoveries our excavations have allowed for a comprehensive stratigraphic analysis to be completed. Results revealed a slightly more complex sedimentological sequence than was recognized by Butzer (1973) with 9 facies in 3 discrete facies associations. The site represents a good aggradational sequence that is unique in the central interior of southern Africa. Of particular interest is facies association 1 at the base of the sequence, which contains the fossiliferous sediments (referred to by Butzer as Horizon 2). This predominantly graveliferous unit includes genetically identical interbedded silty-sand units that together comprise between 1.0 to 3.0 m of fossiliferous deposition. The gravel component represents a high-energy river discharge while the silty-sand units represent abandoned-channel equivalents formed when the paleo-river periodically changed its course. Fossils have been recovered from both units and tend to be concentrated near the interface between these components. Fossil density is low relative to cave infills such as Makapansgat and Sterkfontein. Fossils recovered from the gravels tend to be more eroded though some display excellent preservation while those recovered from the abandoned-channel, silty-sand deposits tend to be relatively well preserved.

AGE OF THE DEPOSIT

Mammuthus subplanifrons was first named for an isolated tooth recovered from Sydney-on-Vaal (Osborn 1928), a fossiliferous unit of the 'Older Gravels' of the Vaal River Gravels in South Africa (Helgren 1979). The oldest specimens of *M. subplanifrons* are from Langebaanweg and are thus dated to approximately 5.0 Ma (Hendey 1981a,b, 1982; Maglio & Hendey 1970). Maglio (1973) suggested that the original Matjhabeng *M. subplanifrons* material described by Meiring (1955) was more derived than specimens known from Langebaanweg (Maglio & Hendey 1970), indicating a probable age near 4.0 Ma for Matjhabeng. In his examination of the geomorphology of the deposit, Butzer (1973) agreed with an estimate of 4.0 Ma for the site. Elsewhere in Africa, *M. subplanifrons* is recorded from the lower Kaiso Formation, Kanam, Chemeron locality J.M. 511, the Sinda Beds of Zaire, and the older Stratigraphic Unit 2 of the Chiwondo Beds, all of which are considered to be early Pliocene (>4.0 Ma) (Bromage *et al.* 1995; Cooke & Maglio 1972; Coppens *et al.* 1978; Howell 1972; Maglio 1973; Maglio & Hendey 1970; Yasui *et al.* 1992). Specimens consistent with *M. subplanifrons* are also known from the Wee-ee Dora in the Aramis Member of the Sagantole Formation (4.1–3.8 Ma) and the Kuseralee Dora in the Kuseralee Member of the Adu-Asa Formation (>4.4 Ma) in the Middle Awash sequence of Ethiopia (Kalb & Mebrate 1993). There do not appear to be any *M. subplanifrons* specimens in sediments younger than 4.0–3.5 Ma in East Africa, thus this taxon can best be ascribed an age of approximately 5.5–3.5 Ma (Maglio 1973).

Megalotragus has been recovered from both Pliocene and Pleistocene sediments throughout Africa. In East Africa the earliest occurrence of *Megalotragus* is in the Lokochot Member of the Koobi Fora Formation, with a maximum age estimate of 3.5 Ma (Harris 1991). Additionally *Megalotragus* fossils have been recovered from elsewhere in the Koobi Fora Formation, in the Nachukui Formation of west Lake Turkana, throughout the Shungura sequence, and in all four Beds of Olduvai Gorge. In South Africa *Megalotragus* fossils are known from Sterkfontein, Makapansgat, Swartkrans, Kromdraai, Coopers, Drimolen, Bolt's Farm, Haasgat, Gladysvale and Plovers Lake in the former Transvaal, as well as numerous sites in the Free State such as Florisbad, Vlakkraal and Mahemspan, among others. As a result, the age of *Megalotragus* appears to span from 3.5–0.009 Ma.

With an age estimate of 5.0–3.5 Ma for *M. subplanifrons,* and 3.5–0.009 Ma for *Megalotragus,* we can presently constrain the probable dates for Matjhabeng to 4.0–3.5 Ma. This range is consistent with earlier reports of 4.0 Ma for the site (Butzer 1973; Maglio 1973), though Matjhabeng is likely to fall nearer the younger end of this range. Recognizing the circularity of the argument (i.e. the age of Matjhabeng is partially established based on the presence of *Megalotragus*), the *Megalotragus* material from Matjhabeng nonetheless represents the oldest occurrence of this taxon yet recorded in South Africa.

ISOTOPIC ANALYSIS OF MATJHABENG FOSSILS

Carbon isotopes derived from enamel hydroxyapatite provide a reliable source of information relating to the dietary behaviour of Cenozoic herbivores (Lee-Thorp & van der Merwe 1991; Quade *et al.* 1992; Sponheimer *et al.* 2006). Variations observed in the $\delta^{13}C$ of carbonate hydroxyapatite of enamel reflect differences in the relative proportions of grass (C_4) and browse (C_3) vegetation consumed by the animal throughout its life. Because of the great potential for ecological information, we selected several samples for destructive analysis to determine their isotopic composition. Approximately 5.0 mg of powder was extracted per dental sample, and the samples were pretreated with sodium hypochlorite (NaOCl) and acetic acid (CH_3COOH). The samples were then combusted and analysed using a GasBench II system in combination with the DeltaPlusXP isotope ratio mass spectrometer to obtain $\delta^{13}C$ values. The results are reported against PDB (Pee Dee belemnite), and the standard NBS-19 (National Bureau of Standards) was used for calibration with a precision of 0.06‰. The results of this isotopic analysis are presented in Fig. 9.

Cerling *et al.* (1997) hypothesized an early emergence of C_4 grasslands in equatorial Africa during the late Miocene, suggesting that these grasslands gradually expanded both north and south over time. Sponheimer *et al.* (2005, 2006a,b) demonstrated considerable dietary flexibility in the early hominins of South Africa, and hypothesized that the ability to consume significant quantities of grassland-based C_4 resources was a fundamental hominin characteristic lacking in other African apes. The location and age of Matjhabeng allows us to test the Cerling *et al.* (1997) C_4 expansion model, to document if grasslands had already become a significant component of the Free State environment in the middle Pliocene. Carbon isotope analysis of a sample of Matjhabeng fossils (Fig. 9) reveals that most of the animals fall into a mixed feeder category, with a distinct preference for grazing. Interestingly, this includes a fragmented tooth of *Ancylotherium,* which is typically considered to have been a dedicated browser. Comparing these data to a series of average isotope values from sites elsewhere in Africa (Sponheimer & Lee-Thorp 2009), Matjhabeng differs from the predominantly browsing fauna of Langebaanweg (Franz-Odendaal *et al.* 2002), and indicates more extensive C_4 grasslands even than later sites such as Makapansgat and Sterkfontein. It thus appears that the Free State was dominated by grasslands from at least the later–early Pliocene. These data represent the earliest isotopic evidence for significant C_4 grasslands in South Africa, and are consistent with a relatively late grassland expansion into southern Africa (Cerling 1992; Segalen *et al.* 2007).

DISCUSSION AND CONCLUSIONS

The Matjhabeng faunal assemblage is predominated by animals considered to be largely grassland-preferring, including mammoths, equids, hippos and ancestral

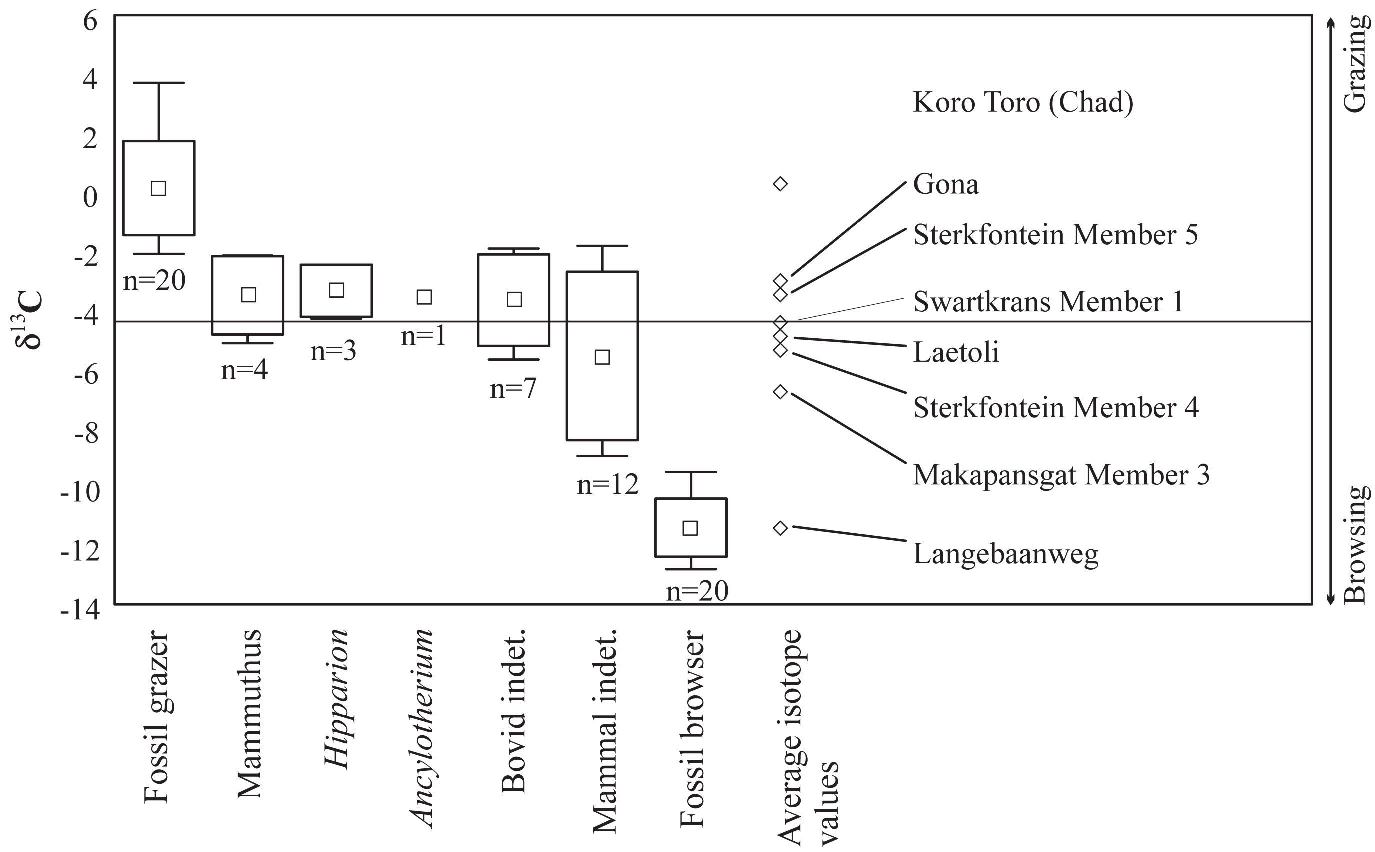

Figure 9. Carbon isotope values for a selection of fossil mammal teeth from Matjhabeng. Comparative 'fossil grazer' and 'fossil browser' data compiled from Swartkrans and Sterkfontein. Grazers are those animals with $\delta^{13}C$ values greater than –2‰, while browsers are those animals with $\delta^{13}C$ values less than –10‰. Animals with values between these ends are referred to as mixed feeders. Average isotope values are calculated by averaging the isotope composition of all specimens sampled from a given site. The grey line represents the average isotope value for all Matjhabeng specimens included in this study, which corresponds to a mixed feeder signal tending towards grazing. These data indicate that grasslands were already extensive by the earlier Pliocene in the Free State, representing the earliest indication of significant grasslands in South Africa. Comparative average isotope values for fossil sites other than Matjhabeng from Sponheimer & Lee-Thorp (2009).

alcelaphines. The presumed browser *Sivatherium* is evident, as is *Ancylotherium,* thus wooded conditions are also indicated. The reptiles and birds demonstrate relatively wetter conditions than are found in the area today. Our isotope data support a primarily mixed feeding/grazing fauna, though the mixed feeding/grazing diet of *Ancylotherium* was unexpected. At present our reconstruction of the paleoenvironment indicates relatively extensive grasslands though these grasslands were part of an environmental mosaic that included notable woodland and probable wetland components. Given that Matjhabeng is a river-deposited locality there is a significant potential for reworking and mixing of materials and thus a potential for time-averaging. We therefore interpret these environmental indicators broadly at the regional scale of the Free State in the earlier Pliocene. Combined with our isotope analysis these data are consistent with a model of major grassland expansion into South Africa by the early Pliocene *c.* 4.0 Ma (Hopley *et al.* 2007; Segalen *et al.* 2007). At present Matjhabeng represents the earliest appearance of significant C_4 grasslands in the central interior of southern Africa. At the same time the Paleo-Sand river was large enough to sustain both hippopotamus and waterfowl. This necessitates perennial channel flow with fresh grasslands available in the vicinity year-round. Periodic fluctuations in river flow are indicated by the interbedded, abandoned channel deposits which developed when the river channel migrated during periods of low stream discharge. Many of the taxa recovered to date are shared by both Langebaanweg and Makapansgat, though some are shared only with Langebaanweg (*Mammuthus*), and some are shared only with Makapansgat (*Ancylotherium, Megalotragus*). These data reflect the intermediary and perhaps transitional nature of this site and highlight the importance of expanding our sample of early Pliocene fossils in South Africa.

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