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New evidence for the lack of C₄ grassland expansions during the early Pliocene at Langebaanweg, South Africa

Tamara A. Franz-Odenaal, Julia A. Lee-Thorp, and Anusuya Chinsamy

Abstract.—Major C₄ grass expansions during the late Miocene in both the Northern and Southern Hemispheres had a major impact on biological communities. We report that the diverse terrestrial fauna of Langebaanweg, South Africa, existed in a local environment that remained C₃-dominated during the late Neogene (~5 Ma). In contrast, other Southern Hemisphere sites at similar latitudes show a clear shift to C₄ grasslands well before 5 Ma. Our results are based on stable isotope analyses of enamel carbonate from four artiodactyl and two perissodactyl families from this locality. We also provide insight into the evolution of the current Mediterranean climate system in this part of South Africa.

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Introduction

During the late Miocene and early Pliocene epochs (between 7 and 5 million years ago), a large-scale vegetation shift occurred when C₄ grasses began a global expansion. Researchers have proposed that this shift was triggered by a decrease in atmospheric CO₂, to levels below 500 parts per million by volume (p.p.m.v.), which would have conveyed advantages to the C₄ photosynthetic pathway (Ehleringer et al. 1991, 1997; Cerling 1993; Cerling et al. 1997b). The evidence for a decrease in pCO₂ is, however, now disputed (Pagani et al. 1999) and the ultimate cause is unresolved. By ~6 Ma, C₄ grasses dominated the grassy components of many low- to midlatitude environments across the globe, and a “C₄ world” has continued to the present day (Cerling et al. 1997b). The expansion of C₄ grasses in East Africa (Cerling 1992, 1993; Morgan et al. 1994; Cerling et al. 1997b), Central North Africa (Zazzo et al. 2000), Asia (Quade et al. 1989, 1992; Cerling 1993), Europe (Quade et al. 1995; Cerling et al. 1997b), and North and South America (MacFadden and Cerling 1996; MacFadden et al. 1996, 1999) has been investigated using carbon isotopic analyses of both paleosols and faunal tooth enamel. Although details of the

timing are unclear, research suggests that this expansion first began at low latitudes and later spread outward to midlatitudes (Cerling et al. 1997b). However, studies from western European and eastern Mediterranean data at mid to high northern latitudes (>36°N) indicate no evidence for a C₄-dominated environment in the last 20 Myr (Quade et al. 1995; Cerling et al. 1997b), in spite of the presence of such grasses at other sites of similar latitudes during this time. The only data available for the Southern Hemisphere at this critical time and at similar midlatitudes are from sites in Argentina, which clearly show a C₃ to C₄ shift at around 8 Ma (MacFadden et al. 1996). Concomitant with the shift from a C₃ to C₄ world, a change in fauna to more savanna-like communities is also evident. Animals with higher-crowned (more hypsodont) dentition begin to dominate faunal assemblages, suggesting the existence of pure grazing taxa (Janis 1993).

This study investigates whether C₄ grasses were present at Langebaanweg (LBW), an early Pliocene site (~5 Ma) in South Africa, by means of isotopic analyses of fossil fauna. LBW is located at 33°S in a region that is today a Mediterranean biome with dry summers and cool, wet winters (Fig. 1). The rich assem-

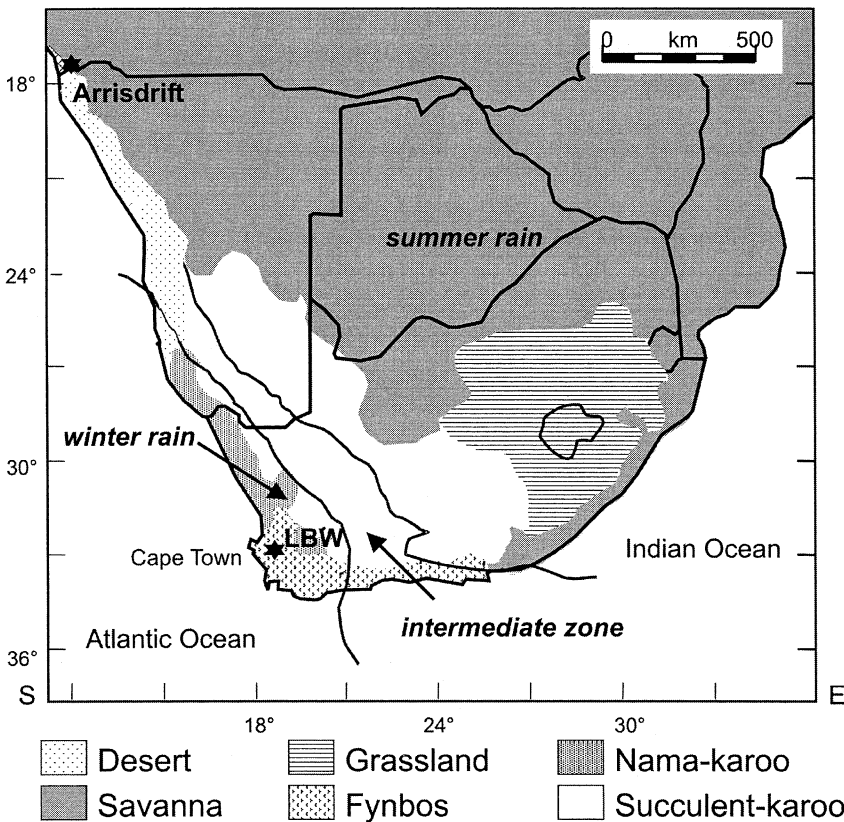


FIGURE 1. Map of the southern African subcontinent showing the present distribution of the main vegetation biomes, summer and winter rainfall regimes, and the position of Langebaanweg (LBW) (modified from Lee-Thorp and Thalma 2000).

blage of vertebrate fossils shows a diverse fauna, most of which are extinct. Hypsodonty indices and phylogenetic relationships to extant forms suggest that the herbivores were mainly large grazers and mixed feeders (Hendey 1983a, 1984). The presence of many large-bodied grazers, such as the white rhinoceros, *Ceratotherium praecox*, suggests the existence of a significant and productive grassy component in the ecosystem. This contrasts sharply with the impoverished mammalian fauna living under the current climate and vegetation regime. According to the C₄ global-expansion model (Cerling et al. 1997b), C₄ grasses could have extended to this latitude by the end of the Miocene, if the present winter rainfall/dry summer climate system was not in place.

Today, local climate is controlled by latitudinal, seasonal movement of the South Atlantic high-pressure system, which operates in two ways. First, it allows penetration of moist

westerlies during the austral winter but prevents penetration of moisture from the east in summer. Second, it induces strong, cold upwelling cells along the west coast, forming the Benguela Upwelling System, which contributes to the marked summer aridity. The vegetation of the southwestern parts of the subcontinent is dominated by "fynbos," a unique, species-rich, sclerophyllous shrubland vegetation recognized as one of the world's six floristic kingdoms (Ellis et al. 1980). Grasses are a very minor component of this biome, and those present are predominately cool-season C₃ grasses (Vogel et al. 1978; Cowling et al. 1997). One of the features of fynbos is that it can grow in the sandy, low-nutrient soils found in this region. As a result, it has a very low nutritional content and supports few large mammals. In contrast, the subcontinent to the east of the Cape Fold Mountains (Fig. 1) experiences a largely summer rainfall, a veg-

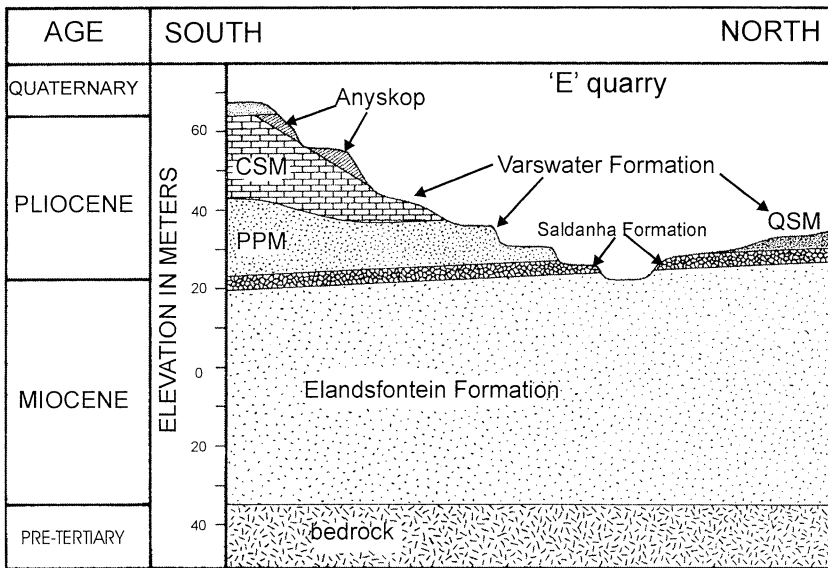


FIGURE 2. Stratigraphy of Langebaanweg (modified from Hendey 1981).

etation dominated by woodlands and C_4 grasslands, as well as a rich mammalian fauna.

Exactly when these two distinct climate and floral systems developed is not well understood. Little is known about the long-term history of the fynbos biome, and except for the late Quaternary, the climates and environments of the region are poorly known (Scott et al. 1997). Limited marine evidence suggests that early forms of the Benguella Upwelling System may have been present in the late Miocene (Siesser 1980), which would imply the existence of a dry summer/wet winter climate regime. However, its development and variability over long time periods is not known until much later. Paleoenvironments of this region during the mid to late Tertiary are largely inferred from the faunal evidence of Arrisdrift in the extreme northwest and LBW in the southwest (Fig. 1). Faunal assemblages at the mid-Miocene Arrisdrift site indicate the presence of forests with some grasses (Hendey 1983a), and the abundance of crocodile remains indicates that temperatures were relatively high throughout the year. The early Pliocene LBW locality has revealed a large, diverse range of vertebrate fossils in the highly fossiliferous Varswater Formation (Fig. 2). Coastal and continental shelf deposits off the

west coast suggest that local sea-level fluctuations were similar to global changes during the Tertiary period. This, together with the faunal evidence, suggests that the Varswater Formation was laid down during the early Pliocene (~5 Ma) and the underlying Elandsfontein Formation during the mid Miocene. Limited pollen data from a single peaty layer within the older Elandsfontein Formation suggest the presence of subtropical forests with some minor fynbos elements (Coetzee and Rogers 1982). In contrast, the predominance of grazing taxa in the Varswater Formation suggests that by the early Pliocene the vegetation was relatively open (Hendey 1976, 1984). A single pollen spectrum from the fossiliferous Varswater Formation was recently reexamined together with two additional samples by Scott (1995). The dominant pollen type belongs to the Ranunculaceae (buttercup family), which likely occurred locally as semi-aquatic plants in a swampy basin. The rest of the sample contains diagnostic elements indicating open vegetation as well as the presence of fynbos. The current understanding is that the subtropical Miocene forests were diminishing at the expense of expanding grasslands during the early Pliocene (Hendey 1981, 1983a,b; Coetzee and Rogers 1982; Scott 1995). This together with the faunal evidence at LBW

(which indicates the existence of a productive biome) is not unlike the situation that is present today in the savanna biomes of the summer rainfall areas in southern and east Africa. On the whole, faunal abundance and diversity, and the patterns of global C₄ grass expansion during the Tertiary, contribute to the suggestion that the vegetation of this region included significant occurrences of C₄ grasses during the mid to late Tertiary period.

In this study, stable carbon and oxygen isotope analyses of tooth enamel carbonate were used to investigate the diets of the fossil fauna at LBW, and hence the composition of the flora. This approach is well established and has been used to provide dietary as well as behavioral information about animals living in savanna environments today (Vogel 1978; Lee-Thorp 1989; Koch et al. 1995; Cerling et al. 1997a, 1999; Lee-Thorp et al. 1997; Cerling and Harris 1999). The method relies on the fact that C₃ and C₄ plants use different photosynthetic pathways. When herbivores eat, the $\delta^{13}\text{C}$ value of the vegetation they consume is incorporated into their tissues such that the $\delta^{13}\text{C}$ value of tooth enamel reflects their diet, with some additional fractionation. The enrichment in $\delta^{13}\text{C}$ between diet and tooth enamel is observed to be 12–14‰ (Lee-Thorp et al. 1989; Cerling and Harris 1999). Typically, tooth enamel from herbivores eating C₃ vegetation have $\delta^{13}\text{C}$ values between -10‰ and -15‰ whereas those feeding on C₄ tropical grasses have $\delta^{13}\text{C}$ values between +2‰ and -2‰. Mixed feeders have values between these extremes. The diets of several fossil species have also been investigated using stable carbon isotopes (Lee-Thorp and van der Merwe 1991; Lee-Thorp et al. 1994; Quade et al. 1995; MacFadden and Cerling 1996; Cerling et al. 1997a, 1999; MacFadden and Shockey 1997; MacFadden et al. 1999; Zazzo et al. 2000).

Stable oxygen isotopes from bone or enamel phosphate have been used extensively to provide information on paleoprecipitation and paleotemperatures (Longinelli 1984; Chappell and Shackleton 1986; Ayliffe and Chivas 1990; Bryant et al. 1994). More recently, oxygen from tooth enamel carbonate has been used to provide information on water-related behavior of fossil animals (Kohn et al. 1996; Sponheimer

and Lee-Thorp 2001). The $\delta^{18}\text{O}$ signature in both enamel phosphate and carbonate is directly related to that of body water, which in turn reflects water usage (uptake and loss) of the animal during tooth development. An animal's physiology therefore acts as a filter that regulates the balance between input (plant water, inspired O₂, and drinking water) and output (water vapor, CO₂, excretion) sources of oxygen. Because plant water (e.g., in leaves) and meteoric rainwater have different $\delta^{18}\text{O}$ signatures, herbivores that obtain most of their water from drinking (i.e., obligate drinkers, which frequently are grazers) can be distinguished from those that obtain water mainly from plants (i.e., non-obligate drinkers, which usually are browsers). In addition, nocturnal versus diurnal feeding behaviors may influence enamel $\delta^{18}\text{O}$ values, because plant water is not enriched at night (Yakir 1992). All $\delta^{18}\text{O}$ values for both modern and fossil hippos are observed to be low, compared with other animals living in the same ecosystem (Quade et al. 1995; Bocherens et al. 1996). The reason for this may be that hippos use different methods from other artiodactyls to keep body temperatures from rising during the hot daytime temperatures. Many artiodactyls either pant or use evaporative cooling to maintain body temperatures below air temperatures (Pough et al. 1996). Hippos, however, spend the hottest parts of the day wallowing in water pools and feed (on land) during the cooler night temperatures (Kingdon 1982). Bocherens et al. (1996) suggested that this method of preventing body temperatures from rising may account for their low $\delta^{18}\text{O}$ values. Although not as well understood as carbon isotope pathways, oxygen isotopes can potentially provide behavioral information about fossil animals, and particularly extinct species, that would otherwise not be available.

A complication of this methodology is the potential for diagenetic alteration of both the $\delta^{13}\text{C}$ and the $\delta^{18}\text{O}$ signal in carbonates from fossil tooth enamel. Several authors have shown that carbon isotopes in enamel survive largely unaltered and that the distinction between C₃ browsers and C₄ grazers is preserved in fossil animals over long periods of time: the present to early Pliocene (Lee-Thorp and van

der Merwe 1987; Bocherens et al. 1996; MacFadden and Cerling 1996; Cerling et al. 1999; MacFadden et al. 1999; Sponheimer and Lee-Thorp 1999); Miocene and beyond (MacFadden and Cerling 1994, 1996; Morgan et al. 1994; Quade et al. 1995; MacFadden et al. 1996; Cerling et al. 1997a, 1999; Zazzo et al. 2000). Oxygen isotopes are more difficult to assess. Seasonal patterns obtained from serial analysis of teeth indicate that the $\delta^{18}\text{O}$ signal is fairly stable (Feranec and MacFadden 2000). Several studies have shown that predictable patterns of water-related behaviors are maintained in fossil faunal assemblages (Bocherens et al. 1996; Sponheimer and Lee-Thorp 1999, 2001). Bocherens et al. (1996) observed that $\delta^{18}\text{O}$ values of hippos were always lower than those of other fauna in both modern and fossil assemblages, and proposed that this distinction provided a good test for the validity of the $\delta^{18}\text{O}$ signal. Although alteration of both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals from fossil tooth enamel carbonate has been found to be insignificant in many studies, this possibility must be assessed for each case study.

A second complication of the stable isotope method is that a variable 2–3‰ difference between the $\delta^{13}\text{C}$ values of modern and fossil animals has been observed, possibly because of changing pCO_2 levels over time. Because modern ecosystems are depleted in ^{13}C by up to 1.5‰, owing to the fossil-fuel effect, there is an apparent offset of this amount when comparing fossil and modern ecosystems (Lee-Thorp and van der Merwe 1987; Cerling et al. 1997b).

Here we investigate the diets of several herbivorous taxa from LBW by means of stable isotope analyses of tooth enamel and provide fresh insight into the early Pliocene paleoclimate of the southwestern region of South Africa.

Material and Methods

The Locality.—The LBW fossil site is situated 13 km inland on the southwest coast of South Africa (Fig. 1). It is believed to have been located at the mouth of a river, as several terrestrial, freshwater, and marine species were found. The Varswater Formation is a complex of deposits of which the two most highly fos-

siliferous members are the Quartzose Sand Member (QSM) and the Pelletal Phosphate Member (PPM) (Fig. 2). All the samples in this study are from the PPM, which consists of two river channel deposits, Bed 3aN and Bed 3aS. These two channels are believed to represent a wet and a dry “season” respectively (Hendey 1980). Although some partially disarticulated specimens occur, most of the fossils are isolated teeth and bones, but all are extremely well preserved. The Varswater Formation has been dated to the early Pliocene (~5 Ma) on the basis of fauna (Hendey 1976), stratigraphy (Hendey 1981), pollen (Coetzee and Rogers 1982), and local sea-level changes (Mercer 1978).

Material.—Sixty-four fossil teeth from the PPM were analyzed (Table 1). These included both browsing and grazing species: Giraffidae (26), Hippopotamidae (15), Suidae (4), Bovidae (9), Rhinocerotidae (4) and Equidae (6) (numbers in parentheses indicate the number of different teeth analyzed). An attempt was made to select molar fragments but this was not always possible. Almost all the teeth analyzed were from Bed 3aN (PPM) except for three Bovidae, two Equidae, and all four Suidae teeth; these were not recorded as belonging to either Bed 3aN or Bed 3aS but rather only to the PPM deposit.

Methods.—Approximately 3 mg of tooth enamel was removed from a broad region at the base of each tooth by a rotary drill fitted with a 1.4-mm diamond-tipped bit. The enamel powder was treated to remove contaminants (according to Sponheimer and Lee-Thorp 1999) as follows: 1.5% sodium hypochloride for 30 minutes followed by 0.1 M acetic acid for 15 min. Between the addition of each of these solutions, samples were centrifuged at high speed and rinsed in distilled water at least three times before proceeding with the next solution. Samples were then freeze-dried for a minimum of 2 hr. 1.8 mg of each pretreated sample was loaded into individual reaction vessels in a Kiel autocarbonate device; CO_2 obtained by acid hydrolysis with 100% phosphoric acid (H_3PO_4) and collected by cryogenic distillation was measured in a Finnigan Mat 252 mass spectrometer. Isotopic ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$) are reported in δ

TABLE 1. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fossil specimens. Means are given with standard deviations for each family. All values are in parts per mil (‰). PPM = Pelletal Phosphate Member.

Sample	Locality	$^{13}\text{C}/^{12}\text{C}$	$^{18}\text{O}/^{16}\text{O}$
Order Artiodactyla			
Family Giraffidae		-11.5 ± 1.1	27.9 ± 1.4
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-12.0	27.7
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-13.5	24.8
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-13.2	28.5
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-13.6	26.8
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.5	29.6
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.4	28.8
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.7	27.9
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.5	27.9
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.7	30.2
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.3	27.2
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.1	27.5
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-9.9	29.0
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.1	30.6
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-12.0	27.8
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.9	27.7
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.6	27.4
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-12.1	26.8
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.3	27.0
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-12.5	29.7
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.4	27.9
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-10.8	28.5
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.1	27.3
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-12.3	29.7
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-11.1	27.0
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-13.5	27.4
<i>Sivatherium hendeyi</i>	Bed 3aN, PPM	-13.0	25.4
Family Hippopotamidae		-12.0 ± 1.5	24.8 ± 1.1
Gen. and sp. not determined	Bed 3aN, PPM	-10.9	27.0
Gen. and sp. not determined	Bed 3aN, PPM	-13.3	23.2
Gen. and sp. not determined	Bed 3aN, PPM	-11.6	26.0
Gen. and sp. not determined	Bed 3aN, PPM	-12.7	25.3
Gen. and sp. not determined	Bed 3aN, PPM	-14.9	24.2
Gen. and sp. not determined	Bed 3aN, PPM	-12.0	23.2
Gen. and sp. not determined	Bed 3aN, PPM	-11.8	24.2
Gen. and sp. not determined	Bed 3aN, PPM	-9.4	24.4
Gen. and sp. not determined	Bed 3aN, PPM	-12.1	25.7
Gen. and sp. not determined	Bed 3aN, PPM	-11.5	25.9
Gen. and sp. not determined	Bed 3aN, PPM	-13.6	24.5
Gen. and sp. not determined	Bed 3aN, PPM	-10.0	25.0
Gen. and sp. not determined	Bed 3aN, PPM	-13.8	24.3
Gen. and sp. not determined	Bed 3aN, PPM	-11.7	23.7
Gen. and sp. not determined	Bed 3aN, PPM	-10.3	25.0
Family Suidae		-11.7 ± 1.0	27.7 ± 0.9
<i>Nyanzachoerus cf. jaegeri</i>	PPM	-12.2	27.9
<i>Nyanzachoerus cf. jaegeri</i>	PPM	-10.3	26.5
<i>Nyanzachoerus cf. jaegeri</i>	PPM	-12.5	27.7
<i>Nyanzachoerus cf. jaegeri</i>	PPM	-12.0	28.6
Family Bovidae		-10.8 ± 0.9	27.6 ± 1.5
<i>Kobus</i> sp.	PPM	-10.7	26.5
<i>Kobus</i> sp.	PPM	-10.7	29.5
<i>Damalacra</i> sp.	Bed 3aN, PPM	-11.4	26.3
<i>Damalacra</i> sp.	Bed 3aN, PPM	-12.3	26.2
<i>Damalacra</i> sp.	Bed 3aN, PPM	-9.3	28.5
<i>Damalacra</i> sp.	Bed 3aN, PPM	-10.5	29.3
<i>Damalacra</i> sp.	Bed 3aN, PPM	-10.3	26.6
<i>Damalacra</i> sp.	Bed 3aN, PPM	-10.3	29.6
<i>Damalacra</i> sp.	PPM	-11.5	26.3

TABLE 1. Continued.

Sample	Locality	$^{13}\text{C}/^{12}\text{C}$	$^{18}\text{O}/^{16}\text{O}$
Order Perissodactyla			
Family Rhinocerotidae		-10.9 ± 0.7	26.2 ± 1.4
<i>Ceratotherium praecox</i>	Bed 3aN, PPM	-11.1	25.5
<i>Ceratotherium praecox</i>	Bed 3aN, PPM	-10.1	28.2
<i>Ceratotherium praecox</i>	Bed 3aN, PPM	-10.5	25.0
<i>Ceratotherium praecox</i>	Bed 3aN, PPM	-11.7	26.2
Family Equidae		-11.3 ± 0.9	27.2 ± 2.0
<i>Hipparion cf. baardi</i>	Bed 3aN, PPM	-11.7	25.1
<i>Hipparion cf. baardi</i>	Bed 3aN, PPM	-12.9	25.1
<i>Hipparion cf. baardi</i>	PPM	-11.0	26.1
<i>Hipparion cf. baardi</i>	Bed 3aN, PPM	-11.2	28.6
<i>Hipparion cf. baardi</i>	Bed 3aN, PPM	-10.7	29.6
<i>Hipparion cf. baardi</i>	PPM	-10.4	28.5

notation, with $\delta^{13}\text{C}$ reported relative to the PeeDeeBelemnite (PDB) international standard and $\delta^{18}\text{O}$ reported relative to Standard Mean Ocean Water (SMOW). Sample values were corrected using known standards (NBS 18, 20) and secondary standards (Carrara Z and Lincoln limestone). Analytical precision is better than 0.1‰. All statistical analyses were performed in STATISTICA (1999 edition).

Results and Discussion

The $\delta^{13}\text{C}$ values from fossil tooth enamel at LBW cluster between -9.3‰ and -14.9‰

(Table 1, Fig. 3). The giraffid, *Sivatherium hendeyi*, and the hippopotamus have a similar wide $\delta^{13}\text{C}$ range (-9.4‰ to -14.9‰) compared with the narrow range for rhinoceros, equid, and suid (-10.1‰ to -12.9‰). The fossil Bovidae, which include animals with variable feeding habits, overlap these two range sets (given the observed known fractionation factor of 12–14‰ between plants and tooth enamel) (Lee-Thorp et al. 1989; Cerling and Harris 1999). These $\delta^{13}\text{C}$ values are well within the range for C₃ grasses and indicate that the southwest Cape was C₃-domi-

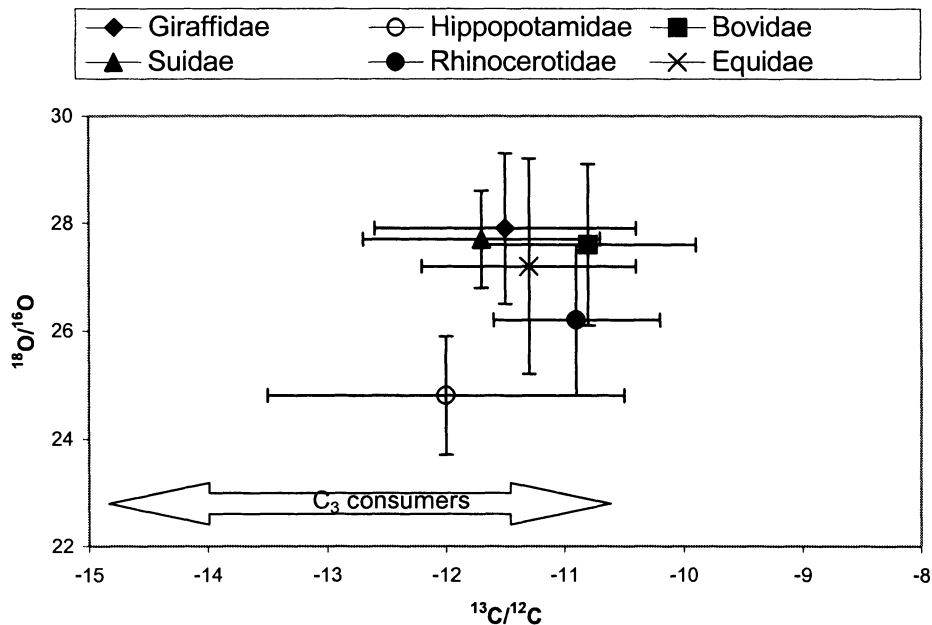


FIGURE 3. Stable carbon and oxygen isotope signals from the Langebaanweg fossil fauna. Double-headed arrow indicates the $\delta^{13}\text{C}$ range for modern C₃ consumers. C₄ consumers are off the scale.

nated during the early Pliocene. Modern bovids from the southwest Cape have low $\delta^{13}\text{C}$ values consistent with a C₃-dominated diet (Lee-Thorp 1989; Lee-Thorp et al. 1989). This contrasts with modern (Van der Merwe et al. 1988; Brink and Lee-Thorp 1992; Sponheimer and Lee-Thorp 2001) and fossil (Brink and Lee-Thorp 1992; Lee-Thorp et al. 1994; Sponheimer and Lee-Thorp 1999) grazing bovids from the central/eastern interior of the country, which have much higher $\delta^{13}\text{C}$ values. These higher $\delta^{13}\text{C}$ values in grazers reflect their diet of C₄ grasses and suggest the presence of a summer rainfall pattern in these parts. The $\delta^{18}\text{O}$ values for modern southwest Cape fauna have not been reported. Using local rainfall values, which average -2.8‰ to -3.8‰ (SMOW) (Harris et al. 1999) and taking into account the 30‰ fractionation between meteoric and body water (Koch 1998), one can calculate what faunal apatite values ought to be (relative to SMOW). If we do this, the LBW faunal values cluster near the values one would expect today in the southwest Cape.

There is, however, some patterning within the assemblage according to species. Bocherens et al. (1996) suggested that $\delta^{18}\text{O}$ values of hippos should be lower than those of most other animals in an assemblage and that this distinction can be used to assess the validity of tooth enamel carbonate $\delta^{18}\text{O}$ signals. $\delta^{18}\text{O}$ values for the LBW hippopotamus ($24.8 \pm 1.1\text{‰}$, $n = 15$) are indeed isotopically distinct ($p < 0.05$) from all the other animals ($27.7 \pm 1.6\text{‰}$, $n = 49$). This suggests that diagenetic alteration is minimal and that the primary isotope signal is preserved.

Faunal evidence from LBW indicates a rich ecosystem of medium- to large-bodied grazers in support of the evolution of hypsodonty in grazing taxa that occurred during the Miocene epoch. According to the C₄ grass expansion model, C₄ grasses had reached low to mid latitudes by the early Pliocene in both Northern and Southern Hemispheres (MacFadden et al. 1996; Cerling et al. 1997b). Stable carbon isotope results reported here indicate that LBW was a C₃-dominated environment during the early Pliocene and that C₄ grasses had not extended to this southerly latitude by 5

Ma, if indeed they were ever present. Furthermore, the evidence for C₃ grasslands suggests that a Mediterranean climate was established in this region by the early Pliocene. This result is in agreement with the data from western Europe (France and Spain [Cerling et al. 1997b]) and the eastern Mediterranean (Greece and Turkey [Quade et al. 1995]), which indicate that Mediterranean ecosystems never supported C₄ grasses.

Pollen data from the mid-Miocene Elandsfontein Formation confirm the presence of limited fynbos-like elements, indicating that even at this time, fynbos was beginning to establish itself. Why, then, did C₃ grasslands give way to fynbos if the climate remained unchanged over time? It has been suggested elsewhere that a nutrient-rich, more alkaline substrate was eliminated at some point during the Pleistocene (Deacon and Deacon 1999). This may have had the effect of opening up the niche for fynbos to flourish.

In a C₃-dominated environment such as LBW, grazers and browsers cannot be distinguished from one another by $\delta^{13}\text{C}$ values, but some more subtle dietary behaviors can be investigated. The $\delta^{13}\text{C}$ values for rhinos and bovids ($-10.8 \pm 0.8\text{‰}$, $n = 13$) are isotopically distinct ($p < 0.05$) from the other animals ($-11.7 \pm 1.2\text{‰}$, $n = 51$), indicating perhaps that different kinds of C₃ vegetation or plant parts were eaten (Table 1, Fig. 3). The slightly higher $\delta^{13}\text{C}$ values (for bovids and rhinos) suggest a preference for open-grassland feeding where irradiance is high and free mixing of biogenic CO₂ with atmosphere can occur (similar to that experienced by leaves at the top of a forest canopy [Quade et al. 1995]). The slightly depleted $\delta^{13}\text{C}$ values for giraffids and hippos suggest that these animals may have been feeding under a partially closed canopy where irradiance is reduced (compared with more open environments).

With the help of modern animals and oxygen isotopes some further reasonable deductions about the behavior of fossil animals may be possible. One might expect the giraffid (*S. hendeyi*) to have been an exclusive browser like the modern giraffe, but the short-necked sivatheres are unlikely to have been able to reach the top of the forest canopy. Their slightly de-

pleted $\delta^{13}\text{C}$ values certainly do not suggest canopy feeding. Using tooth microwear analyses and premaxillae shape, Solounias et al. (1988, 2000) and Solounias and Moelleken (1993) have shown that the diets of the extinct giraffids are highly heterogeneous, with some being mixed feeders and others pure grazers. Recently, pure- C_4 -grazing *Sivatherium* species were found at 3–3.5 Ma in Chad, a North African late Pliocene locality (A. Zazzo personal communication 2000), as well as at 1.8 Ma in Olduvai, Tanzania (N. J. Van der Merwe personal communication 2000). Whether the LBW sivathere was a pure grazer or a mixed feeder or a low-level browser cannot be determined from $\delta^{13}\text{C}$ values alone because of the dominant C_3 signature at LBW. The $\delta^{18}\text{O}$ values of the sivatheres are most similar to those of the bovids and suids, indicating possibly similar water-related behavior. Frequent drinking may therefore have been a behavior of the sivatheres, as in grazing bovids today, which are known to be obligate drinkers.

Variable diets for the white rhinoceros, *C. praecox*, have also been reported recently (Zazzo et al. 2000). Between 5 and 4 Ma, *C. praecox* in North Africa was a mixed feeder, but by 3.5 Ma it was a pure grazer. As previously discussed, their (slightly) enriched $\delta^{13}\text{C}$ values may indicate a preference for open grassland feeding (similar to the diet of the modern white rhino). Grazers tend to be obligate drinkers and have enriched $\delta^{18}\text{O}$ values, yet the $\delta^{18}\text{O}$ values of the white rhino at LBW ($26.2 \pm 1.4\text{‰}$, $n = 4$) are significantly lower ($p < 0.05$) than those of all the other animals, excluding hippos. Modern rhinos are water dependent and cool off during the hot midday temperatures (Kingdon 1982) (as do hippos), thereby lowering their $\delta^{18}\text{O}$ values, and a similar behavior could have applied to *C. praecox*. Alternatively, the fossil rhino may have been a nocturnal feeder (similar to hippos) which also would have the effect of reducing $\delta^{18}\text{O}$ values. It is unlikely that body size could contribute to these slightly depleted values, because the effects of body size are believed to be significant only for small animals (Bryant et al. 1996) and all the LBW fauna analyzed are of a similar medium to large body size.

The results of our investigation at LBW sug-

gest that even subtle differences in stable carbon and oxygen isotope values can shed light on dietary and behavioral differences between taxa. More importantly, the findings presented here offer information relating to C_4 expansions in the Southern Hemisphere as well as local climate and vegetation histories. The fact that C_4 grasses did not dominate at 33°S during the early Pliocene is probably related to the early establishment of the current winter rainfall/dry summer climate regime.

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