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Age and Environmental Significance of a Rare Elephant Tooth (*Loxodonta africana zulu*) from the Windhoek Spring Deposit, Namibia

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Abstract

An elephant molar recovered from the Windhoek Zoo Park Gardens in 1961/62 and stored in the National Museum of Namibia has been identified as a rare specimen of *Loxodonta africana zulu* and has been radiocarbon dated to 6991-7241 cal BP (6240 ± 30 ^{14}C BP). Stable isotope analysis of biogenic apatite in tooth enamel (δ^{13}C = -9.0‰) suggests that the elephant was a mixed feeder but that C4 grass made up a significant part of its diet. The new age and isotope data for the molar confirm previously published pollen and diatom evidence from the spring suggesting that in the Windhoek area the Holocene at ca. 7000 cal BP was wetter than today.

Keywords: rare elephant, *Loxodonta africana zulu*, elephant diet, palaeoenvironment, Namibia, Holocene.

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INTRODUCTION

Windhoek is located in a basin of the central Namibian highlands, the Khomas Hochland, at 1700 m a.s.l. (Fig. 1). The average rainfall is 365 mm/yr. Before modern development, hot ground water (<80°C) emerged from several springs along a north-south oriented fault in the centre of town (Gevers, 1932). The spring water seeped down the slope towards the bottom of the valley where the central business district is today. The springs created extensive swampy areas with relatively lush vegetation (Mossolow, 1965; Stern & Lau, 1989; Scott et al., 1991).

During landscaping work in the Windhoek Zoo Park Gardens in September 1961 the remains of three elephants were found by Municipal workers at a depth of 2 m. The remains included a pelvis, lower jaw and tusk (MacCalman, 1965, 1967). Later, in January 1962, the bones of at least one other elephant were discovered at a depth of 0.35 m some 10 m from the original site. These included a lower jaw, tusks, teeth, a femur, vertebrae and ribs (MacCalman, 1967). The tusk from the original site yielded a radiocarbon age of 5200 ± 140 ^{14}C BP (5611-6268 cal BP). Associated with the bones at both locations was a quartz stone industry including choppers, hammerstones and unretouched flakes considered to be Later Stone Age, suggesting that the two locations were elephant butchery sites (MacCalman, 1967). The elephant tooth that forms the focus of this paper was recovered as part of the 1961-62 excavations and has been stored at the Namibian National Museum since it was collected. The tooth is part of a larger collection of artefacts and elephant remains, including a whole mandible that was recovered from the site.

The bones and stone artefacts were recovered from within or immediately below a sand lens resting on peaty sand and overlain by black peat. MacCalman (1967) interprets the sand lens as a fossil stream channel, within a marsh, fed by the springs on the ridge above the site.

The marshes were drained during the late 1890s to reduce typhoid and malaria outbreaks (Mossolow, 1965) and discharge from the springs above Zoo Park channeled in 1902 (Stern & Lau, 1989). The springs were capped during the late 1950s and their discharge piped into the municipal water supply.

Diatoms in the elephant level showed that salt concentrations were lower at that time indicating a lower evaporation rate (Cholnoky, 1963). In addition, the high frequency of nitrogen heterotrophic *Nitzschia* species indicated a marshy environment polluted by animals showing that the spring was a watering place. MacCalman (1967) reports that pollen analysis by van Zinderen Bakker Sr. showed that the site was in semi-dry savanna (*Rhus*, *Lannea*, *Terminalia*, Aizoaceae, Chenopodaceae), but a high frequency of Cyperaceae indicates locally wet conditions. MacCalman (1967) points out that together the diatom and pollen assemblages suggest wetter conditions than exist today.

Preparatory excavations to construct a high-rise building in Windhoek in 1988, about 125 m downstream (west) of the elephant remains, exposed a 3 m thick sequence of spring deposits. Radiocarbon ages for the sequence ranged from 2410 ± 80 to 7150 ± 80 ^{14}C BP (2180-2720 and 7739-8155 cal BP) at 50 cm and 300 cm, respectively. On the basis of pollen content Scott et al. (1991) subdivided the profile into three zones W1, W2 and W3. Zone W1 had a high proportion of Cyperaceae pollen and together with the diatomaceous nature of the deposits and the good pollen preservation this suggests waterlogged conditions between ca. 8151 and 6500 cal BP. The diatomaceous nature of the W1 deposits matches the sediments in which the elephant fossils were found. Small numbers of arboreal pollen, including Combretaceae, *Commiphora*, Tarchonantheae, and *Rhus* also indicate somewhat wetter conditions (Scott et al., 1991). After ca. 6500 cal BP, there was a decline in Cyperaceae and arboreal pollen and an increase in Cheno/Am and Compositae pollen, all pointing to drier conditions.

Scott et al. (1991) suggest that the swamp in the Windhoek area was surrounded by a semiarid savanna under lowered evaporative conditions at the time the elephants were butchered. This paper attempts to classify the species of elephant, determine the age of the tooth, and obtain information on the elephant's diet and the climate that prevailed during its lifetime.

AGE OF THE TOOTH

Procedures for the preparation of enamel samples for isotopic analysis are critical for obtaining reliable data. In general it must be assumed that the sample has undergone some alteration or contamination in its natural environment, and also that the excavation process may have added modern contaminations as a result of handling and preservation procedures. The carbonates in fossil enamel may be contaminated by secondary carbonates, precipitated in the process of burial either as pore filling cements or as bicarbonates absorbed to the surface of crystals.

A 0.5 gram sample of enamel (powder) was drilled from the tooth. This powder was reacted with 1N acetic acid in a 100 ml Erlenmeyer flask. The flask was periodically evacuated to remove air and /or CO_2 from micro-pores, after which the flask was returned to atmospheric pressure to force fresh acid into the micro-spaces of the sample. The nature of this reaction is a qualitative indication of $CaCO_3$ contamination. This process of evacuation

and re-pressuring was continued at about 20 minute intervals until no substantial release of gas as fine foamy bubbles occurred, even at the vapour pressure of water. The process of evacuation and re-pressurisation to atmospheric pressure was repeated 5 times. The cleaned sample was then washed free of acetic acid by repeated soaking and decantation with demineralised water and then vacuum dried so that it was ready for isotopic analysis of carbon in bioapatite (Cherkinsky, 2009)

The cleaned enamel powder was reacted under vacuum with 1.5 ml of 100% phosphoric acid at 65ºC for 1 hour to recover carbon dioxide. The released CO_2 was cryogenically purified; 90% of the gas was used for AMS radiocarbon dating and the remaining 10% for stable carbon isotope analysis using a conventional mass spectrometer MAT 252. The yield of carbon from the bioapatite was about 0.5% suggesting that any diagenetic carbonates were completely removed during sample preparation. If the yield had been >0.7% this would have suggested that diagenetic carbonates were still present in the sample.

For AMS analysis the cleaned carbon dioxide was catalytically converted to graphite using the method of Vogel et al. (1984). The graphite $^{14}C/^{13}C$ ratio was measured using a 0.5 MV Pelletron AMS instrument and compared with the ratio of the Oxalic Acid I (NBS SRM 4990) standard. The uncalibrated age of the elephant tooth enamel is 6240 ±30 radiocarbon years before 1950 (^{14}C yr BP), using a ^{14}C half-life of 5568 years and is corrected for isotope fractionation. The uncertainty is one standard deviation and reflects both statistical and experimental errors. This age in ^{14}C yr BP (and previously published ages) was calibrated at the 2σ probability level using CALIB 7.0 (Stuiver & Reimer, 1993) and the Southern Hemisphere (SHcal13) atmospheric calibration curve of Hogg et al. (2013) to obtain a calibrated age of 6991-7241 calendar years BP (cal BP) (Table 1).

The spring water at Windhoek is old as indicated by ages on the carbon of 20,800 ± 160 ^{14}C BP (GrN-5292) and 19,500 ± 170 ^{14}C BP (Pta-0599) ^{14}C BP (Scott et al., 1991). Old carbon in the water could influence the ages of aquatics and fossils in the spring and thus ages for the sediments subjected to diatom and pollen analysis. However, Scott et al. (1991) suggest that the sites examined are far enough downslope of the spring eye that the water had time to equilibriate with the atmosphere before old carbon could be incorporated into plants or fossils. In fact, Scott et al. (1991) report ages for the sediment sequence ranging from 2410 ± 80 ^{14}C BP (2180-2720 cal BP) at 50 cm to 7150 ± 80 ^{14}C BP (7739-8155 cal BP) at 300 cm, with the older ages correlating well with our age for the molar.

ESTABLISHING THE SPECIES OF THE ELEPHANT

African elephant taxonomy: *Loxodonta zulu (L. zulu)*

The Family Elephantidae is one of eight families within the Order Proboscidea. The family evolved in Africa approximately 6 million years (Ma) ago, and all three genera, *Loxodonta, Elephas* and *Mammuthus* originated in Africa. *Elephas* and *Mammuthus* spread to Eurasia and the Americas throughout the Plio-Pleistocene. Only two genera survive *Loxodonta* in Africa and *Elephas* in Asia (Todd & Roth, 1996). The Plio-Pleistocene fossil records of *Elephas* and *Mammuthus* are well-known, although specific relationships between fossil species within each lineage are controversial. The evolution of *Loxodonta* is not as well

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known, as this genus remains relatively rare while the more dominant *Elephas* is present in Africa. Early fossil species include the variable *Loxodonta exoptata* from 4.5-2.0 Ma, and *Loxodonta atlantica* is present in northern Africa from 2.5 Ma to 35 ka. The earliest record of *Loxodonta africana* is from Kenya at 500 ka, but the record is sparse from this time period to the Holocene, with the exception of a few fossils from southern Africa that have been attributed to *Elephas (Loxodon) zulu* (Maglio, 1973).

 Elephas (Loxodon) zulu was initially described by Scott (1907), based on material recovered from a locality near Port Durfort, Natal, South Africa (Type: PU 11548, left and right M_3). The fossils were thought by Scott (1907) to be from the Pliocene, although they differed only slightly from living genera. Unfortunately, the location of the locality was not well-documented, and the exact stratigraphic layers from which the fossil originated are unknown. However, discovery of a rhinoceros tooth from the Port Durnford Formation prompted McCarthy and Orr (1978) to attempt to relocate the original fossil site, which was traced to similar strata within a gabhagabha aeolianite formation at Dawson's Rocks. Based on comparison with fossils from these layers and with the Vaal River gravels, McCarthy and Orr (1978) reassigned the original fossils to the Middle Pleistocene. More specimens were recovered from Elandsfontein (400-700 ka), together with the extant species, *Loxodonta africana (*Hendey, 1996; Klein *et al.,* 2007).

 Elephas (Loxodon) zulu was referred to *Elephas zulu* by Hopwood (1926) based on material recovered from the Kaiso Bone Beds near Lake Albert (BMNH 12639 housed in the British Museum of Natural History). Osborn (1938) renamed the species *Loxodonta zulu* and Cooke (1947) maintained *Elephas zulu* as a distinct species because of differences in overall size and crown height. Arambourg (1938) suggested that the southern species fell within the range of variability of *Loxodonta atlantica (Elephas atlanticus*) from the Omo River valley in Ethiopia. This prompted Coppens *et al.* (1978) and Beden (1979) to synonomise *Elephas (Loxodonta) zulu* with *Loxodonta atlantica* from Ternifine. Maglio (1973) considered both northern and southern African species the same, although noting differences between the two groups. Since the type fossils were the only material from southern Africa, and the *L. atlantica* types were from Ternifine, Maglio (1973) separated the geographic groups at the subspecies level, with *Loxodonta atlantica atlantica* in north Africa, and *Loxodonta atlantica zulu* for the southern specimens. Maglio (1973) also notes "The very rare occurrence of this species at Omo and absence from other East African localities in which *Elephas recki* is abundant and the absence of the latter from Ternifine and Elandsfontein suggest that two species were adapted to different ecological situations, and may account for disappearance of *L. atlantica* in the lower Pleistocene of East Africa and its replacement by *E. recki*." (Maglio 1973: 29)

 Maglio (1973) assigned the holotype of *Loxodonta atlantica zulu* to PU 11548 (Left and Right M_3, Scott's (1907) original fossils), from the Middle Pleistocene of South Africa. He described the subspecies as the following: larger than the northern subspecies, closely spaced plates with an LF of 4.3-5.2, 2-3 mm enamel thickness, and simple enamel loops. Maglio (1973) figured SAM 2577 (Right lower M_2) from Elandsfontein and PU 11548 (Left M_3) from Port Durfort, South Africa.

 The shape of the worn enamel figure in fossil specimens of *Elephas* and *Loxodonta* can be quite similar, leading to confusing assignments to genera. Scott (1907) noted that the

South African specimens lacked the characteristic loxodont sinus in the enamel figures, instead showing similarities to *Elephas antiquus* from Europe and *Elephas recki* from East Africa, but he also suggested that the lack of the characteristic lozenge shape supported its ancestral position to *Loxodonta africana*.

Molar morphology and the Windhoek specimen

The enamel of the type specimens of *Loxodonta zulu* is very thick and tightly folded, giving it a characteristic "crimped" appearance. This crinkling of the enamel is again very similar to earlier *Elephas recki* and also *Elephas antiquus* from Europe, supporting early assignments by Scott (1907), Cooke (1947) and others to the *Elephas* genus. Beden (1979) named it *Elephas (Paleoloxodon) zulu* based on these similiarities, and proposed it as a side branch along with *Elephas (Paleoloxodon) iolensis* from North Africa, with both originating from *Elephas recki*. However, molars of *Loxodonta atlantica* and *L. africana* are much narrower than those of *Elephas recki*, and while there is also similarity in the lozenge pattern of the enamel figures, Todd (1997, 2010) has suggested different developmental pathways for the enamel pattern. In *Elephas recki*, the lozenge develops from conules that are anterior and posterior to the main enamel loop. With wear, these conules join the loop, and a pseudolozenge appears. In the loxodont elephants, the initial enamel is lozenge-shaped in early wear. Todd (2010) also proposes that *Loxodonta atlantica* is the direct ancestor of *Loxodonta africana*, supporting Scott (1907) and others. Another interesting note is that the crimping of enamel persists in many specimens of the extant African elephant, particularly those from southern Africa.

The fossil consists of a single tooth plate, with thick enamel and strong longitudinal furrows along the length of the plate. On worn plates, these furrows will create tightly crimped and folded enamel (Fig. 2). The enamel loop is in early stages of wear, and the morphology and size is consistent with an upper M^2. It is the last lamella, indicated by the wear facet and polished surface on the posterior side from articulation with the M^3 posterior in the jaw.

While other "subfossils" have been attributed to *Elephas recki*, the measurements are clearly not in the *E. recki* range (Todd, 2005) (Table 2). The enamel thickness ranges from 2.64-3.75 mm, much thicker than late *Elephas recki* (mean ~2.5 mm). Maximum plate width is 76.36 mm, much narrower than *Elephas recki* (92-94 mm on average). The plate height ranges from 96.8-111.36 mm, but height on a single plate is not very indicative of overall molar height. Maximum width of the enamel figure in the median area is 12.5 mm.

The measurements fit within the comparative sample of M^2 for either *Loxodonta atlantica* or *Loxodonta africana*. The enamel thickness of the specimen is on the high end of the ranges of *L. africana* (2.5-2.9 mm, with a few up to 3.52 mm), and *L. atlantica* (2.3-3.1 mm with some up to 4.21 mm). The enamel is quite folded, a feature that is present, but not consistent in East African *Loxodonta africana*. The overall morphology of the plate compares very well with the sample of *Loxodonta africana zulu* as currently described. Other remains of this elephant (although not formally described) in the National Museum in Windhoek also show characteristics that confirm the interpretation we have made based on examination of the molar.

In terms of age, the oldest occurrence of *L. africana* is from the site of Kanjera in Kenya, dated at 500 ka. The first appearance of *L. atlantica* is 2.52 Ma in the Shungura Formation in Ethiopia, and the last appearance around 34 ka in North Africa (Todd, 2006). This fossil, at approximately 7000 cal BP, postdates the last occurrence of *Loxodonta atlantica*. In addition, all of the *Loxodonta atlantica* specimens are from northeastern and northern Africa, with only a few specimens attributed to southern Africa. Maglio (1973) separated the two sets of specimens into subspecies due to their wide geographic separation, and the lack of other *Loxodonta* fossils for comparison.

"Should *E. zulu* eventually prove to be the actual ancestor of *E. africanus*, it would tend to give the latter a less isolated position, connecting it with Asiatic and European species. At all events, it is extremely interesting and important to find in South Africa an elephant with so many points of resemblance to species characteristic of the northern hemisphere" (Scott 1907:262).

The morphology of the Windhoek specimens more closely resemble *Loxodonta africana* than *Loxodonta atlantica*, and we therefore suggest they be attributed to *Loxodonta africana.zulu*. Rather than a direct ancestor of *Loxodonta africana*, as Maglio (1973) implied, we suggest that *L. a. zulu* resulted from an allopatric isolation event during the Middle Pleistocene in southern Africa, and ultimately suffered a local extinction during the Holocene. These specimens are important to understanding the radiation of elephants throughout Africa during the latest Pleistocene and early Holocene, as well as understanding the effect of climate change and increased human populations on large mammals during this time period.

ISOTOPIC EVIDENCE OF DIET

The African elephant is a mixed feeder consuming variable proportions of browse (C3 plants) and graze (largely C4 grasses) in different environments. Only one species is recognized, *Loxodonta africana*, comprising two extant sub-species. The larger of these, *L. africana africana*, is the savanna elephant and is found in eastern and southern Africa while the smaller, *L. africana cyclotis* inhabits the forests of central and western Africa. Presently there is debate as to whether these two sub-species should be recognised as individual species. In the following discussion we will not differentiate between them. There also remains considerable controversy about the diet of African elephants with many authors suggesting a very high component of grass in the diets of savanna elephants while others regard savanna elephants to be predominantly browsers with little grass in their diet (discussion in Cerling et al., 2004). Preliminary microwear data on teeth of *L. africana*, show even proportions of pits and scratches suggesting that they are mixed feeders (Todd, unpublished data).

The $\delta^{13}C$ of mammal bone collagen and tooth enamel preserves a record of the long-term diets (e.g. DeNiro & Epstein 1978; van der Merwe et al. 1988; Cerling et al. 1997, 1999). Collagen may not survive beyond ~10,000 cal BP but fossil bone and tooth apatite, particularly from tooth enamel, can extend the record to the mid Pleistocene as they are resistant to isotopic exchange (Lee-Thorp & van der Merwe 1987; Quade et al. 1992; Wang & Cerling 1994; Lee-Thorp, 2000). In fact, diagenetic alteration of the $\delta^{13}C$ signal in fossil tooth enamel is not large even for open systems (Lee-Thorp & van der Merwe, 1987; Wang

& Cerling, 1994). Elephant diet has been estimated from $\delta^{13}C$ values for collagen and apatite by comparison with values for animals known to be pure browsers or pure grazers (on C4 grasses) and determining enrichment factors relative to diet. Enrichment of $\delta^{13}C$ between bone collagen and diet is ~5.5‰ (Vogel et al., 1990a) and between bone apatite (including enamel) and diet ~14.1‰ (Cerling et al., 1997; Cerling & Harris 1999). The enrichment factor approach has shown that most elephants are predominantly browsers (e.g. van der Merwe et al. 1988; Cerling et al. 1999). For example, a study by Cerling et al. (1999) found that the mean $\delta^{13}C$ of tooth enamel of forest elephants in Kenya was -13.2‰ (diet = -27.3‰) confirming a predominantly C3 diet while the mean of savanna elephants in four parks was -11.7‰ (diet = -25.8‰) suggesting only a very small percentage of C4 grass in their diet. However, savanna elephants from Amboseli (tooth enamel = -7.7‰) and Tsavo National Park (tooth enamel = -9.7‰) had $\delta^{13}C$ values of -21.8‰ and -23.8‰, respectively, indicating their diet included > ~ 20% C4 grasses (Cerling et al., 1999; see also van der Merwe et al. 1988 for parallel collagen studies).

However studies of $\delta^{13}C$ values of elephant dung in the Kasungu Wildlife Refuge (KWR) in Malawi and later in Kruger National Park (KNP), South Africa revealed much higher levels of C4 grass in the diet than had been suspected previously. In KWR C4 grasses accounted for 0-10% of the diet of savanna elephants in the dry season and about 70% in the wet season, compared to the ~15% C4 contribution indicated by elephant bone collagen (van der Merwe et al., 1988). In KNP the percent of C4 grass in the diet is significant throughout the year with lower values in the dry season from May to October (~ 25–35%), high values during the wet season from December to March (~ 50%), and intermediate values of ~ 40% in April and November (e.g. Codron et al., 2006, 2011). These authors suggest that the different results obtained from collagen/apatite and dung studies may be because elephants are metabolically less efficient in extracting protein from C4 grasses than from C3 plants. A study of Asian elephants by Sukumar and Ramesh (1992) appears to confirm this. They found that relative to the quantity of C3 and C4 plants consumed by Asian elephants, more carbon is incorporated into bone collagen from C3 plants than from C4 plants, possibly because of higher protein content in C3 plants (3-26% dry weight) compared to C4 plants (1.5-10% dry weight).

Elephant diets determined from isotopic studies of elephant hair (e.g. Cerling et al., 2004, 2006) confirm the seasonal importance of C4 grass in the diet revealed by dung studies, documenting in particular the increased consumption of C4 grass during the wet season and low levels of consumption during the dry season (Cerling et al., 2006). In Tsavo National Park the average annual consumption of C4 grass was 10% to 15%, although it reached up to 60% for several weeks at the beginning of the rainy season (Cerling et al. 2004). Codron et al. (2011) suggest that grass is favored when available in abundance, as search time for food is minimized by consuming grass in bulk. Elephants benefit from eating grass when the nutrient content is relatively high, so that browsing (C3 feeding) is favored in the dry season when grass nutrient content decreases and fibre to nutrient ratios increase.

We obtained a $\delta^{13}C$ value of -9.0‰ for enamel drilled from the Windhoek elephant (*L. zulu*) tooth. This is high relative to elephants in Kenya (forest = -13.2‰; 4 savanna environments = -11.7‰) but more comparable with values from Tsavo in Kenya (-9.7‰; range = -7‰ to -13‰). The Tsavo elephants may eat more C4 grass (0% to 25% of their diet)

than elephants in most other parts of Africa perhaps explaining the high enamel δ^{13}C value (Cerling & Harris, 1999; Cerling et al. 1999, 2004). Published bone collagen δ^{13}C values for Namibia, converted to bone apatite values (+8.6‰), are -13.1‰ for the Caprivi, -10.4‰ for Damaraland, -9.7‰ for the northern Namib Desert, -9.3‰ for Etosha, and -7.8‰ for the eastern Kaokoveld (van der Merwe et al., 1988; Vogel et al., 1990a, 1990b).

The δ^{13}C value for the Windhoek elephant tooth enamel is one of the highest obtained from African elephants living in a wide variety of environments. The high average value for the Tsavo elephant population has been explained by a mixed diet that includes a significant amount of grass. Applying the same logic suggests that the Windhoek *L. zulu* may also have consumed a significant amount of grass, particularly during the wet season. If correct, this would imply that ~7000 cal yr BP summer rains were reliable and sufficiently plentiful for the regular growth of grass in the summer wet season. Certainly this would agree with other evidence from the Windhoek spring site (e.g. diatoms and pollen) of wetter conditions at this time compared with today.

DISCUSSION

The age of the *L. zulu* tooth from the Windhoek spring site, together with the previously published age for an elephant tusk from the same site, indicates a Holocene age from ca. 5600 to 7200 cal BP during a wetter period than today. Diatom and pollen assemblages in the sediments from which the elephant remains were recovered (Cholnoky, 1963, van Zinderen Bakker quoted in MacCalman, 1967) and pollen analysis of other spring sediments deposited during this period (Scott et al., 1991) provide evidence of wetter conditions. The δ^{13}C value for the elephant tooth enamel also suggests abundant summer rains at this time, as discussed above.

The existence and timing of an early Holocene wet period at Windhoek is also supported by evidence from other sites in the region (Fig. 1). For example, the Stampriet aquifer south of Windhoek, which is recharged from rainfall in the Windhoek area, shows a sharp increase in excess air around 7000 cal BP that is believed to record a transition from a dry to a wet climate (Stute & Talma, 1997). Rapid accumulation of an 18 m thick sedimentary sequence at Homeb in the lower Kuiseb valley from 9800 to ~6000 cal BP (Bourke et al., 2003), interpreted by Srivastava et al. (2006) as aggrading channel fill and floodplain facies, suggests wetter and more consistent rainfall on the Khomas Hochland immediately west of Windhoek. This climate produced fewer flash floods along the Kuiseb so that fine sediments from the headwaters and upper catchment were transported and deposited in the lower reaches of the river. However, around 4800 cal BP the Kuiseb returned to a flash-flood fluvial regime, similar to the present, leading to the rapid erosion of these silt deposits (Srivastava et al., 2006). Micromammal remains in barn owl pellets at the Mirabib archaeological site in Namibia, which are dominated by gerbil bones from ca. 5950-6800 cal BP (5200-6000 ^{14}C BP), indicate a greater grass cover and more rainfall than later in the record (Brain & Brain, 1977; ^{14}C ages interpolated from their Fig. 2). Evidence of a greater grass cover at Mirabib also supports our interpretation of the *L.zulu* molar enamel δ^{13}C value as indicating more reliable and substantial summer rains ca. 7000 cal BP than today. In addition, sediments in the South Atlantic GeoB 1023-4 marine core, near the mouth of the Kunene River, record a period of increased river flow from 11,000-6000 cal BP, with

maximum humidity from 7000-6000 cal BP (Gingele, 1996). This body of evidence appears to confirm the Windhoek spring elephant age and palaeoenvironmental data that the interval ~ 7200 to 5600 cal BP was wetter than today with increased summer rainfall.

Africa has been considered unique among the continents in having maintained an extraordinarily diverse megafauna spanning the Pleistocene-Holocene epochs. Recently developed information, however, refutes the premise that changes in Africa's megafauna did not occur. At least 24 large mammal species have disappeared from continental Africa during the late Pleistocene or Holocene (Faith, 2013), while many grazer and browser ungulate species underwent considerable population and range changes (Lorenzen et al., 2012). For example, African buffalo populations declined 75-98% since the mid-Holocene (Heller et al., 2008), concurrent with a pronounced transition to a drier climate in many parts of Tropical Africa approximately 4500 cal BP (Heller et al., 2012). Also, among the better sampled taxa, most recent African megafauna extinctions are restricted to the terminal Pleistocene and early Holocene. Where good terrestrial palaeoenvironmental records are present, extinctions are associated with changes in the availability, productivity, or structure of grassland habitats, suggesting that environmental changes played a decisive role in the losses (Faith, 2013). Extinctions or local extirpation at the Pleistocene-Holocene transition of specialized grazers or species that prefer grasslands are therefore presumed to have been driven by declining productivity and availability of grassland habitats (Faith, 2011). It is tempting to suggest that changes in grasslands throughout its range was a contributing factor to the final extinction of *L. zulu* but the isotopic evidence from a single molar, or a single population if additional molars in the National Museum collection were to be analysed, is not sufficient to reach such a conclusion. The coincidence in timing, however, is too significant not to deserve consideration.

CONCLUSIONS

An elephant molar stored in the National Museum of Namibia since 1961/2 has been identified as a rare *L. zulu* specimen. The radiocarbon age of the specimen, 6991-7241 cal BP, confirms the chronology of sediments and microfossils in the layer where the tooth was found, and so confirms the evidence that these provided indicating wetter climatic conditions in central Namibia ca. 7000 cal BP during the early to middle Holocene. The $\delta^{13}C$ of the tooth enamel (-9.0‰) is higher than most other values obtained from southern and eastern Africa and suggests that grass was an important part of the elephant's diet, particularly at times when the grass was most nutritious as during the wet season. The apparent availability of grass ca. 7000 cal BP indicates that summer rains were probably more regular and more abundant than now, a conclusion that agrees with evidence from the Stampriet aquifer of a significant increase in recharge, in-channel Kuiseb River sediments at Homeb suggesting an aggrading depositional fluvial regime, and findings at Mirabib rock shelter of more abundant grass cover at this time (Stute & Talma, 1997; Srivastava et al., 2006; Brain & Brain, 1977).

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Table 1. Radiocarbon age data for elephant remains and sediment from the Windhoek spring.

Lab ID	Material	Depth (cm)	$\delta^{13}C$ (‰)	Age (^{14}C yr BP)	Age (2σ cal BP)
Pta-5348	Sediment	50	-24.0	2410 ± 80	2180-2720
Pta-5044	Sediment	100	-20.8	3850 ± 60	3992-4412
Pta-5030	Sediment	200	-23.8	5630 ± 70	6218-6540
Pta-5179	Sediment	300	-25.6	7150 ± 80	7739-8155
SR-34*	Elephant tusk	213	NA	5200 ± 140	5611-6268
UGAMS-7219	Elephant tooth	NA	-9.0	6240 ± 30	6991-7241

* Gulbenkian Radiocarbon Dating Laboratory, University College of Rhodesia, Salisbury.

Table 2. The Windhoek *L. zulu* tooth compared to other *L. zulu, L. atlantica* and *L. africana* specimens.

Species	L. zulu*		L. atlantica*	L. africana*
	Windhoek	**Other specimens**		
Details	M3	n=4 (includes M3) ***	n=13 (includes M2LM3 and UM3)	n=20 (UM2)
LF	3.4-5.4 for M3**	4.25	4-6 (mean 5.08)	4-5 (mean 4.28)
Number of Plates	12-15 on M3**	11.75 (2 are M3)	8-14	8-9 on M2
Enamel thickness	2.64-3.75 (mean 3.2) 2-3**	3.2-3.94 (mean 3.52)	2.23-4.21 (mean 3.07)	2.147-3.288 (mean 2.747)
Maximum plate width	76.36	68.95	56.01-90.9 (mean 68.1)	62.52-90.13 (mean 72.37)
Plate height	96.8-111.36 (unworn)	45.86 (in jaw)	36.08-122.97 (mean 66.14)	39.973-61.583 (mean 50.34)
Fold index	9.35	2.45-4.35 (mean 3.11)	2.75-4.29 (mean 3.54)	3.46-8.74 (mean 5.94)
Med exp	12.5 (posterior plate)	14.78	12.6-26.03 (mean 18.85)	18.23-28.66 (mean 23.23)

* measurements in cm

**(Maglio, 1973)

*** Specimens BMNH M.12639A, BMNH M.12639B, SAM 4577 and PU 11548
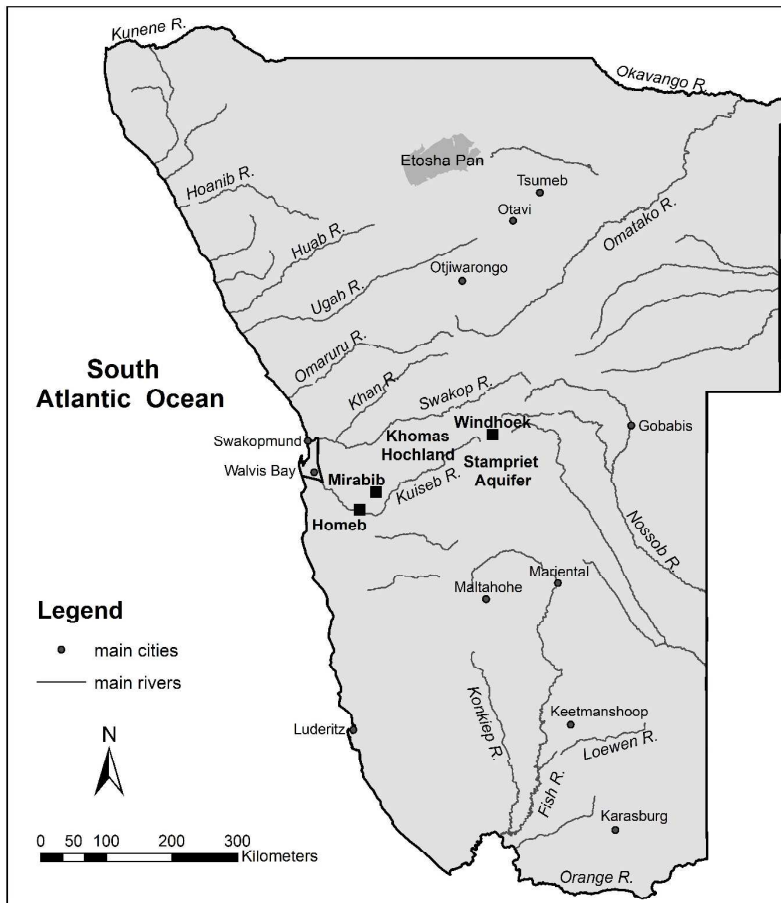
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Figure 1. Map of Namibia showing the location of Windhoek and other sites mentioned in the text. The panhandle (Caprivi Strip) of Namibia is not shown.

Figure 2. Last plate of an upper M^2 of *L. africana zulu* from Windhoek.

Map of Namibia showing the location of Windhoek and other sites mentioned in the text. The panhandle (Caprivi Strip) of Namibia is not shown.
215x166mm (300 x 300 DPI)