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Late Pleistocene and Holocene mammal extinctions on continental Africa



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ABSTRACT

Understanding the cause of late Quaternary mammal extinctions is the subject of intense debate spanning the fields of archeology and paleontology. In the global context, the losses on continental Africa have received little attention and are poorly understood. This study aims to inspire new discussion of African extinctions through a review of the extinct species and the chronology and possible causes of those extinctions. There are at least 24 large mammal (>5 kg) species known to have disappeared from continental Africa during the late Pleistocene or Holocene, indicating a much greater taxonomic breadth than previously recognized. Among the better sampled taxa, these losses are restricted to the terminal Pleistocene and early Holocene, between 13,000 and 6000 yrs ago. The African extinctions preferentially affected species that are grazers or prefer grasslands. Where good terrestrial paleoenvironmental 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. In the broader evolutionary context, these extinctions represent recent examples of selective taxonomic winnowing characterized by the loss of grassland specialists and the establishment of large mammal communities composed of more ecologically flexible taxa over the last million years. There is little reason to believe that humans played an important role in African extinctions.

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1. Introduction

The last ~100,000 yrs witnessed massive extinctions of large mammals across the continents. Understanding what caused these extinctions is one of the most contentious problems in Quaternary science, with debate focusing primarily on the extent to which anthropogenic or climatic drivers are to blame (MacPhee, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006; Wroe et al., 2013). Compared to the losses in North America, Australia, and Eurasia, the late Quaternary extinctions (LQE) on continental Africa have received little attention and are considered to be poorly understood (Martin and Steadman, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006).

Klein (1984b) provided the most comprehensive review of African LQE to date, with particular attention to the South African record. However, within the context of the global megafaunal extinction debate, it is Maglio and Cooke's (1978) volume on the evolution of African mammals that provides the ultimate primary reference for most accounts of African species thought to have disappeared during the late Pleistocene and Holocene (e.g., Martin, 1984; Smith et al., 2003; Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006). The species lists generated from this volume have yet to be updated or vetted by contemporary standards, despite substantial gains in African paleontology over the last several decades (Werdelin and Sanders, 2010). The result is that species now known to have disappeared during the middle Pleistocene routinely appear on lists of taxa thought to have disappeared within the last ~100,000 yrs (e.g., the bovid *Parmularius* and the equid *Hipparion*) (e.g., Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006), whereas more recent additions do not appear at all (e.g., Bagtache et al., 1984; Pickford and Thomas, 1984; Brink, 1999; Faith et al., 2011, 2012).

A comprehensive account of the mammals involved is needed if Quaternary scientists are to begin to understand the causes of African LQE. The goal of this paper is to provide such a synthesis for the late Pleistocene (126,000 to 12,000 yrs ago) and Holocene (<12,000 yrs ago) of continental Africa, in addition to an assessment of the extinction chronology and possible explanations.

2. Africa and the extinctions debate

2.1. Africa in the global context

Despite being poorly understood, the African LQE play an important role in the global extinction debate. The African losses are often characterized as less severe than extinctions elsewhere (Martin, 1984; Barnosky et al., 2004; Koch and Barnosky, 2006). Martin (1984: 380) remarks that the African mammals “escaped being greatly altered by late Pleistocene extinctions” while Koch and Barnosky (2006: 221) consider Africa “a fortunate anomaly.” This is true in the sense that Africa supports an exceptionally diverse large mammal community today (Kingdon, 1982). For example, there are 38 genera of extant African megafauna (>44 kg), compared to fewer than 20 on other continents (Eurasia: 17; North America: 13; South America: 10; Australia: 2) (Koch and Barnosky, 2006).

The apparently anomalous survival of Africa's large mammals is thought by some to reflect long-term co-evolution of human predators and their prey (Martin, 1984; Lyons et al., 2004). The earliest representatives of our genus (*Homo habilis*) appeared in Africa ~2.3 million yrs ago (Kimbel et al., 1997; Antón, 2012), with fossil and genetic evidence pointing to an African origin of *Homo sapiens* between 200,000 and 100,000 yrs ago (White et al., 2003; McDougall et al., 2005; Gonder et al., 2007; Campbell and Tishkoff, 2010; Brown et al., 2012). African hominins incorporated animal tissues into their diet perhaps as early as 3.4 million yrs ago (McPherron et al., 2010; but see Domínguez-Rodrigo et al., 2010) and there is ample evidence for the exploitation of terrestrial prey by ~2.6 to 1.5 million yrs ago (Bunn, 1981; Potts and Shipman, 1981; Bunn and Kroll, 1986; Domínguez-Rodrigo et al., 2005; Pobiner et al., 2008; Domínguez-Rodrigo et al., 2009; Ferraro et al., 2013). Although there is debate about when early hominins became proficient hunters (Marean and Assefa, 1999; Klein, 2001; Domínguez-Rodrigo, 2002; Faith, 2008; Ferraro et al., 2013), the long-term development of hunting behavior is argued to have translated to the evolution of defense mechanisms in African prey, rendering them relatively immune to the impacts of prehistoric hunters (Martin, 1984).

The co-evolution argument is central to Martin's (1967, 1984, 2005) overkill hypothesis, which proposes that human hunters caused

massive extinctions as they dispersed throughout the continents during the last ~70,000 yrs. According to Martin, the greater severity of extinctions in Australia and the Americas was the result of naïve prey that lacked the behavioral defense mechanisms of their African counterparts (see [Wroe et al., 2004](#) for a critique). The presumed vulnerability of non-African faunas was such that invading human hunters were able to wipe them out in a geological instant, meaning that little archeological evidence for overkill is to be expected. Martin also argued that the survival of Africa's megafauna is evidence that late Quaternary climate change is incapable of driving mass extinction of large mammals. No matter what their potential, albeit contentious (e.g., [Grayson and Meltzer, 2003](#); [Wroe et al., 2004, 2013](#)), applicability to extinctions elsewhere, these arguments offer little insight into the losses that occurred in Africa.

2.2. Extinction research in Africa

The study of Pleistocene African mammals was fueled by the discovery of hominin fossils from sites in Southern and East Africa, including the Sterkfontein Caves and Olduvai Gorge ([Fig. 1](#)), following World War II. These discoveries stimulated interest in the associated fauna in order to establish the biochronological, paleoenvironmental, and evolutionary context of the hominin fossils ([Maglio and Cooke, 1978](#)). This tradition continues today, with much of the recent progress in Cenozoic African paleontology driven by paleoanthropological research ([Sanders and Werdelin, 2010](#)).

The extinct mammals discussed here, although corresponding to a much more recent phase of human prehistory, are no exception. The majority of sites yielding extinct late Pleistocene and Holocene mammals are the focus of archeological investigations into the behavioral, ecological, and environmental context of early *H. sapiens* ([Fig. 1](#)). Most of these are caves or rockshelters that were inhabited by Middle Stone Age (MSA: 280,000 to 40,000 yrs ago) or Later Stone Age (LSA: <40,000 yrs ago) humans, with the associated faunal remains typically representing discarded food refuse. While evidence that humans hunted extinct megafauna is scant in the Americas or Australia ([Grayson and Meltzer, 2002](#); [Barnosky et al., 2004](#); [Koch and Barnosky, 2006](#); [Wroe and Field, 2006](#)), there is abundant evidence that MSA and LSA foragers routinely preyed upon extinct mammals in Africa (for two exceptional cases see [Marean, 1997](#); [Milo, 1998](#)).

[Klein \(1972, 1974b, 1980, 1984b\)](#) was the first to address African LQE in the context of the global extinction debate. His critically important work focused on the southern African record, where a long history of archeological research provided the most detailed late Quaternary faunal sequence for the continent. At the time, this record documented the extinction of a handful of open grassland ungulates near the Pleistocene–Holocene transition, between 12,000 and 9500 yrs ago. The association of these extinctions with a major episode of faunal turnover, characterized by the replacement of ungulate grazers by ungulate browsers, suggested that environmental changes were at least partly responsible. Because the extinct taxa survived previous glacial–interglacial transitions, however, Klein reasoned that human impacts

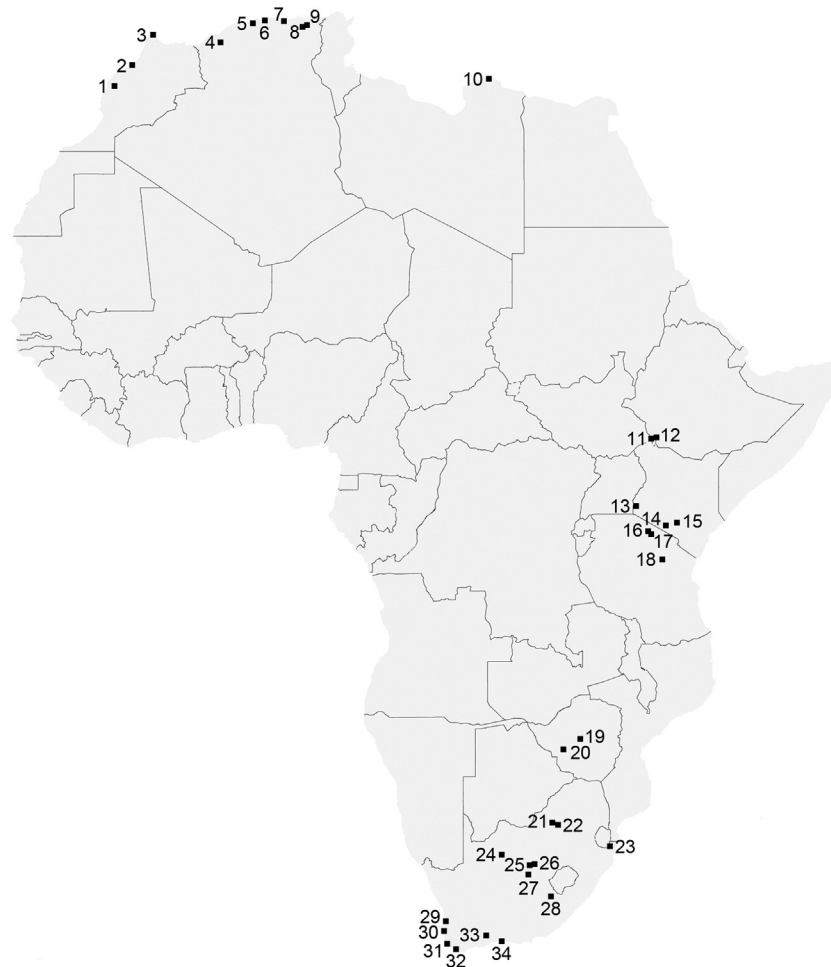


Fig. 1. Location of sites referred to in the text: (1) Jebel Irhoud, (2) El Harhoura 1 & 2, (3) Mugharet el 'Aliya, (4) Tighenif, (5) Beausejour Farm, (6) Les Phacochères, (7) Tamar Hat, (8) Jebel Thaya, (9) Hammam el Meskhoutine, (10) Haua Fteah, (11) Natodameri, (12) Shungura Formation, (13) Rusinga & Mfangano islands, (14) Lainyamok, (15) Lukenya Hill, (16) Gol Kopjes, (17) Olduvai Gorge, (18) Kisese II, (19) Redcliff Cave, (20) Chelmer Farm, (21) Kruger Cave, (22) Sterkfontein & Swartkrans, (23) Border Cave, (24) Wonderwerk Cave, (25) Modder River, (26) Florisbad & Vlakkrans, (27) Koffiefontein, (28) Colwinton, (29) Elands Bay Cave, (30) Elandsfontein, (31) Swartklip, (32) Die Kelders Cave, (33) Boomplaas Cave, (34) Nelson Bay Cave.

were also a necessary contributor. He argued that the Pleistocene–Holocene transition was unique in that it was the first glacial–interglacial transition when large mammal communities were subject to predation by highly effective hunters armed with LSA technology. According to Klein, MSA human populations, although anatomically modern, lacked the cognitive and technological prowess of their LSA successors and had little impact on animal populations.

Subsequent research on African LQE has favored environmental extinction hypotheses (Brink, 1987; Marean and Gifford-Gonzalez, 1991; Brink and Lee-Thorp, 1992; Marean, 1992; Brink, 1994, 1999; Faith, 2011c; Faith et al., 2011, 2012, in press). Anthropogenic hypotheses have fallen out of favor, in part because archeological research over the last several decades has shown the behavioral contrast between MSA and LSA humans proposed by Klein (1980, 1984b) to be untenable (e.g., Marean and Assefa, 1999; McBrearty and Brooks, 2000; Henshilwood and Marean, 2003; Faith, 2008). A better understanding of how environmental change or human impacts may have contributed to the extinctions first requires a detailed account of the species involved.

3. The extinct mammals

There are at least 24 large mammal (>5 kg) species known to have disappeared from continental Africa during the late Pleistocene (126,000 to 12,000 yrs ago) or Holocene (<12,000 yrs ago), all of which are globally extinct (Table 1, Fig. 1). These include species from six genera that are globally extinct (*Megalotragus*, *Rusingoryx*, *Megaceroides*, *Metridiochoerus*, *Kolpochoerus*, *Stephanorhinus*), two that are represented in Africa today only by domesticates (*Bos* and *Camelus*), and one that survives elsewhere (*Elephas*). An extinct caprine antelope from South Africa (Brink, 1999) likely accounts for a seventh globally extinct genus (see below). Although the precise extinction chronology for many of these taxa is poorly known, all of the taxa listed in Table 1 have been recovered from late Pleistocene or Holocene contexts as established by radiometric dates or associated archeological industries. Fossil occurrences associated with late Pleistocene or Holocene radiometric dates are reported in Table 2. Absolute ages associated with extinct mammals are derived primarily from radiocarbon (^{14}C), Uranium

series (U-series or U/Th), Electron Spin Resonance (ESR), or luminescence (TL/OSL) techniques. Radiocarbon ages are calibrated (2σ) using Calib (Stuiver and Reimer, 1993) and the INTCAL09 calibration curve (Reimer et al., 2009). Age ranges discussed here (in calendar years), often derived from multiple sites and dating techniques (Table 2), are rounded to the nearest 1000 yrs and given the suffix “ka.” A summary of the extinct taxa is provided below.

3.1. Order Artiodactyla

3.1.1. *Aepyceros* sp.

The evolutionary history of impalas (*Aepyceros* spp.) was once characterized as a single, gradually changing lineage leading to the modern species (*Aepyceros melampus*) (e.g., Gentry, 1978). However, recent research has documented the presence of several extinct impalas in the Pliocene (Geraads et al., 2009; Gentry, 2011; Geraads, 2012) and Pleistocene (Brink et al., 2012; Faith et al., in press). These include a large-bodied and markedly hypsodont impala recovered from late Pleistocene (100 to 33 ka) deposits along the margins of Lake Victoria in Kenya (Faith et al., in press). Due to the lack of a suitable type specimen, this extinct impala remains to be formally named. Its exceptionally deep mandibles and hypsodont teeth suggest a greater emphasis on grazing in open and dry environments compared to *A. melampus*. The adaptive implications of elevated hypsodonty is consistent with the associated faunal communities, which indicate the dominance of open and seasonally arid grasslands (Tryon et al., 2010, 2012), although provisional isotopic evidence indicates that the extinct impala consumed some dicots (Garret et al., 2010).

3.1.2. *Antidorcas australis*

First recovered from middle Pleistocene deposits at Swartklip along the southern coast of South Africa, the southern springbok (*Antidorcas australis*) was originally described as a subspecies of the modern springbok (as *A. marsupialis australis*) (Hendey and Hendey, 1968). Vrba (1973) subsequently elevated it to specific status, noting that its presence at Swartkrans suggests a wide temporal and geographic distribution worthy of a valid species. She later expressed doubt concerning her attribution of the Swartkrans fossils to *A. australis* (Vrba, 1976), suggesting that the material may instead represent a pre-marsupialis variant. Although the taxonomic status of the Swartkrans material remains uncertain (de Ruiter, 2003; Gentry, 2010a; Hendey (1974) supported the taxonomic validity of *A. australis* when it became clear that it was found together with *Antidorcas recki*, the presumed ancestor of modern springbok, in the early-to-middle Pleistocene deposits at Elandsfontein (see also Klein et al., 2007). With definitive records occurring only along the southern and western coasts of South Africa, the southern springbok is documented in the late Pleistocene (~60 to 50 ka) at Die Kelders Cave (Feathers and Bush, 2000; Klein and Cruz-Urbe, 2000; Schwarcz and Rink, 2000) and perhaps also in the very latest Pleistocene deposits at Nelson Bay Cave (11,950 \pm 150 ^{14}C yrs BP = 13,430 to 14,140 cal yrs BP) as *A. cf. australis* (Klein, 1980, 1983). Where it is found, *A. australis* is associated with open-habitat species including equids and alcelaphine antelopes. Like extant springbok, the southern springbok was probably a mixed feeder, capable of browsing dicots when grasses became unpalatable or scarce (Klein, 1980).

3.1.3. *Antidorcas bondi*

Cooke and Wells (1951) described *Gazella bondi* from Quaternary deposits at Chelmer Farm in Zimbabwe and Vlakkrak in South Africa. In her analysis of antelope remains from Swartkrans, Vrba (1973) later placed the species within *Antidorcas* on the basis of its cranial morphology. Bond's springbok is very well documented in the late Pleistocene to early Holocene (89 to 8 ka) of southern Africa (Klein, 1977; Cruz-Urbe, 1983; Klein, 1984a; Brown and Verhagen, 1985; Klein et al., 1991; Brink and Lee-Thorp, 1992; Plug and Engela, 1992; Plug, 1993, 1997; de Ruiter et al., 2008). Its exceptionally hypsodont teeth,

Table 1
Extinct late Pleistocene and Holocene African mammals. Taxa in bold represent genera that are globally extinct.

| Order | Family | Taxon |
|----------------|-----------------|---------------------------------------|
| Artiodactyla | Bovidae | <i>Aepyceros</i> sp. |
| | | <i>Antidorcas australis</i> |
| | | <i>Antidorcas bondi</i> |
| | | <i>Bos primigenius</i> ^a |
| | | <i>Damaliscus hypsodon</i> |
| | | <i>Damaliscus niro</i> |
| | | <i>Gazella atlantica</i> |
| | | <i>Gazella tingitana</i> |
| | | <i>Hippotragus leucophaeus</i> |
| | | <i>Megalotragus priscus</i> |
| | | <i>Rusingoryx atopocranion</i> |
| | | <i>Syncerus antiquus</i> |
| | | Unnamed caprine antelope |
| | | <i>Camelus</i> sp. ^a |
| | Camelidae | <i>Megaceroides algericus</i> |
| | Cervidae | <i>Metridiochoerus</i> sp. |
| | Suidae | <i>Kolpochoerus</i> sp. |
| Perissodactyla | Equidae | <i>Equus algericus</i> |
| | | <i>Equus capensis</i> |
| | | <i>Equus mauritanicus</i> |
| | | <i>Equus melkiensis</i> |
| Proboscidea | Rhinocerotidae | <i>Stephanorhinus</i> |
| | Elephantidae | <i>Elephas iolensis</i> ^b |
| Tubulidentata | Orycteropodidae | <i>Orycteropus crassidens</i> |

^a Genus represented in Africa by domesticates only.

^b Genus no longer represented in Africa, but survives elsewhere.

together with isotopic evidence, suggest that this small springbok was a specialized grazer (Vrba, 1973; Brink and Lee-Thorp, 1992). Gentry (2010a) notes that in near-mature individuals, the extreme hypsodonty results in incomplete ossification along the inferior border of the mandible's horizontal ramus. In the stratified sequence from Border Cave in South Africa, its abundance tracks that of other open grassland species (Klein, 1977).

3.1.4. *Bos primigenius*

The aurochs (*Bos primigenius*) is the extinct progenitor of domestic cattle. Although it is typically considered a Eurasian taxon (Martinez-Navarro et al., 2007), aurochs fossils are well known from numerous late Pleistocene and early Holocene (115 to 6 ka) sites across North Africa (Churcher, 1972; Churcher and Smith, 1972; Churcher, 1974, 1999; Gautier, 1976; Wendorf and Schild, 1976; Klein and Scott, 1986; Marks et al., 1987; Michel, 1992; Peters, 1992; Vermeersch, 2000; Wengler et al., 2002; Aouraghe, 2004; Nespolet et al., 2008; Michel et al., 2009; Monchot and Aouraghe, 2009; Bougariane et al., 2010; Dibble et al., 2012). North African aurochs typically co-occurs with several species of gazelle (*Gazella* spp.) and equids (*Equus* spp.). Genetic evidence suggests that North African aurochs underwent indigenous African domestication near the onset of the Holocene (Bradley et al., 1996; Hanotte et al., 2002). Although this has prompted some to treat the disappearance of aurochs as a pseudo-extinction (Turvey, 2009), African aurochs persisted well into the Holocene (Table 2), meaning that the domestication process did not involve all populations of the species. Those that were not domesticated ultimately disappeared ~6 ka.

3.1.5. *Damaliscus hypsodon*

Fossils of a small alcelaphine (wildebeest and allies) now known as *Damaliscus hypsodon* were initially reported by Marean (1990) from late Pleistocene ($>11,950 \pm 460$ ^{14}C yrs BP = 12,776 to 15,268 cal yrs BP) archaeological contexts at Lukenya Hill in south-central Kenya. It was subsequently reported from the late Pleistocene at Kiseso II Rockshelter ($>10,720 \pm 132$ ^{14}C yrs BP = 12,375 to 12,946 cal yrs BP) and Gol Kopjes (undated) in northern Tanzania (Marean and Gifford-Gonzalez, 1991) and from late Pleistocene sites (100 to 33 ka) in Kenya's Lake Victoria Basin (Tryon et al., 2010, 2012). This small alcelaphine remained unnamed until recently, when middle Pleistocene specimens from Lainyamok (Kenya) that were previously attributed to *Damaliscus* cf. *dorcus* (Potts and Deino, 1995) were formally described as *D. hypsodon* (Faith et al., 2012). The dietary and locomotor adaptations of *D. hypsodon*, together with its association with oryx (*Oryx beisa*) and Grevy's zebra (*Equus grevyi*) (Faith et al., 2013), suggest that it grazed in open and arid grasslands. As suggested by its name, and like *A. bondi*, its teeth are characterized by greater hypsodonty than any extant African bovid, overlapping with some species of *Equus*.

3.1.6. *Damaliscus niro*

Hopwood (1936) designated a horn core collected by L.S.B. Leakey from Bed IV Olduvai Gorge as the type specimen of *Hippotragus niro*, a species later placed within *Damaliscus* by Gentry (1965). There are numerous records of *D. niro* from the early-to-middle Pleistocene of East and southern Africa (Cooke, 1974; Gentry and Gentry, 1978; Brink, 1987; Vrba, 1997; Suwa et al., 2003; Geraads et al., 2004; Thackeray and Brink, 2004). A late Pleistocene record of *D. niro* was recently reported by de Ruiter et al. (2008) from Plovers Lake in South Africa. The Plovers Lake specimen came from deposits that were disturbed by mining activity. However, the vast majority of *in situ* fossils from this site are from a deposit bracketed by flowstones and dated by U-Series and ESR to between 89 and 63 ka. There are some fossil remains from beneath the primary fossil deposit, but these are also dated to the late Pleistocene (92 ka). Thus, the Plovers Lake *D. niro* most likely dates to between 89 and 63 ka, or perhaps slightly older. Isotopic evidence

from middle Pleistocene specimens in South Africa indicates a diet dominated by C_4 grasses (Codron et al., 2008).

3.1.7. *Gazella atlantica*

The Atlantic gazelle (*Gazella atlantica*) was described by Bourguignat (1870) from late Quaternary cave deposits at Jebel Thaya in Algeria. This North African species is common in late Pleistocene (100 to 37 ka) archaeological and paleontological contexts across Algeria and Morocco (Aouraghe, 2004; Raynal et al., 2008; Michel et al., 2009; Bougariane et al., 2010; Geraads, 2012; Steele, 2012). Klein (1984b) suggests that *G. atlantica* may have persisted into the middle Holocene, although this remains to be substantiated (Turvey, 2009). In the stratified sequence from El Harhoura 2 in Morocco, the occurrences of *G. atlantica* coincide with those of wildebeest (*Connochaetes taurinus*) and hartebeest (*Alcelaphus buselaphus*) (Michel et al., 2009), suggesting a preference for grasslands.

3.1.8. *Gazella tingitana*

In his survey of North African Pleistocene gazelles, Arambourg (1957) described *Gazella tingitana* from Aterian levels at Mugharet el 'Aliya in Morocco, now dated to between 85 and 37 ka (Wrinne and Rink, 2003). Amani and Geraads (1993) subsequently documented this poorly known gazelle from middle-to-late Pleistocene (190 to 90 ka) deposits at Jebel Irhoud (Grün and Stringer, 1991; Smith et al., 2007). There is little paleoecological information available for this taxon, although like other gazelles it may have been a mixed feeder that preferred open habitats.

3.1.9. *Hippotragus leucophaeus*

The first large African mammal to become extinct in historic times, the blue antelope (*Hippotragus leucophaeus*) was endemic to southernmost South Africa and disappeared ~1800 AD (Klein, 1974a; Kerley et al., 2009; Skead, 2011). Although its historic range was limited to some 4300 km² to the east of Cape Town (Kerley et al., 2009), late Pleistocene fossil evidence and rock art suggests a much broader distribution across southern Africa (Klein, 1974a; Loubser et al., 1990; Faith and Thompson, 2013). The blue antelope is commonly found in late Pleistocene assemblages from the southern and western Cape of South Africa, and it is typically more numerous in assemblages dominated by open grassland species, including equids and alcelaphine bovids (Klein, 1983). Evidence from mortality profiles indicates that blue antelope preferentially calved in the western margin of its range and migrated east–west across the southern coast, presumably to track seasonal rains (Faith and Thompson, 2013). A combination of long-term and more recent mechanisms have been invoked to account for its extinction, including climate-driven vegetation change and disruption of migration routes (Faith and Thompson, 2013), competition with domestic livestock within the past 2000 yrs (Klein, 1974a), overhunting by European colonists (Klein, 1974a; IUCN SSC Antelope Specialist Group, 2008b; but see Kerley et al., 2009), and habitat loss and fragmentation due to agricultural expansion during the colonial era (Faith and Thompson, 2013).

3.1.10. *Megalotragus priscus*

The giant wildebeest (*Megalotragus priscus*) was described by Broom (1909a) as *Bubalis priscus* on the basis of a cranial fragment from late Quaternary deposits along the Modder River in central South Africa. The taxon has many synonyms (e.g., *Bubalis helmei*, *Pelorocerus elegans*, *Connochaetes grandis*), although most authorities attribute all giant alcelaphine remains from the late Pleistocene of southern Africa to *M. priscus* (Gentry, 1978; Gentry and Gentry, 1978; Klein, 1980; Brink et al., 1995; Brink, 2005; Gentry, 2010a). The molars of *Megalotragus* are hypsodont (Gentry and Gentry, 1978) and isotopic data indicate a diet of C_4 grasses (Lee-Thorp and Beaumont, 1995; Codron et al., 2008). Together with its massive body size, which exceeds extant alcelaphine antelopes, this suggests a diet involving the unselective

Table 2
Late Pleistocene and Holocene radiometric dates associated with extinct African mammals (excluding blue antelope). ALG = Algeria, EGY = Egypt, KEN = Kenya, LYB = Lybia, MOR = Morocco, SA = South Africa, SUD = Sudan, TAN = Tanzania, TUN = Tunisia, ZIM = Zimbabwe.

| Taxon | Site | Date | Reference |
|--------------------------------|--------------------------|--|---|
| <i>Aepyceros</i> sp. | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Faith et al. (in press) |
| <i>Antidorcas australis</i> | Die Kelders Cave SA | 50.7 ± 4.7 to 79.7 ± 15.6 ka (TL/OSL) | Feathers and Bush (2000) and Klein and Cruz-Uribe (2000) |
| | Nelson Bay Cave SA | 11,950 ± 150 to 18,660 ± 100 ¹⁴ C yrs BP | Klein (1983) and Deacon (1984) |
| <i>Antidorcas bondi</i> | Border Cave SA | 37,700 ± 590 ¹⁴ C yrs BP to 60 ± 3 ka (ESR) | Klein (1977) and d'Errico et al. (2012) |
| | Equus Cave SA | 9830 ± 120 to 27,230 ± 340 ¹⁴ C yrs BP | Klein et al. (1991) and Lee-Thorp and Beaumont (1995) |
| | Heuningneskrans SA | 19,980 ± 260 ¹⁴ C yr BP | Klein (1984a) |
| | Kruger Cave SA | 7570 ± 60 ¹⁴ C yrs BP | Brown and Verhagen (1985) |
| | Plovers Lake SA | 62.9 ± 1.3 to 88.7 ± 1.6 ka (U) | de Ruiter et al. (2008) |
| | Rose Cottage Cave SA | 9250 ± 70 ¹⁴ C yr BP | Wadley (1991) and Plug and Engela (1992) |
| | Redcliff Cave ZIM | 25,650 ± 1800 ¹⁴ C yrs BP | Cruz-Uribe (1983) |
| <i>Bos primigenius</i> | Contrebandiers Cave MOR | 96 ± 4 to 115 ± 3 (OSL) | Dibble et al. (2012) |
| | El-Kilh E71P1 EGY | 16,950 ± 300 to 17,800 ± 300 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | El-Kilh E71P5 EGY | 11,560 ± 80 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Fayum E29H1 EGY | 8070 ± 115 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Isna E71K1 EGY | 18,020 ± 300 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Isna E71K3 EGY | 17,590 ± 300 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Isna E71K9 EGY | 9330 ± 160 to 16,830 ± 290 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Isna E71K14 EGY | 12,690 ± 240 ¹⁴ C yrs BP | Wendorf and Schild (1976) |
| | Makhadma 2 EGY | 12,060 ± 280 to 13,330 ± 170 ¹⁴ C yrs BP | Vermeersch (2000) |
| | Makhadma 4 EGY | 12,320 ± 70 to 12,940 ± 130 ¹⁴ C yrs BP | Vermeersch (2000) |
| | Shuwikhat 1 EGY | 25,000 ± 2500 ¹⁴ C yrs BP | Vermeersch (2000) |
| | Haua Fteah LYB | 7300 ± 30 to 47,000 ± 1500 ¹⁴ C yrs BP | Klein and Scott (1986) |
| | El Harhoura 1 MOR | 5400 ± 290 ¹⁴ C yr BP to >66.5 ± 5.2 ka (U) | Monchot and Aouraghe (2009) and Raynal and Occhietti (2012) |
| | El Harhoura 2 MOR | <51.6 ± 3.6 to 102.6 ± 5.7 (OSL) | Michel et al. (2009) and Jacobs et al. (2012) |
| | El Mnasra MOR | 71 ± 5.3 to 108.8 ± 6.6 (OSL) | Nespoulet et al. (2008) and Jacobs et al. (2012) |
| | Rhafas Cave MOR | 70 (TL) to 107 ± 12 ka (OSL) | Michel (1992) and Mercier et al. (2007) |
| | Wadi Assaka MOR | >30,200 ± 2900 ¹⁴ C yrs BP | Wengler et al. (2002) |
| | Khashm el Girba KG15 SUD | 10,230 ± 270 ¹⁴ C yr BP | Marks et al. (1987) |
| <i>Damaliscus hypsodon</i> | Lukenya Hill Gvjm19 KEN | 13,705 ± 430 ¹⁴ C yrs BP | Marean (1992) |
| | Lukenya Hill Gvjm22 KEN | 13,730 ± 430 to 17,700 ± 760 ¹⁴ C yrs BP | Marean (1992) |
| | Lukenya Hill Gvjm46 KEN | 19,330 ± 945 to 20,780 ± 1050 ¹⁴ C yrs BP | Marean (1992) |
| | Lukenya Hill Gvjm62 KEN | 11,950 ± 460 to 21,535 ± 980 ¹⁴ C yrs BP | Marean (1992) |
| | Mfangano Island KEN | >30,530 ± 390 ¹⁴ C yrs BP | Tryon et al. (2012) |
| | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Tryon et al. (2010, 2012) |
| | Kisese II TAN | >10,720 ± 132 ¹⁴ C yrs BP | Marean and Gifford-Gonzalez (1991) |
| <i>Damaliscus niro</i> | Plovers Lake SA | 62.9 ± 1.3 to 88.7 ± 1.6 ka (U) | de Ruiter et al. (2008) |
| <i>Gazella atlantica</i> | El Harhoura 1 MOR | >66.5 ± 5.2 ka (U) | Monchot and Aouraghe (2009) and Raynal and Occhietti (2012) |
| | El Harhoura 2 MOR | <51.6 ± 3.6 to 99.9 ± 5.8 ka (OSL) | Michel et al. (2009) and Jacobs et al. (2012) |
| | Mugharet el 'Aliya MOR | 37 ± 4 to 85 ± 9 ka (ESR) | Steele (2012) and Wrinn and Rink (2003) |
| <i>Gazella tingitana</i> | Mugharet el 'Aliya MOR | 37 ± 4 to 85 ± 9 ka (ESR) | Steele (2012) and Wrinn and Rink (2003) |
| <i>Megalotragus priscus</i> | Boomplaas Cave SA | 21,100 ± 180 ¹⁴ C yr BP | Klein (1983) and Deacon (1984) |
| | Equus Cave SA | 9830 ± 120 to 27,230 ± 340 ¹⁴ C yrs BP | Klein et al. (1991) and Lee-Thorp and Beaumont (1995) |
| | Nelson Bay Cave SA | 16,700 ± 240 ¹⁴ C yrs BP | Klein (1983) and Deacon (1984) |
| | Plovers Lake SA | 62.9 ± 1.3 to 88.7 ± 1.6 ka (U) | de Ruiter et al. (2008) |
| | Rose Cottage Cave SA | 12,690 ± 120 to 13,360 ± 150 ¹⁴ C yrs BP | Wadley (1991) and Plug and Engela (1992) |
| | Sibudu Cave SA | 61.7 ± 2 to 64.7 ± 2.3 ka (OSL) | Clark (2011) |
| | Wonderwerk Cave SA | 7430 ± 60 ¹⁴ C yrs BP | Thackeray et al. (1981) |
| <i>Megalotragus</i> | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Tryon et al. (2010) and Faith et al. (2011) |
| <i>Rusingoryx atopocranion</i> | Mfangano Island KEN | >30,530 ± 390 | Tryon et al. (2012) |
| | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Faith et al. (2011) and Tryon et al. (2012) |
| <i>Syncerus antiquus</i> | Amekni ALG | 5500 ± 250 to 8670 ± 150 ¹⁴ C yrs BP | Gautier (1987) and Gautier and Muzzolini (1991) |
| | Medjez II ALG | 8550 ± 150 ¹⁴ C yrs BP | Gautier and Muzzolini (1991) |
| | Meniet ALG | 5400 ± 150 ¹⁴ C yrs BP | Gautier (1987) and Gautier and Muzzolini (1991) |
| | Lukenya Hill Gvjm22 KEN | 13,730 ± 430 to 17,700 ± 760 ¹⁴ C yrs BP | Marean (1992) |
| | Mfangano Island KEN | >30,530 ± 390 to 41,846 ± 458 ¹⁴ C yrs BP | Tryon et al. (2012) |
| | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Tryon et al. (2010, 2012) |
| | El Harhoura 1 MOR | >66.5 ± 5.2 ka (U) | Monchot and Aouraghe (2009) and Raynal and Occhietti (2012) |
| | El Harhoura 2 MOR | 51.6 ± 3.6 to 106.7 ± 6.6 ka (OSL) | Michel et al. (2009) and Jacobs et al. (2012) |
| | Mugharet el 'Aliya MOR | 37 ± 4 to 85 ± 9 ka (ESR) | Steele (2012) and Wrinn and Rink (2003) |
| | Boomplaas Cave SA | 12,060 ± 105 to 21,110 ± 180 ¹⁴ C yrs BP | Klein (1983) and Deacon (1984) |
| | Die Kelders Cave SA | 50.7 ± 4.7 to 79.7 ± 15.6 ka (TL/OSL) | Feathers and Bush (2000) and Klein and Cruz-Uribe (2000) |
| | Nelson Bay Cave SA | 11,950 ± 150 to 18,660 ± 100 ¹⁴ C yrs BP | Klein (1983) and Deacon (1984) |
| | Klasies River Mouth SA | 43.4 ± 3.0 to 106.8 ± 12.6 ka (OSL) | Klein (1976) and Feathers (2002) |
| | Sibudu Cave SA | 57.6 ± 2.1 to 59.6 ± 2.3 ka (OSL) | Clark (2011) |
| Unnamed caprine | Boomplaas Cave SA | 9100 ± 135 ¹⁴ C yr BP to 66 ± 7 ka | Faith (2012) and Vogel (2001) |
| | Colwinton Shelter SA | 6270 ± 40 ¹⁴ C yr BP | Brink (1999) |
| <i>Camelus</i> | Bir Tarfawi 14 EGY | 71.4 ± 8.2/–7.1 to 129.2 ± 7.7 ka (OSL) | Gautier (1993) and Stokes (1993) |
| | Wadi Assaka MOR | >30,200 ± 2900 ¹⁴ C yrs BP | Wengler et al. (2002) |
| | Oued el Akarit TUN | 19,900 ± 750 to >34,000 ¹⁴ C yrs BP | Brun et al. (1988) |
| <i>Megaceroides algericus</i> | Tamar Hat ALG | 17,040 ± 400 ¹⁴ C yr BP | Merzoug and Sari (2008) |
| <i>Metridiochoerus</i> | Redcliff Cave ZIM | 25,650 ± 1800 ¹⁴ C yrs BP | Cruz-Uribe (1983) |
| <i>Kolpochoerus</i> | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Tryon et al. (2010); this study |
| <i>Equus algericus</i> | El Harhoura 1 MOR | 5400 ± 290 ¹⁴ C yrs BP to >66.5 ± 5.2 (U) | Monchot and Aouraghe (2009) and Raynal and Occhietti (2012) |
| <i>Equus capensis</i> | Apollo 11 NAM | 12,510 ± 90 to 14,550 ± 90 ¹⁴ C yrs BP | Thackeray (1979) |
| | Equus Cave SA | 9830 ± 120 to 27,230 ± 340 ¹⁴ C yrs BP | Klein et al. (1991) and Lee-Thorp and Beaumont (1995) |

Table 2 (continued)

| Taxon | Site | Date | Reference |
|-------------------------------|-------------------------|---|---|
| | Boomplaas Cave SA | 12,060 ± 105 to 17,830 ± 180 ¹⁴ C yr BP | Klein (1983) and Faith (2012) |
| | Border Cave SA | 47 ± 2 ka (ESR) | Klein (1977) and d'Errico et al. (2012) |
| | Bushman Rock Shelter SA | >47,000 ¹⁴ C yr BP | Badenhorst and Plug (2012) |
| | Byneskranskop 1 SA | 12,730 ± 185 ¹⁴ C yr BP | Schweitzer and Wilson (1982) |
| | Die Kelders Cave 1 SA | 50.7 ± 4.7 to 79.7 ± 15.6 (TL/OSL) ka | Feathers and Bush (2000) and Klein and Cruz-Uribe (2000) |
| | Elands Bay Cave SA | 9600 ± 90 to 12,450 ± 280 ¹⁴ C yrs BP | Klein and Cruz-Uribe (1987) |
| | Rose Cottage Cave SA | 12,690 ± 120 to 13,360 ± 150 ¹⁴ C yrs BP | Wadley (1991) and Plug and Engela (1992) |
| | Wonderwerk Cave SA | 10,000 ± 70 ¹⁴ C yrs BP | Thackeray et al. (1981) |
| | Redcliff Cave ZIM | 25,650 ± 1800 ¹⁴ C yrs BP | Cruz-Uribe (1983) |
| <i>Equus mauritanicus</i> | Contrebandiers Cave MOR | 96 ± 4 to 115 ± 3 (OSL) | Dibble et al. (2012) |
| | El Harhoura 1 MOR | 5400 ± 290 ¹⁴ C yrs BP to >66.5 ± 5.2 ka (U) | Monchot and Aouraghe (2009) and Raynal and Occhietti (2012) |
| | Rhafas Cave MOR | 5400 ± 100 ¹⁴ C yrs BP to <107 ± 12 (OSL) | Michel (1992) and Mercier et al. (2007) |
| | Oued el Akarit TUN | 19,900 ± 750 to >34,000 ¹⁴ C yrs BP | Brun et al. (1988) |
| <i>Equus melkiensis</i> | Mugharet el 'Aliya MOR | 37 ± 4 to 85 ± 9 ka (ESR) | Eisenmann (2006) and Wrinn and Rink (2003) |
| <i>Stephanorhinus</i> | Contrebandiers Cave MOR | 107 ± 9 (OSL) | Dibble et al. (2012) |
| | Haua Fteah LYB | 16,070 ± 100 to 47,000 ± 1500 ¹⁴ C yrs BP | Klein and Scott (1986) |
| | El Harhoura 2 MOR | <52.6 ± 3.3 to 61.9 ± 3.5 (OSL) | Michel et al. (2009) and Jacobs et al. (2012) |
| | El Mnasra MOR | 108.8 ± 6.6 ka (OSL) | Nespoulet et al. (2008) and Jacobs et al. (2012) |
| <i>Elephas iolensis</i> | Natodameri SUD | 35 ka (U) | Coppens et al. (1978) |
| <i>Orycteropus crassidens</i> | Rusinga Island KEN | >28,670 ± 600 ¹⁴ C yrs BP to 100 ka | Tryon et al. (2010, 2012) |

bulk grazing of low quality forage (Bell, 1971; Jarman, 1974; Marean, 1992). Relative to extant alcelaphines, the metapodials of *Megalotragus* are long compared to its upper limbs (Gentry and Gentry, 1978), suggesting a preference for open habitats (Scott, 1985; Plummer and Bishop, 1994). *Megalotragus priscus* is documented in numerous late Pleistocene archeological and paleontological localities (89 to 12 ka) across southern Africa (Klein, 1980; Cruz-Uribe, 1983; Klein, 1983, 1984a; Klein et al., 1991; Plug and Engela, 1992; Brink et al., 1995; Robbins et al., 2000; Clark and Plug, 2008; de Ruiter et al., 2008), with a single early Holocene record dating to 7430 ± 60 ¹⁴C yrs BP (8160 to 8392 cal yrs BP) at Wonderwerk Cave (Thackeray et al., 1981; Thackeray, 1983). In addition to the southern African occurrences, *Megalotragus* remains have also been recovered from late Pleistocene deposits (100 to 33 ka) in Kenya's Lake Victoria Basin (Tryon et al., 2010; Faith et al., 2011; Tryon et al., 2012). It is unclear whether these represent a late form of *Megalotragus kattwinkeli*, known from earlier in the East African Pleistocene, *M. priscus*, or a new species.

3.1.11. *Rusingoryx atopocranion*

Pickford and Thomas (1984) described a new genus of alcelaphine bovid on the basis of a partial cranium recovered from the Wasiriya Beds of Rusinga Island, Kenya. *Rusingoryx atopocranion* was later subsumed into *Megalotragus* by Harris (1991), a decision supported by Vrba's (1997) phylogenetic analysis of fossil alcelaphines. However, renewed fieldwork on Rusinga Island (Tryon et al., 2010) recovered a large sample of *Rusingoryx* remains that provided morphological and phylogenetic evidence supporting its distinction from *Megalotragus*, which is also present in the fossil collection (Faith et al., 2011). The Rusinga specimens are now dated to the late Pleistocene (100 to 33 ka) and additional remains have been recovered from roughly contemporaneous deposits (>35 ka) on nearby Mfangano Island (Tryon et al., 2012). Dental mesowear analysis, isotopic analysis, and its extreme hypsodonty indicate that *R. atopocranion* was a grazer, while its association with Grevy's zebra (*E. grevyi*) and oryx (*O. beisa*) suggests a preference for dry grassland or scrub habitats (Faith et al., 2011).

3.1.12. *Syncerus antiquus*

The giant buffalo (*Syncerus antiquus*) holds the distinction of being the largest African bovid and the first fossil bovid described on the continent. Believing it to be closely related to the Asian water buffalo (*Bubalus bubalis*), Duvernoy (1851) founded the taxon as *Bubalus antiquus* on the basis of a cranial fragment recovered from Quaternary deposits in Algeria. *Bubalus* was subsequently used for several species of giant buffalo, including *Bubalus bainii* from South Africa (Seeley, 1891) and *Bubalus nilssoni* from Kenya (Lönnberg, 1933). Bate (1951)

recognized that these buffaloes were conspecific and not related to *Bubalus*, placing them within *Homoioceras* (as *Homoioceras antiquus*), which was established for a specimen from Sudan (*Homoioceras singae*) (Bate, 1949). Although *H. antiquus* is still in use by some (Brink, 2005; Codron et al., 2008), the type specimen of *H. singae* appears to be a primitive form of extant African buffalo (*Syncerus caffer*) (Gentry, 1978; Gentry and Gentry, 1978), rendering *Homoioceras* unavailable as the genus for *antiquus*. Gentry and Gentry (1978) assigned *antiquus* to *Pelorovis*, as do many today (Klein, 1994; Klein et al., 2007; Tryon et al., 2010), although morphological and systematic evidence is leading to a growing consensus that *antiquus* should be placed within *Syncerus* (Gautier and Muzzolini, 1991; Geraads, 1992; Klein, 1994; Peters et al., 1994; Hadjouis, 2002; Martínez-Navarro et al., 2007; Gentry, 2010a). *Syncerus antiquus* had the broadest geographic distribution of any of the extinct species considered here, occurring in the late Pleistocene (107 to 13 ka) of southern Africa (Klein, 1980, 1983; Cruz-Uribe, 1983; Clark and Plug, 2008; Rector and Reed, 2010; Faith, 2012, 2013b), East Africa (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Tryon et al., 2010, 2012), Central Africa (Peters, 1990), and North Africa (Gautier and Muzzolini, 1991; Aouraghe, 2004; Monchot and Aouraghe, 2009; Steele, 2012). As indicated by fossil remains and rock art, the giant buffalo persisted into the middle Holocene (~6 ka) in North Africa (Gautier and Muzzolini, 1991). Isotopic and mesowear evidence indicate that *S. antiquus* was a grazer (Codron et al., 2008; Stynder, 2009), and its massive body size suggests that it consumed large quantities of low quality forage. The horns of larger individuals extended upwards of 3 m from tip to tip (versus up to 1.4 in *S. caffer*), limiting *S. antiquus* to open habitats (Klein, 1994).

3.1.13. Unnamed caprine

Brink (1999) reported an extinct caprine antelope from the late Pleistocene to early Holocene (66 to 7 ka) at several localities in mountainous regions of South Africa. Morphologically similar fossils were subsequently found in middle Pleistocene (830 to 578 ka) deposits at Gladysvale Cave (Lacruz et al., 2002). This extinct caprine's teeth are markedly hypsodont and its post-crania match those of other caprines adapted to rugged habitats. Due to the lack of a suitably complete type specimen, the taxon remains to be formally described. The species may belong within the extinct genus *Makapania* (Brink, 1999; Lacruz et al., 2002), which is typically thought to belong to the tribe ovibovini (muskoxen and allies) (Gentry, 1970, 2010a), although Brink's (1999) analysis suggests numerous caprine affinities. In the stratified sequence from Boomplaas Cave, its disappearance between 9100 ± 135 and 6400 ± 75 ¹⁴C yrs BP (9866 to 10,095 and 7171 to 7433 cal yrs BP) is associated with the replacement of grazing ungulates by browsers (Faith, 2012, 2013b).

3.1.14. *Camelus*

An extinct camel that perhaps belongs within *Camelus thomasi* is documented at a handful of North African late Pleistocene sites ranging in age from >24 ka to 130 ka (Gautier, 1966, 1993; Wendorf, 1977; Brun et al., 1988; Wengler et al., 2002). *Camelus thomasi* was described by Pomel (1893) from the early/middle Pleistocene at Tighenif in Algeria. Late Pleistocene *Camelus* is often assigned to the same taxon (Gautier, 1966, 1993; Wendorf, 1977), although Harris et al. (2010a) caution that these identifications are suspect as they were made without reference to the Tighenif material. Due to a rather sparse record, it is possible that late Pleistocene *Camelus* represents a different species or that multiple species are represented. The relationship of late Pleistocene *Camelus* to the domestic dromedary (*Camelus dromedarius*) is uncertain (Harris et al., 2010a). Late Pleistocene specimens are 20–30% larger than *C. dromedarius* (Gautier, 1966).

3.1.15. *Megaceroides algericus*

Lydekker (1890) founded *Cervus algericus* on the basis of a maxilla recovered from late Quaternary deposits at Hammam el Meskhoutine in Algeria. The taxonomic position of this and other megalocetine deer is contentious (Lister et al., 2005), and various authorities place *algericus* within *Megaloceros* (Hamilton, 1978; Gentry, 2010b) or *Megaceroides* (Joleaud, 1914; Hadjouis, 1990; Azzaroli and Mazza, 1993; Pfeiffer, 2002; Abbazzi, 2004; Geraads, 2010a). *Megaceroides* is used here, as the large sample of antlers from Les Phacochères in Algeria shows a number of features that distinguish it from Eurasian *Megaloceros*, including the lack of a posterior tine (Hadjouis, 1990). *Megaceroides algericus* is known from various late Quaternary sites across Algeria and Morocco (Arambourg, 1938; Saxon et al., 1974; Hadjouis, 1990; Merzoug and Sari, 2008). In the stratified archeological sequence from Tamar Hat in Algeria, its last appearance is dated to 17,040 ± 400 ¹⁴C yrs BP (19,411 to 21,306 cal yrs BP) (Saxon et al., 1974; Merzoug and Sari, 2008). Possible artistic renditions of the species raise the possibility that it may have persisted into the Holocene (Arkell, 1962; Saxon et al., 1974), although these have been questioned (Turvey, 2009). The brachydont teeth and shallow horizontal mandibular ramus of *M. algericus* suggest it was a browser (Abbazzi, 2004).

3.1.16. *Metridiochoerus*

An extinct giant warthog (*Metridiochoerus* sp.) is reported from the middle-to-late Pleistocene of southern Africa (Klein, 1980; Cruz-Uribe, 1983; Klein, 1984b). The *Metridiochoerus* lineage thrived earlier in the Pleistocene (van Hoepen and van Hoepen, 1932; Harris and White, 1979; Potts, 1998; Suwa et al., 2003; Geraads et al., 2004; Brink, 2005; Bishop, 2010), and Klein (1980, 1984b) suggests that it persists into the late Pleistocene at four southern African localities (Florisbad, Koffiefontein, Vlakkrak, and Redcliff Cave). However, the Florisbad specimens may belong to extant *Phacochoerus* (Brink, 1987) and are probably middle Pleistocene in age (279 to 121 ka) (Grün et al., 1996). Those from Koffiefontein and Vlakkrak were assigned to the late Pleistocene on the basis of their association with MSA artifacts, although the

oldest MSA is now dated to ~280 ka (Tryon and McBrearty, 2006; Morgan and Renne, 2008). This leaves the *Metridiochoerus* specimens from Redcliff Cave in Zimbabwe, which are associated with a radiocarbon date of 25,650 ± 1800 ¹⁴C yr BP (26,257 to 34,125 cal yrs BP), as the sole late Pleistocene record of the taxon (Klein, 1980; Cruz-Uribe, 1983). The teeth of the Redcliff specimens are extremely hypsodont (Klein, 1980) and isotopic data from earlier Pleistocene *Metridiochoerus* indicate that the giant warthog was a grazer with limited dependence on water (Harris and Cerling, 2002).

3.1.17. *Kolpochoerus*

The suid genus *Kolpochoerus* has a long history that extends into the earliest Pliocene (Brunet and White, 2001). The youngest previously documented records of *Kolpochoerus* (*Kolpochoerus majus*) were middle Pleistocene (~500 ka) in age (Geraads et al., 2004; McBrearty and Jablonski, 2005; Faith et al., 2012). Recent collections from the late Pleistocene (100 to 33 ka) Wasiriya Beds on Rusinga Island in Kenya (Tryon et al., 2010, 2012) recovered several dental specimens belonging to *Kolpochoerus*, the most complete of which is illustrated here in Fig. 2. The level of compression of the pillars and cementum most closely matches *K. majus*, although a secure identification will require the recovery of more complete specimens. The Rusinga Island *Kolpochoerus* is associated with other ungulates interpreted as reflecting a dry grassland environment (Tryon et al., 2010; Faith et al., 2011; Tryon et al., 2012). Early Pleistocene *Kolpochoerus* from Lake Turkana was a grazer, but more dependent on water than *Metridiochoerus* (Harris and Cerling, 2002).

3.2. Order Perissodactyla

3.2.1. *Equus algericus*

Bagtache et al. (1984) described a caballine horse (*Equus algericus*) from late Quaternary deposits of Les Phacochères (AKA Allobroges) in Algeria. *Equus algericus* has since been reported from the Neolithic and Aterian deposits at El Harhoura 1 in Morocco (Aouraghe and Debénath, 1999; Aouraghe, 2004; Monchot and Aouraghe, 2009). Its occurrences at this site range in age from the middle Holocene (5400 ± 290 ¹⁴C yrs BP = 6683 to 6805 cal yrs BP) to >66.5 ± 5.2 ka (Raynal and Occhietti, 2012). Little is known about its paleoecology, although like most large species of *Equus* it was probably a bulk grazer that preferred open habitats.

3.2.2. *Equus capensis*

The Cape zebra (*Equus capensis*) is the largest equid known from the African Quaternary, standing 150 cm tall at the withers and with a body mass exceeding 400 kg (Eisenmann, 2000, 2003). *Equus capensis* was founded by Broom (1909b) on the basis of a right mandible recovered from near Cape Town in South Africa. More than a dozen large equids were later described from South African Pleistocene sites in the early 1900s, all of which are now synonymized within *E. capensis* (Churcher and Richardson, 1978). *Equus capensis* is documented at many late

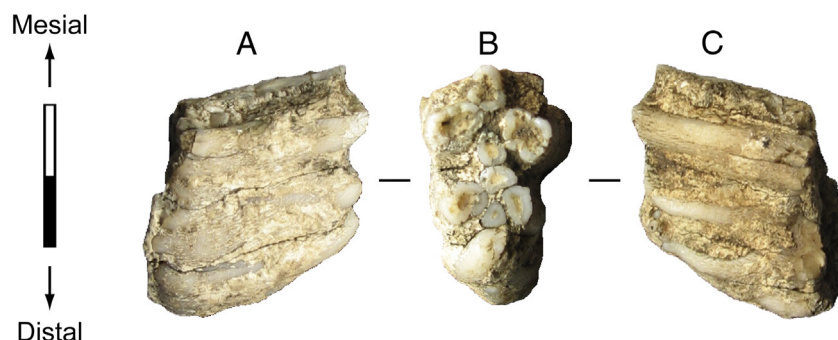


Fig. 2. Distal fragment of *Kolpochoerus* right mandibular M₃ from Rusinga Island (KMN-RU 49738) in (A) lingual, (B) occlusal, and (C) labial views.

Pleistocene sites (90 to 11 ka) across southern Africa, where it disappeared near the Pleistocene–Holocene transition (Klein, 1977; Thackeray, 1979; Klein, 1980; Thackeray et al., 1981; Schweitzer and Wilson, 1982; Cruz-Urbe, 1983; Klein, 1983; Klein and Cruz-Urbe, 1987; Klein et al., 1991; Plug and Engela, 1992; Klein and Cruz-Urbe, 2000; Robbins et al., 2000; Badenhorst and Plug, 2012; Faith, 2012, 2013b). Churcher (Churcher et al., 1999; Churcher, 2006) reports several *E. capensis* specimens spanning the middle Pleistocene and Holocene of Egypt. However, their taxonomic status is equivocal. Believing *E. capensis* to be the direct ancestor of *E. grevyi* (Churcher and Richardson, 1978; Churcher, 2006), Churcher treats the distinction between the two species loosely, using *E. capensis* for fossil remains and *E. grevyi* for modern animals. Ancient DNA evidence now shows that *E. capensis* is more closely related to extant plains zebra (*Equus quagga* – formerly *Equus burchelli*) than to *E. grevyi* (Orlando et al., 2009). Thus, the Egyptian specimens may belong to extant Grevy's zebra or to an extinct North African taxon, perhaps *Equus mauritanicus*. Isotopic data show that *E. capensis* was a grazer (Lee-Thorp and Beaumont, 1995; Codron et al., 2008) and Klein (1980) observes that it is more numerous in fossil localities from what are today more arid regions of southern Africa.

3.2.3. *Equus mauritanicus*

The extinct zebra *Equus mauritanicus* is a poorly defined North African taxon created by Pomel (1897) from late Quaternary material in Algeria. Churcher and Richardson (1978) regarded it as a subspecies of the extant plains zebra (*E. quagga* – formerly *E. burchelli*). However, Eisenmann (1980) and Eisenmann and Baylac (2000) examined several skulls of *E. mauritanicus* and found them to be morphologically distinct from plains zebra, whereas its massive teeth overlap in size with southern African *E. capensis* (Eisenmann, 2003). Bernor et al. (2010) agree that *E. mauritanicus* is not *E. quagga*, but they caution that the taxon needs a more clear definition and further study. Although its taxonomic status is uncertain, there are no extant African zebras that it could reasonably belong to and *E. mauritanicus* is used here for the extinct taxon that is routinely reported from late Pleistocene to Holocene (115 to 6 ka) localities in North Africa (Higgs, 1967; Brun et al., 1988; Michel, 1992; Aouraghe and Debénath, 1999; Monchot and Aouraghe, 2009; Dibble et al., 2012; Steele, 2012).

3.2.4. *Equus melkiensis*

Bagtache et al. (1984) described an extinct equid (*Equus melkiensis*) probably related to the wild ass (*Equus africanus*) from Les Phacochères in Algeria, also the type site of *E. algericus*. Eisenmann (2006) reports *E. melkiensis* from several presumably late Pleistocene sites in Algeria and Morocco, although the record from Mugharet el 'Aliya is the only one that can be securely assigned to the late Pleistocene (85 to 37 ka) (Wrinn and Rink, 2003). Like many of the extinct North African taxa, there is little known about its paleoecology. Extant wild asses inhabit arid environments and are able to subsist on very poor quality forage (Bauer et al., 1994).

3.2.5. *Stephanorhinus*

The extinct rhinoceros *Stephanorhinus* is a Eurasian taxon that migrated into North Africa near the end of the middle Pleistocene (Amani and Geraads, 1993; Geraads, 2012). The phylogeny and systematics of Pleistocene African rhinoceroses are problematic and have not kept pace with work in Eurasia (Fortelius et al., 1993; Heissig, 1999; Billia, 2008; Geraads, 2010b). As a result, *Dicerorhinus* is sometimes used for *Stephanorhinus*, although the former now has a more restricted definition (Fortelius et al., 1993). At least one, but perhaps two species of *Stephanorhinus* disappeared from North Africa during the late Pleistocene. The narrow-nosed rhinoceros (*Stephanorhinus hemitoechus*) is reported from a handful of late Pleistocene (109 to 53 ka) localities in North Africa (Nespoulet et al., 2008; Raynal et al., 2008; Michel et al., 2009; Jacobs et al., 2012). *Stephanorhinus kirchbergensis* is also reported

from the late Pleistocene (>40 to 19 ka) at the Huah Fteah in Libya (Klein and Scott, 1986). The two species have often been confused in the past (Billia, 2008) and Geraads (2010b) suggests that only *S. hemitoechus* is present in the North African late Pleistocene.

3.3. Order Proboscidea

3.3.1. *Elephas iolensis*

The terminal representative of one of the more long-lived and widespread African elephant lineages, *Elephas iolensis* was founded by Pomel (1895) on the basis of a lower molar from Beausejour Farm in Algeria. The species is known from middle/late Pleistocene sites across Africa (Maglio, 1973; Coppens et al., 1978; Abbate et al., 2010; Sanders et al., 2010). A specimen of *E. iolensis* from Natodameri in South Sudan has been directly dated by U–Th to 35 ka and provides the latest record of the taxon (Coppens et al., 1978). The molars of *E. iolensis* are more hypsodont than any other African elephant (Maglio, 1973; Coppens et al., 1978), suggesting a specialized grazing adaptation.

3.4. Order Tubulidentata

3.4.1. *Orycteropus crassidens*

MacInness (1956) described a large extinct aardvark (*Orycteropus crassidens*) from the late Pleistocene Wasiriya Beds (100 to 33 ka) on Rusinga Island in Kenya (Tryon et al., 2012). The taxon is also known from the early-to-middle Pleistocene at nearby Kanjera (Behrensmeyer et al., 1995; Lehman, 2009). Pickford (1975) regarded *O. crassidens* as a subspecies of extant *Orycteropus afer*, although Lehman (2009) summarizes morphological and phylogenetic evidence supporting the validity of the species.

3.5. Problematic species

There are a handful of taxa absent from Table 1 that are often cited as having become extinct during the late Pleistocene or Holocene (Martin, 1984; MacPhee and Flemming, 1999; Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006; Turvey, 2009), but whose taxonomic status or last appearances require revision.

3.5.1. *Hipparion lybicum*

A three-toed (hipparionine) horse referred to as *Hipparion lybicum* often appears on lists of extinct late Pleistocene taxa (Barnosky et al., 2004; Lyons et al., 2004; Koch and Barnosky, 2006). This can be traced to Churcher and Richardson (1978), who synonymized over a dozen taxa from across Africa into *H. lybicum* and suggested that it persisted into the late Pleistocene at a number of sites. *Hipparion lybicum* is no longer recognized as a valid taxon (Bernor et al., 2010) and none of the supposed late Pleistocene occurrences can be confidently placed in this time frame. Current evidence indicates that hipparionine horses disappeared from Africa early in the middle Pleistocene (~500 ka) (Geraads et al., 2004; Bernor et al., 2010; Geraads, 2010a). All Pliocene and Pleistocene three-toed horses from Africa are now assigned to the genus *Eurygnathohippus* (Bernor et al., 2010).

3.5.2. *Giraffa gracilis*

Arambourg (1947) described a lightly built species of giraffe (*Giraffa gracilis*) from the Shungura Formation in Ethiopia, although the taxon is now regarded as a junior synonym of *Giraffa stillei* (Harris et al., 2010b). Churcher (1978) describes the age range of this taxon as late Pliocene to late Pleistocene. However, Churcher does not mention any specific late Pleistocene occurrences and none of his tables or figures provide age ranges indicating the presence of *G. gracilis* or *G. stillei* beyond the middle Pleistocene. In the decades since then, there are still no records of an extinct late Pleistocene giraffe (Harris et al., 2010b).

3.5.3. *Parmularius*

Parmularius is an extinct genus of alcelaphine antelope most closely related to *Damaliscus*, which includes extant blesbok (*Damaliscus dorcas*) and topi (*Damaliscus lunatus*). Its misplaced status as an extinct late Pleistocene taxon can be traced to Maglio's (1978) list of Cenozoic African mammals, which indicates an age range for *Parmularius* from the early to the late Pleistocene. This conflicts with Gentry's (1978) assessment of *Parmularius* in the same volume and with current evidence indicating the extinction of the genus near the early-to-middle Pleistocene boundary (Vrba, 1997; Geraads et al., 2004; Gentry, 2010a).

3.5.4. *Equus quagga*

The extinct quagga (*Equus quagga quagga*), noted for the lack of stripes on its rear half, was historically widespread on the South African plains south of the Orange River. It disappeared in the wild in the second half of the 19th century and the last individual died in the Amsterdam Zoo in 1883. From the 1980s until recently there was substantial debate over its taxonomic status and relationship to the more widespread plains zebra (formerly *E. burchelli*) (Bennett, 1980; Thackeray, 1988; Klein and Cruz-Urbe, 1995; Thackeray, 1997; Klein and Cruz-Urbe, 1999; Eisenmann and Brink, 2000; Groves and Bell, 2004). Genetic evidence has resolved this debate by showing that quagga and plains zebra belong to the same species (Leonard et al., 2005), a position also adopted by the IUCN (Hack and Lorenzen, 2008) and paleontological authorities (Bernor et al., 2010). The correct name for extant plains zebra is now *E. quagga*, which has priority over *E. burchelli*.

3.5.5. *Gazella rufina* (= *Eudorcas rufina*)

The red gazelle (*Eudorcas rufina*) was thought to have disappeared from Algeria near the end of the 19th century. The only known specimens ($n = 3$) were purchased from markets in northern Algeria and the taxon has never been documented in the wild. One of these specimens has since been identified as belonging to extant red-fronted gazelle (*Eudorcas rufifrons*), prompting the IUCN to change its conservation status from extinct to data deficient in 2008 (IUCN SSC Antelope Specialist Group, 2008a).

4. Chronology and explanations

At the continental scale, the last appearance dates (LADs) of the extinct African taxa range in age from >63 ka (*D. niro*) to the middle Holocene (6 ka) (*B. primigenius*, *S. antiquus*, *E. mauritanicus*, *E. melkiensis*). There is good reason to believe that this chronology is structured to a large extent by sampling. Fig. 3 plots the number of dated sites against the youngest associated radiometric age for each extinct taxon, excluding blue antelope (data from Table 2). There is a

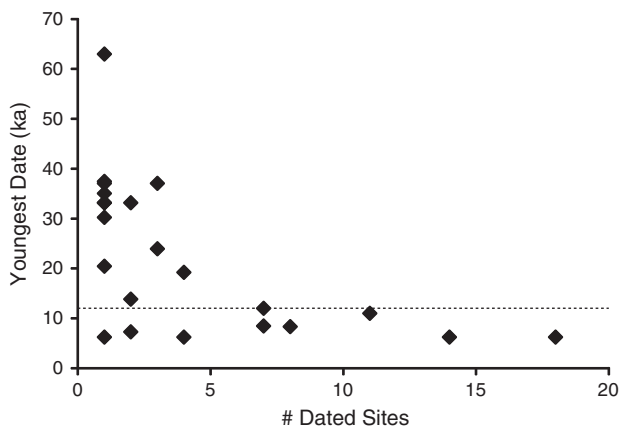


Fig. 3. The number of dated sites against the youngest associated radiometric date for each extinct taxon, excluding blue antelope (data from Table 2). Dashed line corresponds to the Pleistocene-Holocene transition.

significant negative relationship between the number of dated sites in which a taxon occurs and its youngest radiometric date (Spearman's rho: -0.670 , $p < 0.001$). All of the taxa ($n = 6$) that have been documented in 7 or more dated sites are associated with fairly recent LADs (~13 to 6 ka), whereas those ($n = 17$) that occur in fewer dated sites, either because they are rare in the fossil record or because their occurrences are undated, are characterized by a broader range of LADs (63 to 6 ka). As has been argued in the context of North American extinctions (Faith and Surovell, 2009), this suggests that additional sampling of the fossil record, or dating of samples that have not been dated, will lead to the establishment of substantially younger LADs for some taxa. Although the better-sampled taxa suggest that the extinctions may have been restricted to the terminal Pleistocene and early Holocene, the regional perspective indicates that losses occurred at different times in different places.

4.1. Southern Africa

An abundance of stratified late Quaternary archeological and paleontological sites across southern Africa provides the best regional chronology of large mammal extinctions on continental Africa (Table 2). In agreement with previous characterizations (Klein, 1980, 1984b), the last appearances of *E. capensis*, *S. antiquus*, and likely *A. australis* broadly correspond with the Pleistocene-Holocene transition. However, there is now good evidence from stratified and well-dated cave deposits that *M. priscus*, *A. bondi*, and the extinct caprine antelope persisted for several thousand years into the Holocene (Thackeray et al., 1981; Thackeray, 1983; Brown and Verhagen, 1985; Plug and Engela, 1992; Brink, 1999; Faith, 2012). The last appearances of *Metridiochoerus* and *D. niro* occur prior to the Last Glacial Maximum, although both are so rare in the late Pleistocene record (1 locality each) that they may have persisted for much longer without being detected (Faith and Surovell, 2009).

The extinct southern African species share a number of ecological characterizations. All show paleoecological associations or morphological adaptations indicating a preference for open grasslands. Many are characterized by extreme hypsodonty and, with the possible exception of *A. australis*, all were likely grazers. *Equus capensis*, *S. antiquus*, and

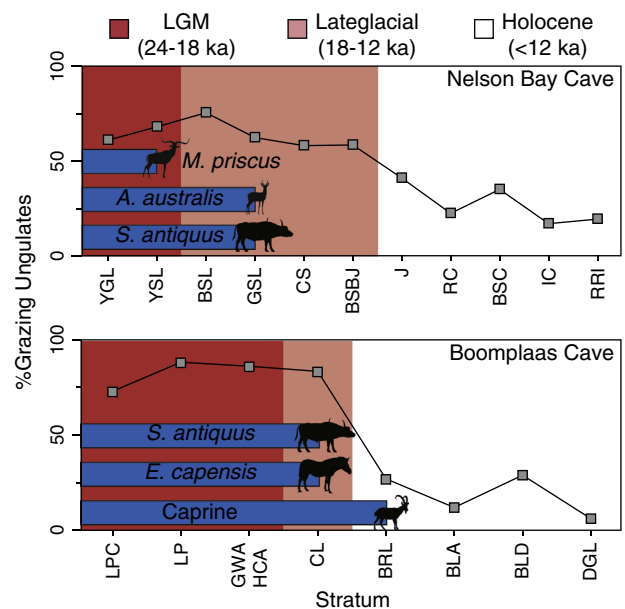


Fig. 4. Last appearances of extinct ungulates at Nelson Bay Cave (data from Klein, 1983) and Boomplaas Cave (data from Klein, 1983; Faith, 2012, 2013b) relative to the abundance of grazing ungulates across stratigraphic units. Shaded area indicates stratigraphic units dating to the Last Glacial Maximum (LGM: 24–18 ka) and Lateglacial (18–12 ka). The stratigraphy and chronology of both sites follow Deacon (1984), with radiocarbon age estimates calibrated using the INTCAL09 calibration curve (Reimer et al., 2009).

Metridiochoerus were among the largest of their respective lineages, suggesting a requirement for greater quantities of grassy forage and more expansive home ranges. In light of these similarities, the extinctions have been attributed primarily to a decline in the availability or productivity of grassland habitats since the end of the Last Glacial Maximum (Klein, 1980, 1984b; Brink, 1987, 1999; Brink and Lee-Thorp, 1992; Faith, 2011c, 2012). Evidence for this is derived primarily from large mammal faunal assemblages, which indicate progressive declines in grazer abundances and diversity over the last 18,000 yrs. This is illustrated here in Fig. 4, which shows how ungulate extinctions at Nelson Bay Cave (Klein, 1983) and Boomplaas Cave (Faith, 2012, 2013b) correspond to a long-term decline of grassland ungulates. Potential mechanisms behind this decline could include vegetation change due to altered rainfall regimes, increased seasonality, or elevated atmospheric CO₂ concentrations (Brink, 1987; Brink and Lee-Thorp, 1992; Brink, 2005; Faith, 2011c, 2013a, 2013b; see also Faith, 2011a).

Klein (1980, 1984b) argued that environmental change alone is an inadequate explanation for the extinctions. Noting that the extinct taxa endured glacial–interglacial transitions since at least the beginning of the middle Pleistocene, he suggests that the late Pleistocene and Holocene losses occurred because of intensified predation by human hunters armed with LSA technology. Their survival during previous episodes of pronounced climate change is attributed to the presumably ineffective technology and limited hunting ability of MSA humans. However, a growing body of evidence indicates that this behavioral contrast is probably inaccurate and there is no evidence for intensified LSA predation pressure on large mammals (Marean and Assefa, 1999; McBrearty and Brooks, 2000; Faith, 2008; Dusseldorp, 2010; Wadley, 2010; Faith, 2011b). More importantly, Klein's argument overlooks the substantial extinctions that did occur prior to the late Pleistocene.

The southern African fossil record documents the extinction of at least 22 large mammals from ~1.0 million yrs ago to the end of the middle Pleistocene, including the dirk-toothed cat *Megantereon whitei*, the giant baboon *Theropithecus oswaldi*, the hippopotamid *Hippopotamus gorgops*, the suids *Kolpochoerus* and three species of *Metridiochoerus*, two species of three-toed horse *Eurygnathohippus*, an unnamed wild ass, an elephant (*Loxodonta atlantica*), a sivather (Sivatherium *maurusium*), and at least ten bovids, including *Aepyceros helmoedi*, *A. recki*, *Damaliscus* aff. *lunatus*, ?*Damaliscus* sp. nov., *Gazella* sp., *Hippotragus gigas*, *Megalotragus eucornutus*, ?*Parmularius* sp. nov., *Rabaticeras arambourgi*, and the enigmatic “spiral horn” antelope (Cooke, 1974; Brink, 1987, 1994, 2005; Klein et al., 2007; Bishop, 2010; Brink et al., 2012). Some of these taxa may have evolved into other forms (e.g. *L. atlantica*, *A. recki*, *M. eucornutus*, *R. arambourgi*), but most disappeared without leaving any surviving representatives. Like the species that disappeared during the late Pleistocene and Holocene, many of these taxa are known or thought to have been open habitat grazers (Codron et al., 2008; Stynder, 2009). With this long term history in mind, there is little reason to argue that extinctions during the late Pleistocene and Holocene were the unique result of LSA human impacts. Rather, they represent part of a long-term extinction pattern, perhaps the result of elevated climate variability (e.g., Potts, 1998; Faith et al., 2012) or increased niche specialization (Codron et al., 2008).

4.2. East Africa

The East African LQE are only beginning to come to light, with the relevant taxonomic and chronological data still being established (Marean and Gifford-Gonzalez, 1991; Faith et al., 2011, 2012; Tryon et al., 2012; Faith et al., in press). Emerging evidence indicates some parallels with southern Africa. In the stratified archeological sequence from Lukenya Hill in south-central Kenya, *D. hypsodon* and *S. antiquus* disappear between the end of the Last Glacial Maximum and the onset of the Holocene (Marean and Gifford-Gonzalez, 1991; Marean, 1992). Other extinct East African taxa include *Megalotragus* sp., *R. atopocranion*, the

unnamed impala (*Aepyceros* sp.), *Kolpochoerus* sp., and *Orycteropus crassidens*, but they are known only from open air deposits broadly dated to the late Pleistocene (33 to 100 ka) (Faith et al., 2011; Tryon et al., 2012; Faith et al., in press). The extinct ungulates were all associated with faunal communities indicative of arid grassland habitats and, with the exception of the extinct impala, all were likely grazers (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Garret et al., 2010; Tryon et al., 2010; Faith et al., 2011; Tryon et al., 2012; Faith et al., 2013). The disappearance of *D. hypsodon* and *S. antiquus* is attributed to a loss of arid grasslands at the onset of the Holocene together with increased competition from mesic-adapted grazers (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Faith et al., 2011, 2012, 2013), likely the result of a marked increase in precipitation (Bonnefille et al., 1990; Bonnefille and Chalieu, 2000; Kiage and Liu, 2006; Wolff et al., 2011).

Evidence from Kenya indicates that although the magnitude of extinctions over the last ~100,000 yrs is not particularly large in terms of the number of taxa lost, the extinctions radically reconfigured the large mammal community by eliminating the dominant taxa (Faith et al., 2012). *Damaliscus hypsodon* is the most abundant large mammal recovered from the late Pleistocene deposits at Lukenya Hill (Marean, 1992). In the Lake Victoria Basin, the dominant species include *R. atopocranion* followed by *D. hypsodon* (Faith et al., 2011; Tryon et al., 2012). At both localities, extinct species account for more than 50% of the large mammals (>5 kg). This represents an important departure from the southern African record, where extinct taxa typically represent a smaller component of late Pleistocene faunas.

4.3. North Africa

North Africa documents the largest number of extinct taxa (Table 2), although its losses have received the least attention. The extinctions chronology is weak, as many of the relevant paleontological and archeological sites were excavated between 1850 and 1950 with little stratigraphic control. Even the more recently excavated late Pleistocene sites lack absolute dates and precise chronologies, leaving the late Pleistocene record poorly resolved (Geraads, 2012). It is clear that the North African extinctions extended into the Holocene, as evidenced by the late survival of *B. primigenius*, *S. antiquus*, *E. mauritanicus*, and *E. melkiensis* (Table 2). The middle Holocene extinction of *S. antiquus* corresponds with an abrupt climatic shift toward extreme aridity (Lézine, 1989; Lézine et al., 1990; DeMenocal et al., 2000; Foley et al., 2003). Its extinction during this arid phase may be related to competition with pastoralists and livestock for increasingly scarce water (Gautier and Muzzolini, 1991), a factor linked to the decline of water-dependent African ungulates that inhabit arid to semi-arid habitats today (Moehlman et al., 1998; Williams, 2002; Moehlman et al., 2008a, 2008b; Faith et al., 2013).

The disappearance of two species of *Gazella*, three species of *Equus*, and other large-bodied hypsodont species (*E. iolensis*, *Camelus*, *B. primigenius*, *S. antiquus*) in North Africa indicates that grazers or open habitat species were predominately affected. These ecological parallels imply that environmental mechanisms likely played a role. However, pending the establishment of a refined extinction chronology and terrestrial paleoenvironmental records, the North African extinctions will remain poorly understood. With the recent surge of paleoanthropological interest in the region (Hublin and McPherron, 2012), substantial progress can be expected in the near future.

5. Extinctions in ecological and evolutionary context

Ecomorphological evidence, paleoenvironmental associations, or taxonomic analogy indicate that many of the extinct taxa preferred open grassland habitats (20 of 24; Table 3). This is particularly clear within the bovids and equids (Table 1). The bovid tribes Antilopini and Alcelaphini, both of which include species with hypsodont teeth and cursorial postcranial adaptations, are considered the archetypal

Table 3

Inferred dietary habits of extinct species. Those in bold likely preferred grassland habitats, as indicated by ecomorphological adaptations, paleoenvironmental associations, or taxonomic analogy (see Section 3).

| Taxon | Diet |
|--------------------------------|--------------|
| <i>Aepyceros</i> sp. | Mixed feeder |
| <i>Antidorcas australis</i> | Mixed feeder |
| <i>Antidorcas bondi</i> | Grazer |
| <i>Bos primigenius</i> | Grazer |
| <i>Damaliscus hypsodon</i> | Grazer |
| <i>Damaliscus niro</i> | Grazer |
| <i>Gazella atlantica</i> | Mixed feeder |
| <i>Gazella tingitana</i> | Mixed feeder |
| <i>Hippotragus leucophaeus</i> | Grazer |
| <i>Megalotragus priscus</i> | Grazer |
| <i>Rusingoryx atopocranion</i> | Grazer |
| <i>Syncerus antiquus</i> | Grazer |
| Unnamed caprine antelope | Grazer |
| <i>Camelus</i> sp. | Brower |
| <i>Megaceroides algericus</i> | Brower |
| <i>Metridiochoerus</i> sp. | Grazer |
| <i>Kolpochoerus</i> sp. | Grazer |
| <i>Equus algericus</i> | Grazer |
| <i>Equus capensis</i> | Grazer |
| <i>Equus mauritanicus</i> | Grazer |
| <i>Equus melkiensis</i> | Grazer |
| <i>Stephanorhinus</i> | ? |
| <i>Elephas iolensis</i> | Grazer |
| <i>Orycteropus crassidens</i> | Insectivore |

open grassland lineages (Vrba, 1980; Greenacre and Vrba, 1984; Bobe and Behrensmeyer, 2004; Bobe, 2006). Species belonging to these tribes account for 22 of 82 (27%) extant African bovids recognized by the IUCN (2012), yet they account for the majority (8 of 13 = 62%) of the extinct bovids (Fisher's exact test: $p = 0.022$). The four extant species of *Equus* (*E. quagga*, *E. zebra*, *E. grevyi*, and *E. africanus*) are bulk grazers that also prefer open habitats, spanning a continuum from extremely arid scrublands (*E. africanus*) to more mesic grasslands (*E. quagga*). The late Pleistocene and Holocene extinctions halved the number of African equids (Table 1). With this long-term pattern in mind, it is perhaps not surprising that the conservation outlook for two of the extant species is grim, with *E. grevyi* and *E. africanus* classified as endangered and critically endangered, respectively (Moehlman et al., 2008a, 2008b).

Diet is also a significant correlate of extinction. Table 3 reports the inferred diets of the extinct African large mammals. These are based on a combination of stable carbon isotopes, dental mesowear analysis, ecomorphology, or analogy with extant relatives (references provided in species descriptions). Focusing on the ungulates, which include all extinct taxa but *O. crassidens*, it is evident that grazers are substantially over-represented. Reed (1998) summarized the dietary habits of 67

extant African ungulates, illustrated here in Fig. 5. Species identified as fresh-grass grazers or fruit/leaf eaters are included in the grazer or browser category, respectively, as these finer dietary classes cannot be readily identified in fossil taxa. A chi-square test shows the distribution of dietary classes among extinct taxa (Fig. 5) to differ significantly from extant ungulates ($\chi^2 = 11.994$, $p = 0.007$). Adjusted residuals, which are to be read as standard normal deviates, show that this is driven by the dominance of grazers ($AR = 3.28$, $p = 0.001$) and rarity of browsers ($AR = -2.81$, $p = 0.005$) among extinct species. As reviewed below, there is reason to believe that the preferential loss of grazers and open habitat taxa is rooted in long-term environmental and evolutionary processes.

Paleoenvironmental evidence documents an expansion of open and arid-to-semi-arid C_4 grasslands throughout Africa since the late Miocene (Cerling and Hay, 1988; Cerling, 1992; Cerling et al., 1997; Bobe and Behrensmeyer, 2004; DeMenocal, 2004; Bobe, 2006; Levin et al., 2011). Among large herbivores, this is associated with the diversification of grassland lineages (e.g., the bovid tribes Alcelaphini and Antilopini) and morphological adaptations to grazing in open habitats, including an increase in hypsodonty, enlarged body size, and the development of cursoriality (reviewed in Potts and Behrensmeyer, 1992; Bobe, 2006). Fossil evidence from East Africa and southern Africa documents a reversal of this trend over the last million years, however, with the loss of many large-bodied or hypsodont forms (Potts, 1998; Brink, 2005; Codron et al., 2008; Faith et al., 2012). For example, ~15 species of Alcelaphine bovid disappeared in the last million years (Vrba, 1997; Gentry, 2010a; and Table 1), leaving only 6 survivors (*A. buselaphus*, *Beatragus hunteri*, *D. dorcas*, *D. lunatus*, *Connochaetes gnou*, *C. taurinus*). Consistent with the long-term trend, many of the extinct grazers reviewed here are exceptionally hypsodont (*Aepyceros* sp., *D. hypsodon*, *R. atopocranion*, *A. bondi*, *E. capensis*, *Metridiochoerus*, *E. iolensis*) or among the largest of their respective lineages (*M. priscus*, *S. antiquus*, *Metridiochoerus*, *E. capensis*, *Camelus*).

The disappearance of large-bodied hypsodont grazers over the last million years corresponds with the establishment of high-amplitude 100 kyr glacial cycles and increased climate variability (Potts, 1998; DeMenocal, 2004). Terrestrial records spanning the Pleistocene–Holocene transition indicate that extinctions are associated with substantial changes in the structure, distribution, or productivity of grassland habitats (Klein, 1980; Avery, 1982; Klein, 1983; Marean and Gifford-Gonzalez, 1991; Marean, 1992; Faith, 2011c, 2012) and the same was likely true of previous glacial–interglacial transitions. In light of this evidence, it is probable that the extinctions within the hyper-diverse grazing niche were the result of high-amplitude late Quaternary glacial–interglacial cycles that altered the structure of grassland habitats and eliminated the feeding niches of more specialized taxa during interglacials. The result of this process can be described as selective taxonomic winnowing, characterized by the gradual loss of specialists and the establishment of a large mammal community composed of more versatile species capable of persisting across a broader range of environmental conditions (see also Potts, 1998; Faith et al., 2012).

6. Conclusion

The most recent comprehensive examination of LQE on continental Africa identified 11 species and 6 genera that disappeared during the late Pleistocene and Holocene (Klein, 1984b). In the last few decades this figure has expanded to include at least 24 species and 9–10 extinct genera (Table 1), revealing a much greater taxonomic breadth than previously considered (Klein, 1984b; Barnosky et al., 2004; Koch and Barnosky, 2006). This represents the loss of 14% of Africa's large mammals (>5 kg) and 25% of its megafauna (>44 kg) (data from Smith et al., 2003; *Antidorcas* excluded from megafauna). In East Africa alone, the number of securely dated extinct late Pleistocene mammals has risen from two to seven in only the last several years (Tryon et al., 2010; Faith et al., 2011, 2012; Tryon et al., 2012; Faith et al., in press).

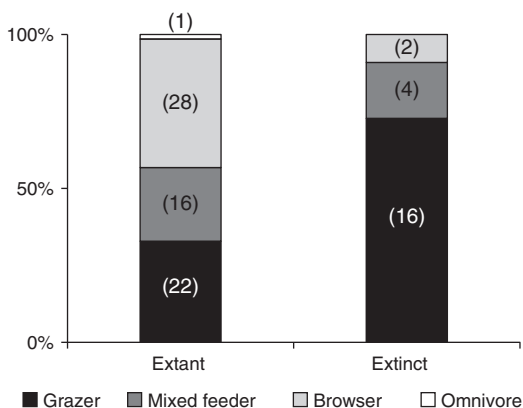


Fig. 5. Dietary habits of extant (from Reed, 1998) and extinct African ungulates. Number of species indicated in parentheses.

These recent increases, together with the geographic bias in sampling (Fig. 1), suggest that much more remains to be understood.

It is now clear that the magnitude of large mammal extinctions on continental Africa over the last ~100,000 yrs is substantial. In terms of the number of extinct taxa that are securely dated to this time frame, the African extinctions exceed those in Europe and Asia (Grayson, 2007; Louys et al., 2007), match those from Australia (Wroe and Field, 2006; Field et al., 2008; Faith and O'Connell, 2011; Wroe et al., 2013), and are surpassed only by the losses in the Americas (Grayson, 1991, 2007; Cione et al., 2009; Faith and Surovell, 2009). Nevertheless, Africa remains the “fortunate anomaly” (Koch and Barnosky, 2006:221) in the sense that the majority of its large mammals survived the extinctions, in contrast to the situation in the Americas or Australia.

The African extinctions can be broadly characterized as involving the loss of species that are grazers or prefer open habitats. Where good extinction chronologies and paleoenvironmental records are available, these losses are readily accounted for by environmental change. In the broader temporal context, these losses represent the more recent examples of a long-term environmentally-driven extinction process over the last million years. Taken together, there is little reason to believe that humans played a major role in African extinctions.

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