Late Pleistocene of Africa

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Late Pleistocene of Africa

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Introduction

The Late Pleistocene vertebrate record of Africa plays a key role in our understanding of human evolution and the development of modern biotic environments. Africa's large landmass and location on the equator helped support prolific radiations of large terrestrial mammals, and this past mammalian diversity has survived to modern times to a greater extent here than on other continents. Furthermore, Africa is truly the cradle of humanity, with many significant steps in human evolution occurring here, including the origins of physically and behaviorally modern humans during the Late Pleistocene (*see* Global Expansion 300,000-8000 years ago, Africa). This article explores the Late Pleistocene vertebrate record of Africa, spanning 126–11.5 ka, paying particular attention to large terrestrial mammals, but also considering smaller vertebrates. Because of the significance of humans in the Late Pleistocene of Africa, much of what we know about the other vertebrates from this time comes from archeological assemblages (*see* Interactions with Hominids; Overview; Global Expansion 300,000-8000 years ago, Africa). **Figure 1** provides the geographic location for each fossil sample discussed below, and **Table 1** provides the relevant references. **Table 2** provides the scientific names for all the species whose common names are used below.

Modern Physical and Environmental Setting

Africa's large landmass, over 30 million km^2 or one-fifth of the land surface of Earth, and its position straddling the equator means that it contains a

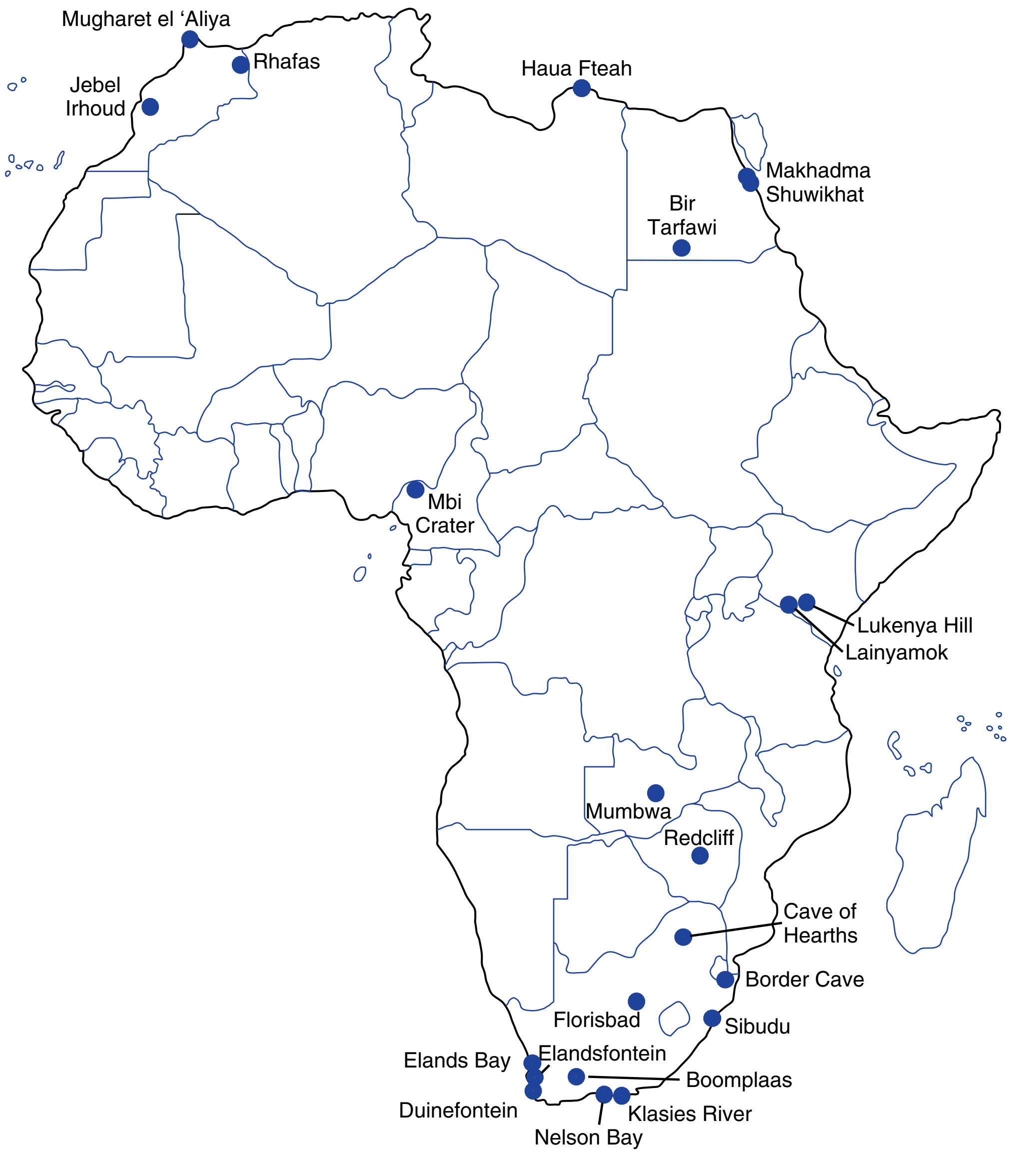

Figure 1 Map of the sites discussed in the text. **Table 1** provides references.

diversity of habitats, which support highly diverse vertebrate communities. The continent is characterized by moderately elevated tablelands. In general, the east and south are higher, and elevation decreases moving north and west. The Atlas Mountains in the far northwest are an exception. This physical geography greatly influences the distribution of moisture, and therefore influences plant communities and ultimately the faunal communities. In general, Africa is a warm and dry continent, and patterns of rainfall largely determine vegetation patterns because of the plants' dependence on water availability (**Fig. 2**). Annual rainfall is distributed broadly in a western pointing horseshoe-shaped pattern centered on the equator, although rainfall diminishes in the eastern highlands. For the most part, rain falls during the summer. The Cape and Mediterranean littorals are exceptions, with dry summers and wet winters creating unique ecosystems. The dominating desert, the large, extremely dry Sahara, lays to the north of this horseshoe, but deserts are also found on the African Horn and the southwestern coast. Savanna and open woodland cover about 40 percent of the continent, mainly south of the Sahara (Turner and Antón 2004). Heavy rains in the tropical highlands create extensive river systems that bring life-giving water to otherwise dry areas. In Africa, the availability of surface drinking water is the single most limiting climatic influence for the majority of mammals (Kingdon 1997: 449).

Africa's physical geography and climate have not always been this way. Major changes caused by movements of continents and the resulting rise of

Table 1 List of sites discussed in the text and references for additional information about each site

Site	*Country*	*References*
Bir Tarfawi	Egypt	Gautier (1993)
Boomplaas	South Africa	Klein (1978a)
Border Cave	South Africa	Klein (1977); Avery (1992)
Cave of Hearths	South Africa	Cooke (1963); Latham and Herries (2004)
Duinefontein 2	South Africa	Klein *et al.* (1999); Feathers (2002); Cruz-Uribe *et al.* (2003)
Elands Bay	South Africa	Klein and Cruz-Uribe (1987)
Elandsfontein Main	South Africa	Klein and Cruz-Uribe (1991); Klein *et al.* (in preparation)
Florisbad	South Africa	Cooke (1963); Grün *et al.* (1996)
Haua Fteah	Libya	Klein and Scott (1986)
Jebel Irhoud	Morocco	Thomas (1981); Grün and Stringer (1991); Amani and Geraads (1993); Amani and Geraads (1998)
Klasies River	South Africa	Klein (1976); Avery (1987)
Lainyamok	Kenya	Potts and Deino (1995)
Lukenya Hill	Kenya	Marean and Gifford-Gonzalez (1991); Marean (1992)
Makhadma 2 and 4	Egypt	Vermeersch (edr.) (2000)
Mbi Crater	Cameroon	Cornelissen (2002)
Mugharet el ‘Aliya	Morocco	Wrinn (in preparation) Wrinn and Rink (2003)
Nelson Bay Cave	South Africa	Klein (1972)
Mumbwa Cave	Zambia	Klein and Cruz-Uribe (2000)
Redcliff Cave	Zimbabwe	Klein (1978b); Cruz-Uribe (1983)
Rhafas Cave	Morocco	Michel (1992)
Shuwikhat 1	Egypt	Vermeersch (ed.) (2000)
Sibudu Cave	South Africa	Plug (2004)

mountains, rifting, and volcanoes have created profound variations in the deep past. However, glacial cycles and the related changes in sea levels and precipitation have had the greatest effect on Late Pleistocene African vertebrate communities (Link: 121, 389). Kingdon (1997: 455) summarizes the pattern of change as occurring along two poles (see also Adams (1997)). During cool, dry times, arid habitats have expanded north and south, contracting again when more moisture is available; during warm, wet periods, tropical forests expanded east and west along the equator, again contracting during cooler, drier times (**Fig. 2**). These changes have resulted in the repeated fragmentation of habitats, isolating plants and animals but ultimately increasing biodiversity.

The Fossil Records

Southern Africa

For the most part, an essentially modern fauna was in place in southern Africa by about 270 ka. This faunal community persisted until the Pleistocene to Holocene boundary 11.5 ka and is sometimes referred to as the Florisian Land Mammal Age (Klein, 1984a). However, a more precise dating of the transition from the more archaic middle mid-Pleistocene assemblages (sometimes referred to as the Cornelian Land Mammal Age) to more modern late mid-Pleistocene and Late Pleistocene assemblages remains elusive (*see* Mid-Pleistocene of Africa), and in eastern Africa, it appears that a modern fauna was in place by 330 ka (Potts and Deino, 1995). In southern Africa, the deposits at Duinefontein 2 (DFT2) appear to straddle this transition. The upper horizon at DFT2 contains an essentially modern fauna and has been dated to ca. 270 ka using optically stimulated luminescence (OSL) (*see* Optically-Stimulated Luminescence). The lower horizon at the site contains an extinct alcelaphine antelope, characteristic of more archaic assemblages. OSL indicates that the sands between the two horizons accumulated 290 ka, providing a minimum age for the more archaic assemblage. The nearby site of Elandsfontein Main (EFTM) contains a very large assemblage of vertebrate remains, a high percentage of which are extinct. Among the bovids alone, when extinct subspecies are counted, 89% (16/18) of the EFTM taxa are now extinct, while only 20% (4/20) of the species in nearby Late Pleistocene faunas are extinct; even when a more conservative approach is taken and only species are compared, 67% (12/18) of the EFTM species are extinct while only 14% (3/21) of the Late Pleistocene species are extinct. The EFTM deposits are not suitable for direct radiometric dating, so their age can be estimated only by comparing species presence and absence with East African deposits, which are more readily radiometrically dated (*see* K/Ar and Ar/Ar Dating). This comparison

Table 2 List of the commons names of animals discussed in the text, along with their scientific names

Common name	*Scientific name*
Mammals	Mammalia
Monkeys, apes, and allies	Primates
Human	*Homo sapiens*
Baboon	*Papio* sp.
Lemurs	Lemuridae
Bats	Chiroptera
Insectivores	Insectivora
Tenrecs	Lipotyphla
Hares, pikas, and rabbits	Lagomorpha
Cape hare	*Lepus capensis*
Scrub hare	*Lepus saxatilis*
European rabbit	*Oryctolagus cuniculus*
Rodents	Rodentia
North African crested porcupine	*Hystrix cristata*
Cape porcupine	*Hystrix africaeaustralis*
Giant gerbil[*]	*Gerbillus grandis*
Cape dune molerat	*Bathyergus suillus*
Common molerat	*Cryptomys hottentotus*
Carnivores	Carnivora
Dogs	Canidae
Golden jackal	*Canis aureus*
Black-backed jackal	*Canis mesomelas*
Red fox	*Vulpes vulpes*
Hunting dog	*Lycaon pictus*
Weasels, badgers, and polecats	Mustelidae
European polecat	*Mustela putorius*
Genets and civets	Viverridae
Mongooses	Herpestidae
Egyptian mongoose	*Herpestes ichneumon*
Hyenas	Hyaenidae
Striped hyena	*Hyaena hyaena*
Brown hyena	*Parahyaena brunnea*
Spotted hyena	*Crocuta crocuta*
Cats	Felidae
Wild cat	*Felis sylvestris*
Sand cat	*Felis margarita*
Serval	*Leptailurus serval*
Caracal	*Caracal caracal*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Bears	Ursidae
Brown bear	*Ursus arctos*
Fur seals and sea lions	Otariidae
Cape fur seal	*Arctocephalus pusillus*
Hyraxes	Hyracoidea
Hyrax	*Procavia* sp.
Elephants	Proboscidea
African elephant	*Loxodonta africana*
Odd-toed ungulates	Perissodactyla
Zebras, horses, and relatives	Equidae
Burchell's (plains) zebra	*Equus burchellii*
Quagga[*]	*Equus quagga*
Mountain zebra	*Equus zebra*
Grevy's zebra	*Equus grevyi*
Giant Cape zebra[*]	*Equus capensis*
Rhinoceroses	Rhinocerotidae
Black rhinoceros	*Diceros bicornis*
White rhinoceros	*Ceratotherium simum*
Merck's rhinoceros[*]	*Dicerorhinus kirchbergensis*

(*Continued*)

Table 2 (*Continued*)

Common name	*Scientific name*
Even-toed ungulates	Artiodactyla
Hippopotamuses	Hippopotamidae
Hippopotamus	*Hippopotamus amphibius*
Madagascan hippopotamus*	*Hippopotamus laloumena*
Madagascan dwarf hippopotamus*	*Hippopotamus lemerlei*
Madagascan pygmy hippopotamus*	*Hexaprotodon madagascariensis*
Pigs and hogs	Suidae
Boar	*Sus scrofa*
Bushpig	*Potamochoerus larvatus*
Giant hog	*Hylochoerus meinertzhageni*
Warthog	*Phacochoerus africanus*
Giant warthog*	*Metridiochoerus/Stylochoerus*
Deer	Cervidae
Camels, llamas, and relatives	Camelidae
Wild camel*	*Camelus thomasi*
Giraffes and okapis	Giraffidae
Giraffe	*Giraffa camelopardalis*
Bovids, antelopes, gazelles, and relatives	Bovidae
Oxen	Bovini
Cape/African buffalo	*Syncerus caffer*
Long-horned buffalo*	*Pelorovis antiquus*
Aurochs	*Bos primigenius*
Spiral-horned bovids	Tragelaphini
Bushbuck	*Tragelaphus scriptus*
Kudu	*Tragelaphus strepsiceros*
Eland	*Taurotragus oryx*
Duikers	Cephalophini
Bush duiker	*Sylvicapra grimmia*
Blue duiker	*Cephalophus monticola*
Dwarf antelopes	Neotragini
Dwarf antelope	*Neotragus batesi*
Grysbok	*Raphicerus melanotis*
Steenbok	*Raphicerus campestris*
Oribi	*Ourebia ourebi*
Reduncines and kobs	Reduncini
Mountain reedbuck	*Redunca fulvorufula*
Reedbuck	*Redunca redunca*
Lechwe	*Kobus leche*
Waterbuck	*Kobus ellipsiprymnus*
Gazelline antelopes	Antilopini
Gazelles	*Gazella* sp.
Thomson's gazelle	*Gazella rufifrons*
Springbok	*Antidorcas marsupialis*
Bond's springbok*	*Antidorcas bondi*
Southern springbok*	*Antidorcas australis*
Hartebeest, wildebeest and allies	Alcelaphini
Impala	*Aepyceros melampus*
Blesbok/bontebok	*Damaliscus dorcas*
Korrigum	*Damaliscus lunatus*
Hartebeest	*Alcelaphus buselaphus*
Giant hartebeest*	*Megalotragus priscus*
Blue wildebeest	*Connochaetes taurinus*
Black wildebeest	*Connochaetes gnou*
Horse-like antelopes	Hippotragini
Roan antelope	*Hippotragus equinus*
Sable antelope	*Hippotragus niger*
Blue antelope*	*Hippotragus leucophaeus*
Oryx	*Oryx gazella*
Sheep and goats	Caprini
Barbary sheep	*Ammotragus lervia*

(*Continued*)

Table 2 (*Continued*)

Common name	*Scientific name*
Reptiles	Reptilia
Angulate tortoise	*Chersina angulata*
Spur-thighed tortoise	*Testudo graeca*
Birds	Aves
Penguin	*Spheniscus demersus*
Cormorant	*Phalacrocorax* sp.
Flightless birds	Struthioniformes (ratites)
Ostrich	*Struthio camelus*
Elephant or marsh birds*	*Aepyornis maximus*

*Indicates extinct species.

indicates that the archaic fauna at EFTM accumulated sometime between 400 and 700 ka, or perhaps during an even older interval between 600 ka and 1 Ma. These results indicate that an essentially modern faunal community came into place in southern Africa sometime between 270 ka and 400 ka. After 270 ka, in the bovids, only subtle changes occurred. At DFT2, kudu horns were smaller and more tightly spiraled, and black wildebeest horns had smaller frontal bosses and failed to pass downward as they pass forward; by the Late Pleistocene, the animals had evolved to more closely resemble today's animals. Once the essentially modern faunal community came into place during the late mid-Pleistocene, no extinctions of large mammals occurred until the very end of the Late Pleistocene (*see* Late Pleistocene Megafaunal Extinctions).

Throughout southern Africa, it is possible to identify changes in mammalian faunal communities in response to Late Pleistocene glacial cycles, but these changes are best documented along the southern and western coasts of South Africa, where good contextual data are available on large, well-documented faunal assemblages (Klein, 1980). The most notable aspect of the Late Pleistocene faunas from this region is the overwhelming abundance of grazing species, especially alcelaphines and equids, compared to the late Holocene and historic fauna, which is domination by browsers and mixed feeders, indicating that grasses were much more common during the Late Pleistocene than at the present.

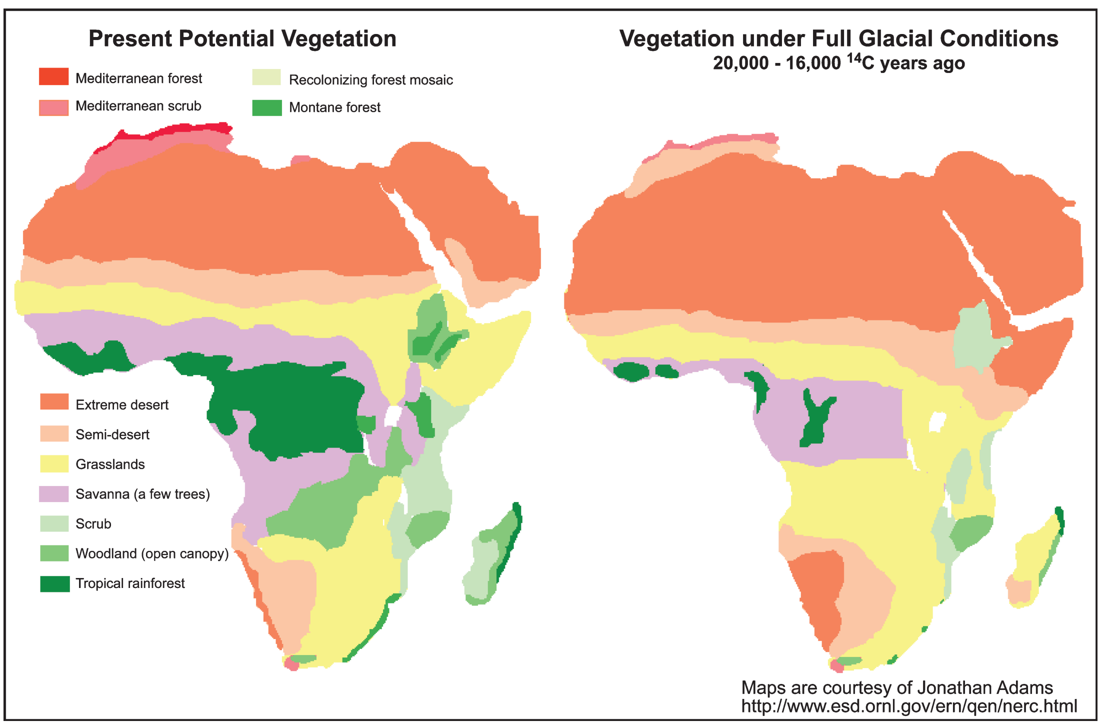

Figure 2 Distribution of the major vegetation zones of Africa in the present day (left) and during the Last Glacial Maximum (right). Note that under the colder, drier glacial conditions, the central forests contract east-west while the deserts expand north-south. Maps from Adams (1997) accessible at http://www.esd.ornl.gov/ern/qen/nerc.html.

This contrast is most striking at Nelson Bay Cave, on the southern coast of South Africa. The faunal assemblages from the levels spanning 18.5–12 ka are dominated by grazing ungulates, including quagga, alcelaphines, long-horned buffalo, and springbok, as well as ostrich, which also prefers open environments; none of these taxa were present in the vicinity of the site historically. However, the dominant taxa of the younger deposits include bushpig, bushbuck, grysbok, and Cape buffalo, which also were found historically in the region of the site. A similar transition occurred at Melkoutboom Cave, located inland northeast of Nelson Bay Cave, where the terminal Pleistocene fauna was also dominated by equids (either mountain zebra or quagga or both) and alcelaphines, while the Holocene deposits resembled the modern local fauna with bushbuck, kudu, blue duiker, grysbok, and bushpig. Again, a similar change is seen on the western coast of South Africa in Elands Bay Cave where the terminal Pleistocene fauna contains relatively more large grazers than the late Holocene component. All of these assemblages indicate that the faunal communities underwent a marked transition as environments changed from the terminal Pleistocene to the Holocene.

A similar contrast is found during the more ancient periods of the Late Pleistocene at the site of Klasies River, further east along the coast from Nelson Bay Cave. Similar to Nelson Bay Cave, the historic fauna included bushpig, bushbuck, grysbok, and Cape buffalo, and also blue duiker and hartebeest. These taxa are also found in the Holocene levels of the site, as well as in the oldest deposits, which possibly correspond to oxygen isotope stage (OIS) 5e, the Last Interglacial, which began 126 ka (*see* Oxygen Isotope Stratigraphy of the Oceans). As the sequence progresses through OIS 5, the relative abundance of taxa that prefer open habitats (alcelaphines and equids) fluctuates with those that prefer more closed habitats (bushbuck and grysbok). Further to the northeast at Border Cave, again a similar contrast is apparent, but the historic fauna is more characteristic of an open environment, with warthog, Burchell's zebra, and alcelaphines. These grazers are also present during the warmer times between OIS 5d and 3, but during colder times, a fauna that prefers more bush is present with bushpig, Cape buffalo, tragelaphines, and impala. Klasies River and other coastal sites also show evidence of changing sea levels and sea temperatures during the Late Pleistocene, as seen in the changing abundances and taxa of marine birds and mammals, especially penguins, cormorants, and Cape fur seals. During warmer times, when the seas were higher, these animals are common, but they are rare during cold times when sea levels were lower, such as during the terminal Pleistocene at Nelson Bay Cave and Elands Bay Cave.

In the northern part of southern Africa (Namibia, Botswana, Zimbabwe, Mozambique, and Angola), less is known about the Late Pleistocene faunal community. Contrasts between glacial and interglacial communities are not as clear, because the record is more sparse and because regions closer to the equator likely experienced less climatic and therefore faunal changes than southern South Africa. The late (and mid-) Pleistocene record from Zambia is better known (Brooks, 2003). Here, fossil assemblages, such as from Mumbwa Cave, closely resemble the modern faunal community with an abundance of Burchell's zebra, warthog, and alcelaphines; any deviation from the modern pattern is in the direction of adding even more grazing ungulates, such as blesbok, springbok, and mountain reedbuck, and bovids that are tied to water, such as lechwe and waterbuck. At Redcliff Cave, Zimbabwe, blesbok, springbok, and mountain reedbuck are more common during what appears to be moister conditions in OIS 2 and 4, but these animals were not documented in the region historically. In eastern South Africa, the historic and Late Pleistocene faunas are dominated by grazers, but during the moister times of the Late Pleistocene, lechwe, waterbuck, Cape buffalo, impala, and roan antelope appear, suggesting open woodlands were present. Blue wildebeest, sable/roan antelope, waterbuck, impala, and hartebeest in the Late Pleistocene deposits of Sibudu Cave, near the coast in KwaZulu-Natal, South Africa, indicate that more open savannas existed there during ancient times than during the present. In sum, the data indicate that open grasslands were much more common in southern Africa during the Late Pleistocene than they have been historically.

The above discussion has focused on bovids, equids, and suids, because these taxa are most common in the fossil record and because changes in their distributions and abundances more closely follow changes in vegetation. Carnivores have more widespread distributions than ungulates, reflecting their more generalized habitat requirements (Turpie and Crowe, 1994). Throughout the Late Pleistocene of southern Africa, lions, brown and spotted hyenas, black-backed jackals, and wild cats are frequently found in fossil assemblages, along with occasional leopards, servals, caracals, hunting dogs, and a variety of mustelids and viverrids. Of the smaller mammals, typical species include baboons, hyraxes, hares, porcupines, and Cape dune molerats, when the local environments are suitable. Hippopotamuses were common throughout southern and eastern Africa wherever permanent water and open grazing were available, both historically and in the Late Pleistocene. Both black and white rhinoceroses make regular appearances in Late Pleistocene assemblages, along with occasional elephants. Historically, giraffes were found throughout the central and northern parts of southern Africa, especially where savannahs and open woodlands were common, but they are rare in the fossil record. A few examples are known, as in Florisbad and Cave of Hearths, but their chronological position of these fossils within the late mid- or Late Pleistocene is unclear. The presence of giraffe in Florisbad especially indicates that past environments were very different from the historically treeless local vegetation. An example of Late Pleistocene giraffe more securely dated to OIS 3 was found in Sibudu Cave, KwaZulu-Natal, South Africa, located in an environment that has not supported giraffes in the recent past, but may have prehistorically.

In sum, the mammalian assemblages from the Late Pleistocene of southern Africa closely resemble the modern-day fauna of the region, but the distribution of the taxa changed through time in response to climatic influences on vegetation. Although almost all the taxa found historically in southern Africa are seen in the fossil record, there are six exceptions: giant Cape zebras, giant warthogs, long-horned buffalo, giant hartebeest, Bond's springbok, and southern springbok (**Fig. 3**). Although these taxa appeared throughout southern Africa during the Late Pleistocene (the southern springbok appeared only on the southern and western coasts of South Africa, while Bond's springbok was everywhere else), the best sites for determining the dates of their extinctions come from the coasts of South Africa. In this region, long-horned buffalo, giant hartebeest, southern springbok, and Cape zebras are last seen between 12 and 9.5 ka (Klein, 1984b). These terminal Pleistocene dates coincide with the major environmental changes described above that occurred with the transition to the Holocene, but hunting by humans may have also played a role (global evidence reviewed in Barnosky *et al.* (2004)) (*see* Late Pleistocene Megafaunal Extinctions). Over-hunting by humans almost certainly caused the next set of extinctions in southern Africa: the last blue antelope was last seen around 1800 and the last-known quagga died in 1883 (Klein, 1987; Rau, 1986). However, recently studies of DNA preserved in a few of their bones and skins stored in museums have provided some data about their taxonomic status and phylogentic relationships (Higuchi *et al.*, 1984; Leonard *et al.*, 2005; Robinson *et al.*, 1996) (*see* Ancient DNA).

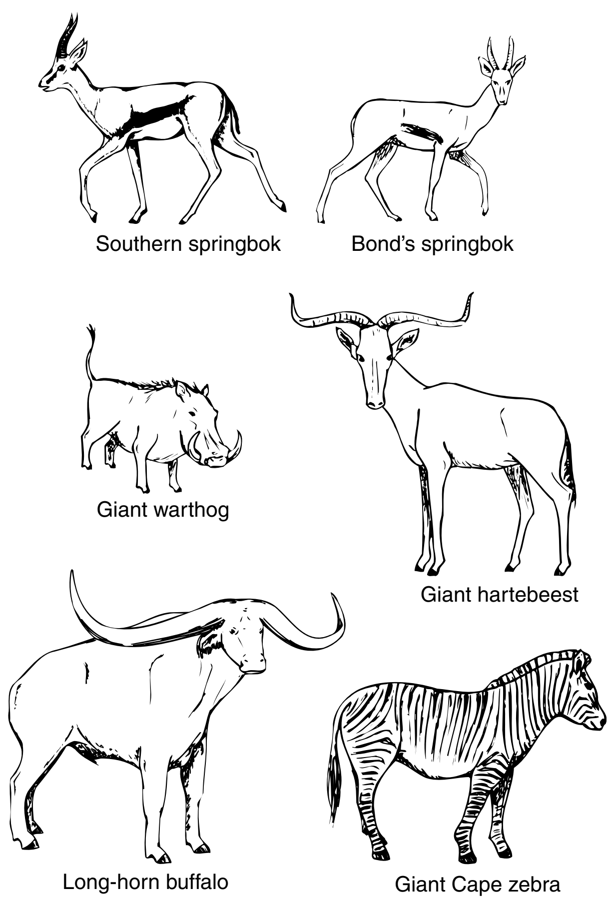

Figure 3 Depictions of African mammals that went extinct at the end of the late Pleistocene. Drawings are courtesy of Richard G. Klein.

Compared to other regions of Africa, fossil samples from southern Africa are large enough and frequent enough to examine changes in body size within a species through time and across space. This is done for two reasons. First, the average size of individuals in a species may vary in relation to temperature and precipitation, thereby being useful paleoenvironmental reconstruction. Size variation is examined between geographic locations of modern populations to understand the causes of the variation. Then these parameters can be inferred from the size of fossil specimens. This variation in size has been studied in carnivores (Klein, 1986), rock hyrax (Klein and Cruz-Uribe, 1996), Cape dune molerats (Klein, 1991), and common molerats (Avery, 2004). The second reason for studying size variation is because it may provide information about human predation pressure on a species, and from this, it is possible to infer human population densities. This has been examined using the angulate tortoise. Tortoises grow continuously throughout their lives, and if they frequently preyed upon, their median size will decrease. Studies of tortoise size from archeological assemblages show that Late Pleistocene tortoises typically were larger than Holocene tortoises (Klein and Cruz-Uribe, 1983; Steele and Klein, in press).

Northern Africa

Most of our knowledge about Late Pleistocene vertebrates from northern Africa comes from coastal regions of the Maghreb, including Morocco, Algeria, Tunisia, and Libya, although Egypt is also well represented. One of the challenges to understanding the vertebrate record from this region is the lack of good chronological control. However, recent efforts to explore the Late Pleistocene archeological record of especially Morocco is changing this, and hopefully this challenge will be overcome soon. The northern African paleontological record is interesting because it contains elements of Eurasian faunas, as well as traditional African species. These immigrants include bears, cervids, and boars. The European component almost certainly entered northern Africa from the northeastern corner through what is today Egypt. An analysis of the zoogeographical affinities of mammals in the Maghreb showed that only bats were able to cross the Straits of Gibraltar and colonize from the north; all other taxa moved in from the east or crossed the Sahara from the south (Dobson and Wright, 2000).

As in southern Africa, the Late Pleistocene species from northern Africa closely resemble modern species. However, it is unclear when exactly this fauna came into place, as very few reliable samples exist from the later mid-Pleistocene, when the change is documented in eastern and southern Africa (Geraads, 2002). The site of Jebel Irhoud, Morocco, lacks the later arriving cervids and boars and contains an alcelaphine with simple teeth and a large gerbil, indicating a late mid-Pleistocene age, of perhaps 150 ka (*see* Mid-Pleistocene of Africa). Electron spin resonance (ESR) has placed the site between 90 and 190 kyr old, and it is possible that the material accumulated throughout this time span (*see* Electron Spin Resonance Dating). The abundance of alcelaphines, oryx, and gazelles in the sample suggests that the environment was a dry savanna. In contrast, the terminal Pleistocene and early Holocene (12–4 ka) was especially moist, and most of the mammals present in during the Late Pleistocene reappeared during the Holocene, so the clear break between Late Pleistocene and Holocene records, which is seen in southern Africa, is not as apparent in northern Africa. However, a few species go extinct during the Holocene, including camels, cervids, and long-horned buffalo (Klein, 1984b).

In general, the faunal remains also indicate the presence of savannas in the Maghreb during the Late Pleistocene. In Haua Fteah, Libya, in Mugharet el 'Aliya and in Rhafas Cave, Morocco, and in nearby sites, the most abundant taxa are Barbary sheep, aurochs, and various gazelle, but hartebeests and equids are also present. Rhinoceroses (both white and Merck's) and elephants are also found, along with both the Cape hare and European rabbit. More rare species include porcupine, hippopotamus, deer, long-horned buffalo, eland, and blue wildebeest. Both warthogs and boar have been identified. Unfortunately, the current data available for the Maghreb do not allow us to make as detailed comparisons between glacial and interglacial cycles as in southern Africa. The fauna at Haua Fteah suggests that Barbary sheep were more abundant during drier periods and that aurochs was more abundant during wetter ones.

The carnivores of this time period are equally diverse (Aouraghe, 2000), and include golden jackals, red foxes, lions, leopards, wildcats, sand cats, caracals, spotted hyenas, Egyptian mongooses, and European polecats. Bears and striped hyenas were also present. The bears, foxes, and polecats provide another link to Eurasian faunas that make the Maghreb's faunal community unique. Among nonmammals, spur-thighed tortoises and ostriches are also common, mirroring the assemblages often seen in southern Africa.

Late Pleistocene vertebrates are best known in northern Africa from the Maghreb, because the geology of this region allows for many deep caves, which permit good bone preservation. Unfortunately, most of the Late Pleistocene sites from the eastern part of northern Africa are open-air sites, where bone is poorly preserved. What data are available, from sites such as Bir Tarfawi, Shuwikhat 1, and Makhadma 2 and 4 Egypt, indicate that the faunal communities were roughly similar between the western and eastern regions of northern Africa. Various gazelles are present, along with hartebeest, aurochs and/or long-horned buffalo. Equids, white rhinoceroses, hippopotamuses, and warthogs were also found in the east, along with porcupines, hares, and ostriches. The mix of carnivores is also similar between the two regions. The eastern region was unique because of the presence of wild camels, giraffes, and reduncines. Some assemblage also include rodents whose modern ranges are much further south in much wetter places, indicating that the fossil assemblages accumulated when the region received higher rainfall than today.

Eastern Africa

While eastern Africa has enjoyed a long history of paleontological research, most of this research has focused on the Pliocene and Early Pleistocene, because these phases are associated with the hunt for early hominin fossils (*see* Overview). Recent attention on modern human origins during the Late Pleistocene is changing this, but large, well-preserved, and well-dated Late Pleistocene faunal assemblages remain rare.

The oldest-dated fossil assemblage in eastern Africa that contains no extinct species, essentially a modern fauna, is from Lainyamok, Kenya, and dated to about 330 kyr old by Ar/Ar (*see* K/Ar and Ar/Ar Dating). This date places the assemblage firmly in the mid-Pleistocene and indicates that modern species existed in eastern Africa throughout the Late Pleistocene (*see* Mid-Pleistocene of Africa). Some nearby Late Pleistocene assemblages, such as those found on Lukenya Hill, Kenya, contain the long-horned buffalo, which was also common in the Late Pleistocene assemblages from southern and northern Africa, and may contain another extinct species, a small alcelaphine. However, other authors argue that these small alcelaphines are bontebok or blesbok. Blesbok also are common at Redcliff, suggesting that they once extended from South Africa through Central Africa to eastern Africa. The small alcelaphine is not found in local Holocene samples, but they are present in small numbers in Holocene samples in northern Tanzania. Oryx and Grevy's zebra are also found in the Lukenya faunas but not locally historically, suggesting that in the past, the region was more arid than today and their modern ranges were expanded to encompass Lukenya. Other common Late Pleistocene species include hartebeest, wildebeest, Thomson's gazelle, and Burchell's zebra, and mountain reedbuck, oribi, steenbok, bush duiker, and warthog are also present.

Madagascar

Although Madagascar is typically considered part of Africa, its isolation from Africa for 165 Myr and from India for 88 Myr allowed its flora and fauna to evolve along a unique path. Located almost 400 km from the coast of Africa at Mozambique, very limited faunal exchange occurred until the first humans arrived ca. 2 ka. Only ca. 100 species of mammals lived on the island before colonization by humans, and this faunal community is characterized by high endemicity (about 80% of its flora and fauna are unique to the island) and taxonomic imbalance. While the mammalian community included primates (lemurs), insectivores (lipotyphlans), rodents, carnivores, hippopotamuses, and bats, very few of the typically African species ever reached the islands: no elephants, rhinoceroses, camels, giraffes, bovids, felids, or canids successfully made the crossing. Recent genetic studies indicate that most of the clades of nonvolant (nonflying) mammals to reach Madagascar did so with single colonization events, either by swimming or by rafting from Africa; lemurs arrived 62–66 Ma, and carnivores arrived later between 18 and 24 Ma (Yoder *et al.*, 2003, 1996). However, the presence of three species of hippopotamuses, each with different ancestors, suggests that they may have arrived in three separate colonization events (Faure and Guérin, 1990; Stuenes, 1989). Knowledge of the Late Pleistocene fossil record of Madagascar is limited, but much work has been done on the subfossil record (terminal Pleistocene and Holocene), especially of lemurs, which provide an impressive example of adaptive radiation in primates. The subfossil record adds 17 extinct species to the ca. 30 still-living lemurs (Godfrey and Jungers, 2002) and allows the study of their ancient DNA, further confirming their single and ancient origin (Karanth *et al.*, 2005) (*see* Ancient DNA). Among non-mammals, Madagascar was also home to giant tortoises and giant ratites (flightless birds), known as elephant birds, marsh birds, or vorompatra. These taxa probably existed on the landmass before it broke away from Africa. The long persistence of lemurs and the other unique species on an isolated island and then their rapid and recent extinction has caused much discussion about whether their demise is related to climatic change, human hunting, or human habitat disturbance (deforestation, increased erosion, change in fire regime, introduction of new species) (Burney, 1999; Goodman and Patterson, 1997) (*see* Late Pleistocene Megafaunal Extinctions).

Western and Central Africa

Very little is known about the Late Pleistocene vertebrate record from western and central Africa, because bone preservation tends to be poor and because few researchers have conducted paleontological and archeological research in the region. What little evidence that is available for the region, such as found in Mbi Crater, Cameroon, indicates that during the terminal Pleistocene animals tended to be more characteristic of open habitats, with hartebeest, korrigum, roan antelope, waterbuck, warthog, reedbuck, and bush duiker being present. Forest cover, while consistently present during the Late Pleistocene, increased in the Holocene, as seen by increasing numbers of various duikers, bushbuck, dwarf antelope, bush pig, giant hog, and leopards.

Summary

Most of the mammal species found in the Late Pleistocene vertebrate records of Africa were also found on the continent historically. However, many changes in the species' ranges, abundance, and associations make Late Pleistocene faunal communities look different from today's communities. As the climate changed in the past, so did the vegetation. Many times in the fossil record, species are found in places where today their descendants live hundreds, if not thousands, of kilometers away, indicating that their past ranges were either completely shifted to different location or expanded to encompass new locations. Late Pleistocene climatic and vegetation changes created unique habitats, many of which do not exist today. Each species' unique responses to these dramatic changes meant that mammal communities were formed that do not have analogs today, meaning that species were often found together in fossil assemblages that are not found together historically. Only a handful of African species went extinct during the transition from the Late Pleistocene to the Holocene.

See also: **Archaeological Records**: Overview; Global Expansion 300,000-8000 years ago, Africa. **Glaciations**: Overview. **K/Ar and Ar/Ar Dating**. **Luminescence Dating**: Optically-Stimulated Luminescence; Electron Spin Resonance Dating. **Paleoceanography, Physical and Chemical Proxies**: Oxygen Isotope Stratigraphy of the Oceans. **Sea Level Studies**: Overview. **Vertebrate Records**: Late Pleistocene Megafaunal Extinctions; Mid-Pleistocene of Africa. **Vertebrate Studies**: Ancient DNA; Interactions with Hominids.

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Late Pleistocene of North America

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Introduction

A synopsis is provided here of the Late Pleistocene terrestrial vertebrate faunas of continental North America. The term 'Pleistocene' has a complicated early history and was originally equated to the glacial deposits in England (Bell *et al.*, 2004). The International Commission on Stratigraphy has placed the Pleistocene epoch (with the three ages: Lower, Middle, and Upper) within the Neogene period (http://www.stratigraphy.org/). The beginning of the Lower Pleistocene is placed at 1.806 Ma and ends at 0.781 Ma. The Middle Pleistocene is fixed between 0.781 and 0.126 Ma, with the Upper Pleistocene ending at 0.0115 Ma (Berggren *et al.*, 1995). Within chronostratigraphy, this system must be followed; however, overall this scheme does little to help elucidate the variations found within the changing climate (glacial–interglacial) and vertebrate faunas of the North American Pleistocene.

Subsequent to the first usage of the term, temporal relationships among the terrestrial Pleistocene deposits of North America were traditionally based on their affiliations to the classical four major glaciations (Nebraskan, Kansan, Illinoian, and Wisconsin), including interglacials between. Deep-sea sedimentary cores have shown that as many as 22 discrete glacial pulses over the past two million years are recognized (Richmond and Fullerton, 1986), which leaves the glacial and interglacial names basically useless in North America and are abandoned for use with faunal assemblages except for the most recent glaciation, Wisconsin. This