

involves water withdrawal due to the presence of segregated ice surrounding the mummies that dehydrates them in the frozen ground. He further states that underground frost mummification should not be confused with freeze-drying that occurs when a body is frozen and moisture is removed by sublimation, a process accelerated by a partial vacuum.

See also: Vertebrate Overview. Vertebrate Studies: Ancient DNA.

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Late Pleistocene Megafaunal Extinctions

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Introduction

From the late nineteenth century, the work of paleontologists was beginning to reveal the fact that many of the large animals that had lived during what was then known as the Great Ice Age are no longer living

today. The great evolutionary biologist, Alfred Russel Wallace, wrote the following memorable comment on this phenomenon in 1876:

We live in a zoologically impoverished world, from which all the hugest, and fiercest, and strangest forms have recently disappeared; and it is, no doubt, a much better world for us now they have gone. Yet it is surely a marvellous fact, and one that has hardly been sufficiently dwelt upon, this sudden dying out of so many large mammalia, not in one place only but over half the land surface of the globe. (1876: 150)

Thirty years later, speculating on the causes of this extinction event, Wallace ventured the following:

Looking at the whole subject again, with the much larger body of facts at our command, I am convinced that the rapidity of ... the extinction of so many large Mammalia is actually due to man's agency, acting in co-operation with those general causes which at the culmination of each geological era has led to the extinction of the larger, the most specialised, or the most strangely modified forms. (1911: 264)

Thus, the comments of Wallace set the stage for a modern discussion of this phenomenon. Today, we know a great deal more about the timing of these extinctions, the number of species involved, and the geographic patterns of extinction, but much of the mystery remains, and the debate over the cause(s) of the Late Pleistocene megafaunal extinction continues to rage on in the current literature.

Definition of Megafauna

The fossil evidence from many continents points to the extinction mainly of large animals at or near the end of the last glaciation. These animals have been termed 'megafauna.' The most common definition of megafauna is an animal with an adult body weight of over 44 kg (Martin, 1984). These animals were worst affected because they exist at relatively low density in the landscape, mature late, and have few offspring. They are slow to recover numbers after any collapse of population. In many regions of the world, the Pleistocene megafauna was dominated by herbivorous mammals, such as the woolly mammoth and woolly rhinoceros. However, in biologically isolated regions of the world, such as Australia and New Zealand, the Pleistocene megafauna also included other vertebrate groups, such as large, flightless birds, and giant turtles and lizards. One of the most curious aspects of Late Pleistocene megafaunal extinctions is that they affected some continents far more than others (Table 1). For reasons which are still being debated, Australia and the Americas were

Table 1 Megafaunal extinctions (genera) during the last 100 kyr (after Wroe *et al.*, 2004)

| Continent | Extinct | Living | Total | Extinct (%) | Landmass (km ²) |
|---------------|---------|--------|-------|-------------|-----------------------------|
| Africa | 7 | 42 | 49 | 14.3 | 30.2 × 10 ⁶ |
| Europe | 15 | 9 | 24 | 60.0 | 10.4 × 10 ⁶ |
| North America | 33 | 12 | 45 | 73.3 | 23.7 × 10 ⁶ |
| South America | 46 | 12 | 58 | 79.6 | 17.8 × 10 ⁶ |
| Australia | 19 | 3 | 22 | 86.4 | 7.7 × 10 ⁶ |

much harder hit than Africa and Asia. In the next section, we discuss the extinction patterns of the various continents.

Extinctions before the end of the Last Glaciation

The extinction of Pleistocene megafaunal species was not a singular event, but rather a process that spanned many thousands of years. It was also time transgressive on the various continents, so it was not tied to a single, global climatic change. One of the difficulties in developing an understanding of megafaunal extinction is that it is very difficult to pin down an exact time when a given species ceased to exist, just by examining the fossil record. When the fossil bones of a given species fail to appear above a certain stratigraphic horizon in a region, we assume that this species died out, at least in that region. However, as the old proverb says, 'absence of evidence is not evidence of absence.' The discovery of any younger fossils will, of course, mean that the extinction date has to be revised. One of the most startling examples of this concerns the woolly mammoth, probably the best-known Pleistocene megafaunal mammal, based on its appearance on the logos of Quaternary research organizations (see the cover of this Encyclopedia). Until quite recently, paleontologists believed that the woolly mammoth became extinct at the end of the last glaciation, perhaps 12.8 ka (Elias, 1999). Then a Russian paleontologist discovered woolly mammoth bones from Wrangel Island, off the northeast coast of Kamchatka. These bones were radiocarbon dated, and found to be only 4.079 kyr old (Long *et al.*, 1994). Thus, the date of extinction for this species had to be revised by 8.7 kyr, placing its last appearance well within the Holocene.

The Wrangel Island woolly mammoth story is a cautionary tale, and it also highlights a different aspect of the demise of the megafauna: extinction

versus extirpation. Extirpation is the dying out of a species in a given region. For instance, the fossil evidence indicates that woolly mammoths were extirpated from mainland North America by 12.8 ka. Extinction refers to the worldwide demise of a species. There is a very important difference between these two phenomena, because during the Pleistocene, extreme environmental changes caused the regional extirpation of countless numbers of species in the middle and high latitudes, time and again. However, as long as populations of a given species were able to survive in other regions (perhaps only a single population in one region), then that species had a chance to survive until environmental conditions in its former range became more favorable again. The fossil record of the Pleistocene is replete with examples of the regional waxing and waning of plant and animal populations, in the face of climate change and glaciation. Extinction, however, is permanent. When a species' unique genotype is lost to the world, it cannot come back. In the next section, we examine the regional history of the timing of megafaunal extinctions (keeping in mind the caveats discussed above about evidence of absence).

Australia

The continent of Australia has been geographically isolated from much of the rest of the world for many millions of years. The only group of mammals to successfully colonize Australia were the primitive group of marsupials. In marsupial mammals, the female typically has a pouch (marsupium) in which it rears its young through early infancy, thereby differing from placental mammals, which give birth to fully formed young. Placental mammals have dominated the mammalian faunas of the other continents since the late Tertiary, but the marsupials were the only mammal group in Australia. In the absence of competition from placental mammals, the Australian marsupials radiated a rich and diverse Pleistocene megafauna, including giant lumbering herbivores, such as *Procoptodon*, a giant kangaroo (Fig. 1C), and *Diprotodon*, a rhinoceros-sized marsupial (Fig. 1A). The megafaunal group that suffered the greatest number of extinctions in the Late Pleistocene were the short-faced kangaroos in the subfamily Sthenurinae. Approximately 14 species of sthenurines died out in the Late Pleistocene; only one species survives today. The hind feet of these kangaroos had a single toe, with a broad, flattened claw that resembled (and may have acted as) a horse's hoof. Unlike horses, however, sthenurines were probably quite slow moving.

Giant wombats and wallabies also roamed the grasslands of Pleistocene Australia. One of the most unusual of these was the giant wombat, *Phascolonus gigas* (Fig. 1B), that weighed up to 200 kg, and was built for burrowing. Flannery (1994) speculated that it was the giant dirt piles adjacent to these burrows that alerted human hunters to the presence of these animals, ultimately leading to their demise.

In the place of placental mammal predatory groups such as wolves, large cats, and bears, the marsupial predators of Australia included *Thylacoleo*, the

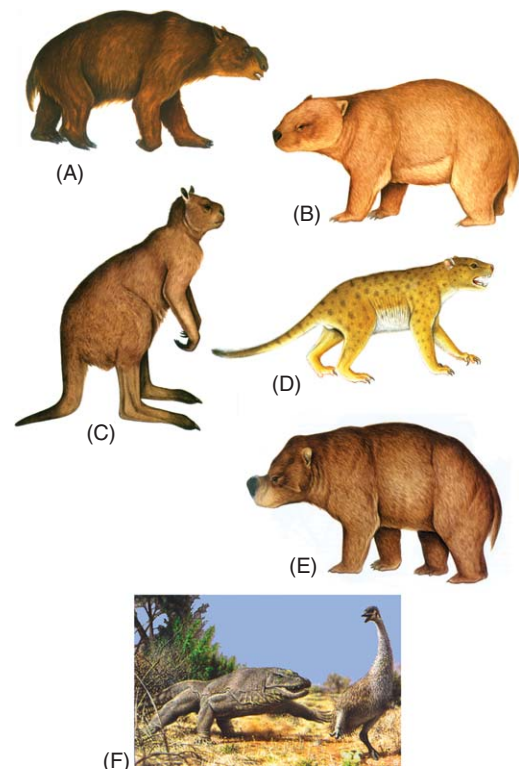


Figure 1 Australian megafaunal species that became extinct in the late Pleistocene. (A) *Diprotodon optatum* from Long J, Archer M, Flannery T, and Hand S (2002) *Prehistoric Mammals of Australia and New Guinea. One Hundred Million Years of Evolution.* p. 87. Johns Hopkins University Press; (B) *Phascolonus gigas* from Long J, Archer M, Flannery T, and Hand S (2002) *Prehistoric Mammals of Australia and New Guinea. One Hundred Million Years of Evolution.* p. 113. Johns Hopkins University Press; (C) *Procoptodon goliah* from Long J, Archer M, Flannery T, and Hand S (2002) *Prehistoric Mammals of Australia and New Guinea. One Hundred Million Years of Evolution.* p. 158. Johns Hopkins University Press; (D) *Thylacoleo carnifex* from Long J, Archer M, Flannery T, and Hand S (2002) *Prehistoric Mammals of Australia and New Guinea. One Hundred Million Years of Evolution.* p. 105. Johns Hopkins University Press; (E) *Zygomaturus trilobus* from Long J, Archer M, Flannery T, and Hand S (2002) *Prehistoric Mammals of Australia and New Guinea. One Hundred Million Years of Evolution.* p. 99. Johns Hopkins University Press; (F) *Megalania* chasing *Genyornis*, from University of California – Berkeley website: <http://www.geology.ucdavis.edu>

equivalent of a Pleistocene lion (Fig. 1D), and *Sarcophilus*, an ancestral Tasmanian Devil. Based on its skull and teeth, *Thylacoleo* was a ferocious predator. It had an enormous set of stabbing front teeth and powerful claws. Paleontologists have equated it with the modern leopard, killings its prey, then dragging the carcass up a tree to feed (Long *et al.*, 2002). *Sarcophilus*, the Tasmanian Devil, had a Pleistocene relative that was about 16% larger than the modern species. It was not, technically, part of the megafauna, weighing only 10 kg, but as with the modern species, the Pleistocene variety probably ‘fought above its weight.’

Other groups of vertebrates flourished in the absence of placental mammals in Australia. These included a large flightless bird, *Genyornis* (Fig. 1F), crocodiles, giant horned turtles, and the giant predatory ‘ripper lizard,’ *Megalania* (Fig. 1F). The Australian Pleistocene bestiary could well fit Wallace’s description of ‘large, fierce, and strange.’ Then, beginning about 50 ka, they started dying off (Table 2).

There are a number of important fossil sites in Australia that have yielded abundant, well-preserved megafaunal remains. Perhaps the best known of these are the caves contained in Naracoorte Caves

Table 2 Timing of extinction of the Australian Pleistocene megafauna

| <i>Taxon</i> | <i>Common name</i> | <i>Last 100 ka</i> | <i>100–50 ka</i> | <i>50–16 ka</i> | <i>16–11.5 ka</i> | <i>11.5–0 ka</i> | <i>Reference</i> |
|----------------------|-----------------------|--------------------|------------------|-----------------|-------------------|------------------|------------------------------|
| Reptilia | | | | | | | |
| Varanidae | | | | | | | |
| <i>Megalania</i> | Giant ripper lizard | | | X | | | Roberts <i>et al.</i> , 2001 |
| Meiolanidae | | | | | | | |
| <i>Meiolania</i> | Giant horned turtle | | | X | | | Roberts <i>et al.</i> , 2001 |
| <i>Ninjemys</i> | Giant horned turtle | X | | | | | Flannery and Roberts, 1999 |
| Crocodylidae | | | | | | | |
| <i>Palimnarchus</i> | Pleistocene crocodile | | | X | | | Roberts <i>et al.</i> , 2001 |
| <i>Quinkana</i> | Saw-toothed crocodile | | | X | | | Roberts <i>et al.</i> , 2001 |
| Boiidae? | | | | | | | |
| <i>Wonambi</i> | Giant madtsoiid snake | | X | | | | Roberts <i>et al.</i> , 2001 |
| Aves | | | | | | | |
| <i>Genyornis</i> | Giant ratite bird | | | X | | | Roberts <i>et al.</i> , 2001 |
| Mammalia | | | | | | | |
| Marsupialia | | | | | | | |
| Diprotodontidae | | | | | | | |
| <i>Diprotodon</i> | <i>Diprotodon</i> | | | X | | | Roberts <i>et al.</i> , 2001 |
| <i>Euryzygoma</i> | <i>Euryzygoma</i> | X | | | | | Flannery and Roberts, 1999 |
| <i>Euowenia</i> | <i>Euowenia</i> | X | | | | | Flannery and Roberts, 1999 |
| <i>Nototherium</i> | <i>Nototherium</i> | X | | | | | Flannery and Roberts, 1999 |
| <i>Zygomaturus</i> | <i>Zygomaturus</i> | | X | | | | Roberts <i>et al.</i> , 2001 |
| Palorchestidae | | | | | | | |
| <i>Palorchestes</i> | Marsupial tapir | | | X | | | Roberts <i>et al.</i> , 2001 |
| Vombatidae | | | | | | | |
| <i>Phascalomys</i> | Hairy-nosed wombat | X | | | | | Flannery and Roberts, 1999 |
| <i>Phascolonus</i> | Giant wombat | | | X | | | Roberts <i>et al.</i> , 2001 |
| <i>Ramsayia</i> | Pleistocene wombat | X | | | | | Flannery and Roberts, 1999 |
| Thylacoleonidae | | | | | | | |
| <i>Thylacoleo</i> | Marsupial ‘lion’ | | | X | | | Roberts <i>et al.</i> , 2001 |
| Macropodidae | | | | | | | |
| <i>Protemnodon</i> | Giant wallaby | | | X | | | Flannery and Roberts, 1999 |
| <i>Procoptodon</i> | Giant kangaroo | X | | | | | Flannery and Roberts, 1999 |
| <i>Simosthenurus</i> | Short-faced kangaroo | | | X | | | Roberts <i>et al.</i> , 2001 |
| <i>Sthenurus</i> | Pleistocene kangaroo | | X | | | | Roberts <i>et al.</i> , 2001 |

After Barnowsky AD, Koch PL, Feranec RS, Wing SL, and Shabel AB (2004) Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306: 70–75.

National Park, South Australia. These are limestone solution caves that formed in the Early Pleistocene. The caves acted as giant pit-fall traps in the last 500 kyr. To date, 118 species of vertebrate animals have been recorded representing four of the major vertebrate groups: the amphibians, reptiles, birds, and mammals. Many of these qualify as megafauna, based on their estimated size. Mammoth Cave, another limestone cave, lies near the southwest tip of Australia in New South Wales. More than 10,000 Late Pleistocene bones have been found in the cave, some greater than 35 kyr old. The fossils include the remains of a Tasmanian devil, the ‘marsupial lion’ (*Thylacoleo*), the giant echidna (*Zaglossus hacketti*), and a Pleistocene short-faced kangaroo (*Simosthenurus*). Pleistocene fossil localities are dotted across much of southern and eastern Australia (Fig. 2). While the cave sites, such as the ones described above, have yielded spectacular bone piles, there are hundreds of open-air sites as well. For more complete inventories of sites, see Horton (1989) and Roberts *et al.* (2001).

The Australian megafauna contained many large animals (Fig. 3), but few that were true giants compared with the many megafaunal species in Eurasia

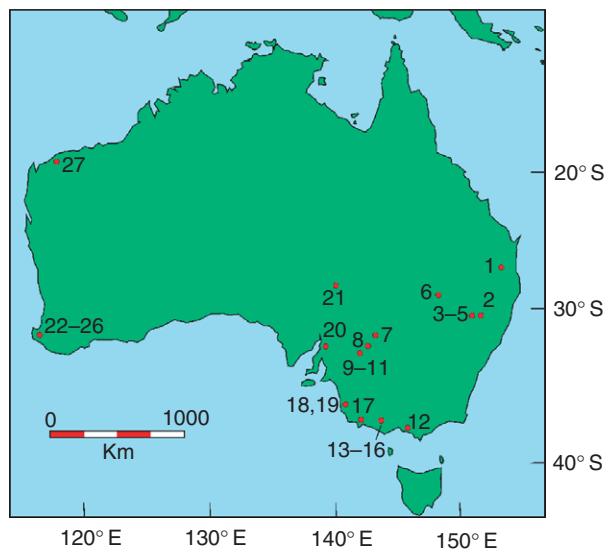


Figure 2 Map of Australia, showing important late Pleistocene fossil localities from which megafaunal remains have been found, and radiometric dates have been analyzed by Roberts *et al.* (2001). 1, Ned’s Gully; 2, Mooki River; 3, Cox’s Creek (Bando); 4, Cox’s Creek (Kenloi); 5, Tambar Springs; 6, Cuddie Springs; 7, Lake Menidee (Sunset Strip); 8, Willow Point; 9, Lake Victoria (Site 50); 10, Lake Victoria (Site 51); 11, Lake Victoria (Site 73); 12, Montford’s Beach; 13, Lake Weering; 14, Lake Corangamite; 15, Lake Weeranganuk; 16, Lake Colongulac; 17, Warrnambool; 18, Victoria Fossil Cave (Grant Hall); 19, Victoria Fossil Cave (Fossil Chamber); 20, Wood Point; 21, Lake Callabonna; 22, Devil’s Lair; 23, Kudjal Yolgha Cave; 24, Mammoth Cave; 25, Moondyne Cave; 26, Tight Entrance Cave; 27, Du Boulay Cave.

and the Americas that weighed several tons. Flannery (1994) attributes the paucity of extremely large megafaunal species in Australia to the low level of nutrients available in Australian soils. Also, because of Australia’s geographic isolation earlier than the evolution of placental mammals on other continents, vertebrate groups other than mammals, such as flightless birds and reptiles, played a larger role in Australian Pleistocene faunas than they did elsewhere. Notable among these were giant snakes, lizards, and crocodiles (although for an opposing view, see Wroe (2002)).

The story of Australian megafaunal extinction is confounded by a relatively poor chronology, and new information is being obtained with great frequency, but the main pulse of extinction came here much

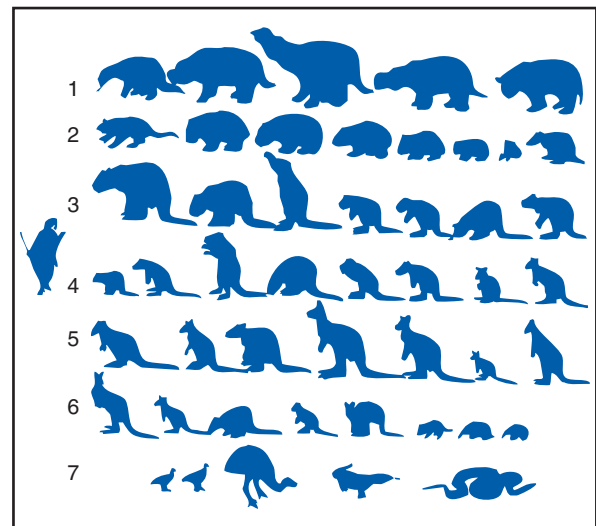


Figure 3 Silhouettes of most of the extinct late Pleistocene Australian vertebrate species drawn to scale (human hunter provides scale). Row 1, right to left: tree-feller (*Palorchestes azeal*), marsupial ‘rhino’ (*Zygomaturus trilobus*), large and small diprotodons (*Diprotodon optatum*, *Diprotodon minor*), *Euowenia* (*Euowenia grata*); Row 2, marsupial lion (*Thylacoleo carnifex*), five species of extinct wombats (*Ramsayia curvirostris*, *Phascolonus gigas*, *Phascolomys major*, *Phascolomys medius*, *Vombatus hacketti*, *Phascolarctos stirtoni*), giant rat-kangaroo (*Propleopus oscillans*); Row 3, seven species of giant short-faced kangaroos (*Procoptodon goliah*, *Procoptodon rapha*, *Procoptodon pusio*, *Sthenurus maddocki*, *Sthenurus brownei*, *Sthenurus occidentalis*, *Sthenurus orientalis*); Row 4, eight species of extinct kangaroos (*Sthenurus gilli*, *Sthenurus atlas*, *Sthenurus tindalei*, *Sthenurus pales*, *Sthenurus oreas*, *Sthenurus andersoni*, *Troposodon minor*, *Wallabia indra*); Row 5, seven species of extinct or dwarfed kangaroos (*Protemnodon roechus*, *Protemnodon anak*, *Protemnodon brehus*, *Macropus ferragus*, *Macropus* (*Osphranter*) *birdselli*, *Macropus siva*, *Macropus titan*); Row 6, extinct or dwarfed marsupials and monotremes (*Macropus tama*, *Macropus thor*, *Macropus piltonensis*, *Macropus goodi*, *Macropus stirtoni*, *Sarcophilus laniarius*, *Zaglossus hacketti*, *Zaglossus ramsayi*); Row 7, extinct birds and reptiles (*Progura naracoortensis*, *Progura gallinacea*, *Genyornis newtoni*, *Megalania prisca*, *Wonambi naracoortensis*). (From Murray, P., 1987).

earlier than elsewhere in the world. Roberts *et al.* (2001) dated the youngest sedimentary layers containing megafaunal species, using a variety of methods, including optically stimulated luminescence (OSL) and U/Th. They placed the extinctions all within a window from 51.2 to 39.8 ka (95% confidence interval). Barnowsky *et al.* (2004) cite the following statistics: of 21 extinct genera of Australian megafauna, 12 persisted to at least 80 ka, and at least six persisted to between 51 and 40 ka. Wroe *et al.* (2004) produced a slightly different reckoning of these events, with 19 genera becoming extinct in the Pleistocene, rather than 21. The differences are mostly due to different taxonomic classification schemes, but the bottom line remains the same: roughly 86% of the Australian megafauna died out before 16 ka, leaving only three genera of large mammals in the Holocene. The timing of these extinctions, and possible associations with human hunting, are a matter of some controversy. The interpretation of the fossil record at the Cuddie Springs site (Fig. 2, No. 6) is a good example of this.

Cuddie Springs is an ancient lake bed in the semiarid zone of north-central New South Wales. Pleistocene megafaunal remains have been found there in a clay pan in the center of the lake bed. The fossil bones were discovered in the 1870s when a well was sunk in the center of the ancient lake bed. Paleontological research began there in earnest in the 1930s, and five megafaunal species have been identified from the site. The work there eventually led to the discovery of stone tools and evidence of butchering of animals (cut marks on fossil bones). The most significant archeological discovery was made in one of the lower levels at the Cuddie Springs site. A small flaked stone tool (possibly an arrowhead or scraper) was found lodged between a *Diprotodon* mandible and a *Genyornis* femur. The tool had traces of dried blood, and wear patterns consistent with its use in butchering. But when did these events take place?

Radiocarbon dating of butchered remains indicates that this activity took place between about 40 and 31 ka. However, there are numerous problems to be considered when radiocarbon dating of collagen extracted from bones that have been repeatedly wetted and dried in a hot climate, so these ages are suspect. Roberts *et al.* (2001) subsequently obtained OSL dates between 30 and 27 ka on sand grains from the megafaunal fossil beds, but they dismiss the apparent age of the site on the grounds that sediment mixing has occurred there, and that the remains must have been reworked. Field and Fullager (2001), who have worked at the site, refute this interpretation. In their view, the megafauna disappeared from the

Cuddie Springs record around 28 ka, well after the arrival of humans in Australia. The view of the archeologists who have studied Cuddie Springs is that after the lake dried out, people lived on and around the clay pan, broadening their resource base to include a range of plant foods. Megafauna appear to be just one of a range of food resources exploited during this time. The archeological evidence suggests no specialized strategies for hunting megafauna. Thus, depending on which interpretation of the Australian fossil record one chooses to believe, the megafauna either died out very shortly after the arrival of humans, about 50 ka, or it persisted for tens of thousands of years afterward.

The Americas

The ancient megafauna of the Americas was very different from that of Australia, but this is not to say that the Americas were not home to some very strange beasts during the Pleistocene. Many forms of Pleistocene mammals remain familiar to us today, even if they are no longer native to the New World. The predators include lions and cheetahs, bears, and wolves, albeit larger-sized versions than exist today. Many of the Pleistocene herbivores also have modern counterparts, such as camels, horses, bison and musk oxen, deer, and elephants. Again, their Pleistocene counterparts were generally larger than the Holocene survivors. These include a host of different giant armadillo-like creatures known as glyptodonts (Fig. 4G). These were particularly important in the Pleistocene fauna of South America. South America was geographically isolated from the rest of the world during the heydays of mammalian evolution in the Tertiary (65–3 Ma). With the formation of the Isthmus of Panama, about 3 Ma, a land connection finally allowed the interchange of mammalian faunas from North and South America. Some large herbivores, such as the mastodon (Fig. 4I) and some related proboscideans, were able to colonize South America, but the large variety of ground sloths persisted through this interval, and some species of ground sloths and armadillos spread into North America. Some of the ground sloths were true giants. For instance, *Megatherium* was about 6 m long, and weighed 4,000 kg.

Of the North American megafauna that existed at the beginning of the last glaciation, only three genera are known to have become extinct before 16 ka. The timing of the extinction of 12 genera remains relatively uncertain (Barnowsky *et al.*, 2004), but the remaining extinctions (20 genera) apparently took place between 16 and 11.5 ka (Table 3).

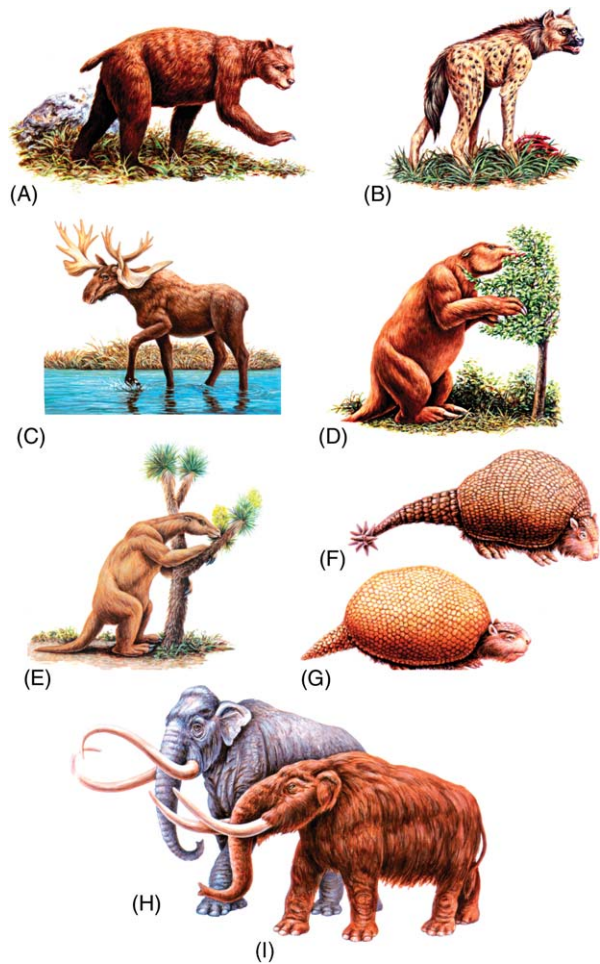


Figure 4 American megafauna that became extinct in the late Pleistocene. (A) *Arctodus simus* from Lange (2002) p. 101; (B) *Chasmaporthetes ossifragus* from Lange (2002), p. 113; (C) *Cervalces scotti* from Lange (2002) p. 140; (D) *Eremotherium rusconii* from Lange (2002), p. 84; (E) *Nothrotheriops shastensis* from Lange (2002), p. 91; (F) *Doedicurus* from Lange (2002), p. 72; (G) *Glyptotherium arizonensis* from Lange (2002), p. 72; (H) *Mammuthus columbi* from Lange (2002), p. 167; (I) *Mammuthus americanum* from Lange (2002), p. 167. Reproduced from Lange IM (2002) *Ice Age Mammals of North America. A Guide to the Big, the Hairy, and the Bizarre*. Mountain Press Publishing Company.

The South American extinction data are much more vague, because less work has been done here. Of the 48 genera of megafauna that have become extinct in the last 100 kyr, we have more or less certain evidence that 17 died out between 16 and 11.5 ka (Table 4). Twenty-seven genera died out sometime in the last 100 kyr, but the timing of their extinction remains uncertain (Barnowsky *et al.*, 2004). Four megafaunal genera are known to have persisted into the early Holocene, and then died out. All told, the North American megafauna suffered a 73% reduction in genera by the end of the Pleistocene, and the South America megafauna suffered almost an 80% reduction in genera.

Regions Suffering few Late Pleistocene Megafaunal Extinctions

In contrast, some regions of the world saw few megafaunal extinctions during the Late Pleistocene. Some of these regions, such as Africa and southern Asia, preserve the only living examples of the types of animals that died out elsewhere, such as lions, hyenas, elephants, native horses, and rhinoceroses. Their survival in these parts of the globe begs the question of the cause of their extinction elsewhere.

Africa

Of all the continents, Africa was the least affected by the Late Pleistocene megafaunal extinction. The modern African fauna includes 42 genera of large mammals; only seven genera died out during the last 100 kyr, according to Wroe *et al.* (2004). Barnowsky *et al.* (2004) listed four genera that became extinct in Africa sometime during the last 100 kyr (Table 5). These include a genus of Pleistocene elephants (*Elephas*) of which the only surviving species is the Asian elephant (*Elephas maximus*), a genus of Pleistocene three-toed horses, a Pleistocene camel, and a Pleistocene bison. Since about 11.5 ka, the haartebeest, a genus of African buffalo (*Parmularius*), and the genus of modern cattle (*Bos*) became extinct in Africa. Thus, the African megafauna suffered the loss of only about 14% of their genera in the last 100 kyr – the smallest faunal decline of any continent.

Eurasia

Eurasia, like Africa, suffered relatively few megafaunal extinctions in the Late Pleistocene (Table 6). Of the ten genera that died out, one became extinct sometime between 100 and 50 ka (the straight-tusked elephant), one was extirpated from Europe (the hippopotamus), and two more became extinct between 50 and 16 ka (the interglacial rhinoceros, *Stephanorhinus*, a cave bear, *Ursus spelaeus*, and a heavy-bodied, Asian antelope, *Spirocerus*) (Barnowsky *et al.*, 2004). The spotted hyena, woolly rhinoceros (Fig. 5B), and mammoths (Fig. 5A) died out in Eurasia between 16 and 11.5 ka, except for the Wrangel Island mammoth population, discussed above. Finally, the musk ox (*Ovibos*) and giant deer (*Megaloceros*) (Fig. 5C) became extinct after 11.5 ka. Recent research has shown that the giant deer survived until about 7.7 ka in western Siberia, more than 300 yr after it was previously thought to have died out (Stuart *et al.*, 2004). Such revisions for the age of extinction will undoubtedly continue to push extinction dates into younger time horizons in the coming years.

Late Pleistocene archeological sites at Mezlin, Mezhirich, and elsewhere in the Ukraine were

Table 3 Timing of extinction of the North American Pleistocene megafauna

| <i>Taxon</i> | <i>Common name</i> | <i>Last 100 ka</i> | <i>100–50 ka</i> | <i>50–16 ka</i> | <i>16–11.5 ka</i> | <i>11.5–0 ka</i> | <i>Reference</i> |
|-----------------------|----------------------------|--------------------|------------------|-----------------|-------------------|------------------|-------------------------------|
| Mammalia | | | | | | | |
| Xenarthra | | | | | | | |
| Glyptodontidae | | | | | | | |
| Glyptotherium | | X | | | | | Martin and Steadman, 1999 |
| Megalonychidae | | | | | | | |
| <i>Megalonyx</i> | Ground sloth | | | | X | | Stuart, 1991 |
| Megatheriidae | | | | | | | |
| <i>Eremotherium</i> | Giant ground sloth | X | | | | | Martin and Steadman, 1999 |
| <i>Nothrotheriops</i> | Shasta ground sloth | | | | X | | Stuart, 1991 |
| Mylodontidae | | | | | | | |
| <i>Glossotherium</i> | Giant ground sloth | | | X | | | Stuart, 1991 |
| Pampatheriidae | | | | | | | |
| <i>Pampatherium</i> | Pampas ground sloth | | | | X | | Johnson, 1987 |
| Rodentia | | | | | | | |
| Castoridae | | | | | | | |
| <i>Castoroides</i> | Giant beaver | | | | X | | Steadman <i>et al.</i> , 1997 |
| Hydrochoeridae | | | | | | | |
| <i>Hydrochaeris</i> | Capybara | X | | | | | Martin and Steadman, 1999 |
| <i>Nechoerus</i> | | X | | | | | Martin and Steadman, 1999 |
| Carnivora | | | | | | | |
| Ursidae | | | | | | | |
| <i>Arctodus</i> | Short-faced bear | | | | X | | Stuart, 1991 |
| <i>Tremarctos</i> | Spectacled bear | | | | X | | Emslie and Morgan, 1995 |
| Felidae | | | | | | | |
| <i>Homotherium</i> | Sabertoothed cat | | | X | | | FAUNMAP, 2003 |
| <i>Miracinonyx</i> | American cheetah | | | | X | | Emslie, 1986 |
| <i>Panthera</i> | Lion | | | | X | | Stuart, 1991 |
| <i>Smilodon</i> | Sabertoothed cat | | | | X | ? | Stuart, 1991 |
| Proboscidea | | | | | | | |
| Elephantidae | | | | | | | |
| <i>Mammuthus</i> | Mammoth | | | | X | ? | Stuart, 1991 |
| Gomphotheriidae | | | | | | | |
| <i>Cuvieronius</i> | Mastodon-like proboscidean | | | X | | | Koch <i>et al.</i> , 1998 |
| Mammutidae | | | | | | | |
| <i>Mammut</i> | Mastodon | | | | X | ? | Stuart, 1991 |
| Perissodactyla | | | | | | | |
| Equidae | | | | | | | |
| <i>Equus</i> | Horse | | | | X | | Stuart, 1991 |
| Tapiridae | | | | | | | |
| <i>Tapirus</i> | Tapir | | | | X | | Beck, 1996 |
| Artiodactyla | | | | | | | |
| Tayassuidae | | | | | | | |
| <i>Mylohyus</i> | Peccary | | | | X | | Stuart, 1991 |
| <i>Platygonus</i> | Flat-headed peccary | | | | X | | Stuart, 1991 |
| Camelidae | | | | | | | |
| <i>Camelops</i> | Camel | | | | X | | Stuart, 1991 |
| <i>Hemiauchenia</i> | Prehistoric llama | | | | X | | Stuart, 1991 |
| <i>Paleolama</i> | Pleistocene llama | | | | X | | Stuart, 1991 |

(Continued)

Table 3 (Continued)

| Taxon | Common name | Last 100 ka | 100–50 ka | 50–16 ka | 16–11.5 ka | 11.5–0 ka | Reference |
|----------------------|---------------------------|----------------|-----------|----------|------------|-----------|---------------------------|
| Cervidae | | | | | | | |
| <i>Bretzia</i> | Pleistocene deer | X | | | | | Martin and Steadman, 1999 |
| <i>Cervalces</i> | Stag-moose | | | | X | | Stuart, 1991 |
| <i>Navahoceros</i> | Pleistocene mountain deer | X | | | | | Martin and Steadman, 1999 |
| <i>Torontoceros</i> | Pleistocene caribou | X | | | | | Martin and Steadman, 1999 |
| Antilocapridae | | | | | | | |
| <i>Stockoceros</i> | Four-homed pronghorn | X | | | | | Martin and Steadman, 1999 |
| <i>Tetrameryx</i> | Pronghorn | X | | | | | Martin and Steadman, 1999 |
| Bovidae | | | | | | | |
| <i>Bootherium</i> | Helmeted musk ox | X | | | | | Martin and Steadman, 1999 |
| <i>Euceratherium</i> | | | | | X | | Stuart, 1991 |
| <i>Saiga</i> | Saiga antelope | X | | | | | Martin and Steadman, 1999 |

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originally held up as evidence of large-scale hunting of woolly mammoths, because the huts built by ice age hunters were made almost exclusively of carefully piled mammoth bones. For instance, the Mezhirich site contains the stacked bones of at least 149 individual mammoths. The bones subsequently yielded radiocarbon ages ranging from 22 to 14 ¹⁴C kyr BP (Lister and Bahn, 1997). Upon closer inspection, they were found to be in various states of preservation, and many had been gnawed by carnivores. It now appears that the humans who made shelters from mammoth bones had not killed the mammoths in massive attacks, but had rather collected most, if not all, of the bones of dead mammoths from the treeless landscape for use as building materials. The bone huts thus bear testimony to a huge, thriving mammoth population in this region during the Late Pleistocene.

Theories on the Causes of Late Pleistocene Extinction

To return to a question posed earlier, why should some regions of the world have been relatively immune from megafaunal extinctions, while others suffered losses of up to 80% of their large animal genera? What can we glean from the geographic patterns discussed above? Finally, what role, if any, did human beings play in the demise of these large animals? The last question has driven the study of the Late Pleistocene megafaunal extinctions in the last 40 yr. Researchers who have

worked on this topic seem to be divided into two main camps: those who believe that humans played a significant role in these extinctions, and those who lay the blame on natural environmental change. As we shall see, the debate has become quite heated at times, with some of the environmental-change champions (perhaps prematurely?) declaring victory over their opponents in the human-induced extinction camp.

Martin's Pleistocene Overkill Hypothesis

In 1967, paleontologist Paul Martin wrote a highly influential chapter entitled 'Prehistoric Overkill' for a book entitled *Pleistocene Extinctions, the Search for the Cause*. In this publication, and in his subsequent (1984) book chapter, he propounded the theory that humans were the chief cause of Late Pleistocene megafaunal extinctions. Martin's theory rested on several tenets that have since been attacked by other authors. He argued that (1) the large Pleistocene mammals were decimated in these extinctions; (2) small mammals (except on islands) were relatively untouched by extinction during the Late Pleistocene; (3) large mammals survived best in Africa; (4) the extinctions were often quite sudden; (5) the extinctions took place at different times on different continents; (6) the extinctions occurred without replacement by new taxa; (7) the extinctions followed in man's footsteps; and (8) the archeology of extinction is obscure. Martin argued that large mammals were the preferred prey of Paleolithic hunters who specialized in big game hunting. Species living in continents not previously

Table 4 Timing of extinction of the South American Pleistocene megafauna

| <i>Taxon</i> | <i>Common name</i> | <i>Last 100 ka</i> | <i>100–50 ka</i> | <i>50–16 ka</i> | <i>16–11.5 ka</i> | <i>11.5–0 ka</i> | <i>Reference</i> |
|----------------------------|-------------------------|------------------------|----------------------|---------------------|-----------------------|----------------------|---------------------------------|
| MAMMALIA | | | | | | | |
| Xenarthra | | | | | | | |
| Dasypodidae | Pleistocene armadillos | | | | | | |
| <i>Eutatus</i> | | | | | X | | Vizcaino <i>et al.</i> , 2003 |
| <i>Propaopus</i> | | | | | X | | Faure <i>et al.</i> , 1999 |
| Glyptodontidae | Pleistocene glyptodonts | | | | | | |
| <i>Chlamydotherium</i> | | | | | X | | Ficcarelli <i>et al.</i> , 2003 |
| <i>Doedicurus</i> | | | | | X | | Borrero <i>et al.</i> , 1998 |
| <i>Glyptodon</i> | | | | | X | | Faure <i>et al.</i> , 1999 |
| <i>Heteroglyptodon</i> | | X | | | | | McKenna and Bell, 1997 |
| <i>Hoplophorus</i> | | | | | | X | Faure <i>et al.</i> , 1999 |
| <i>Lomaphorus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Neosclerocalyptus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Neothoracophorus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Parapanochthus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Panochthus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Plaxhaplous</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Sclerocalyptus</i> | | X | | | | | Martin and Steadman, 1999 |
| Megalonychidae | Two-toed sloths | | | | | | |
| <i>Valgipes</i> | | X | | | | | Martin and Steadman, 1999 |
| Megatheriidae | | | | | | | |
| <i>Eremotherium</i> | Giant ground sloth | | | | X | | Ficcarelli <i>et al.</i> , 2003 |
| <i>Megatherium</i> | Giant ground sloth | | | | X | | Borrero <i>et al.</i> , 1998 |
| <i>Nothropus</i> | Aquatic sloth | X | | | | | Martin and Steadman, 1999 |
| <i>Nothrotherium</i> | Ground sloth | X | | | | | Martin and Steadman, 1999 |
| <i>Ocnopus</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Perezfontanatherium</i> | Ground sloth | X | | | | | McKenna and Bell, 1997 |
| Mylodontidae | | | | | | | |
| <i>Glossotherium</i> | Giant ground sloth | | | | X | | Coltorti <i>et al.</i> , 1998 |
| <i>Lestodon</i> | Giant ground sloth | X | | | | | Martin and Steadman, 1999 |
| <i>Mylodon</i> | Giant ground sloth | | | | X | | Borrero, 2003 |
| Pampatheriidae | | | | | | | |
| <i>Pampatherium</i> | Pampas ground sloth | X | | | | | Martin and Steadman, 1999 |
| Scelidotheriidae | | | | | | | |
| <i>Scelidotherium</i> | Sloth | | | | X | | Ficcarelli <i>et al.</i> , 2003 |
| Litopterna | | | | | | | |
| Macrauchiidae | | | | | | | |
| <i>Macrauchenia</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Windhausenia</i> | | X | | | | | Martin and Steadman, 1999 |
| Notoungulata | | | | | | | |
| Toxodontidae | | | | | | | |

(Continued)

Table 4 (Continued)

| Taxon | Common name | Last 100 ka | 100–50 ka | 50–16 ka | 16–11.5 ka | 11.5–0 ka | Reference |
|----------------------|----------------------------|----------------|--------------|-------------|---------------|--------------|---------------------------------|
| <i>Mixotoxodon</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Toxodon</i> | | | | | X | | Martinez, 2001 |
| Rodentia | | | | | | | |
| Hydrochoeridae | | | | | | | |
| <i>Nechoerus</i> | Capybara | | | | | X | Ficcarelli <i>et al.</i> , 2003 |
| Octodontidae | | | | | | | |
| <i>Dicolpomys</i> | | X | | | | | Martin and Steadman, 1999 |
| Carnivora | | | | | | | |
| Canidae | | | | | | | |
| <i>Theriodictis</i> | Wolf-like canid | X | | | | | Martin and Steadman, 1999 |
| Felidae | | | | | | | |
| <i>Smilodon</i> | Sabertoothed cat | | | | | | Ficcarelli <i>et al.</i> , 2003 |
| Ursidae | | | | | | | |
| <i>Arctodus</i> | Short-faced bear | X | | | | | Martin and Steadman, 1999 |
| Proboscidea | | | | | | | |
| Gomphotheriidae | | | | | | | |
| <i>Cuvieronius</i> | Mastodon-like proboscidean | | | | X | | Dillehay and Collins, 1991 |
| <i>Haplomastodon</i> | Mastodon-like proboscidean | | | | | X | Ficcarelli <i>et al.</i> , 2003 |
| <i>Notiomastodon</i> | Mastodon-like proboscidean | X | | | | | Martin and Steadman, 1999 |
| <i>Stegomastodon</i> | Mastodon-like proboscidean | | | | X | | Núñez <i>et al.</i> , 1994 |
| Perissodactyla | | | | | | | |
| Equidae | | | | | | | |
| <i>Equus</i> | Horse | | | | | X | Ficcarelli <i>et al.</i> , 2003 |
| <i>Hippidion</i> | Pleistocene horse | | | | X | | Alberdi <i>et al.</i> , 2001 |
| <i>Onohippidion</i> | Pleistocene horse | | | | | | Martin and Steadman, 1999 |
| Artiodactyla | | | | | | | |
| Camelidae | | | | | | | |
| <i>Eulamaops</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Hemiauchenia</i> | Prehistoric llama | | | | X | | Martinez, 2001 |
| <i>Palaeolama</i> | Pleistocene llama | | | | | X | Faure <i>et al.</i> , 1999 |
| Cervidae | | | | | | | |
| <i>Agalmaceros</i> | Pleistocene deer | X | | | | | Martin and Steadman, 1999 |
| <i>Antifer</i> | March deer | | | | X | | Núñez <i>et al.</i> , 1994 |
| <i>Charitoceros</i> | | X | | | | | Martin and Steadman, 1999 |
| <i>Morenelaphus</i> | Pampas deer | X | | | | | Martin and Steadman, 1999 |
| Tayassuidae | | | | | | | |
| <i>Platygonus</i> | Flat-headed peccary | X | | | | | Martin and Steadman, 1999 |

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inhabited by people would have had little or no fear of humans, making them easier to kill. For the continents of North and South America and Australia, newly colonized by humans during the last ice age, Martin envisioned waves of human hunters, fanning out

across new lands, killing the large mammals in a 'blitzkrieg,' thus bringing on megafaunal extinction. Such decimation failed to occur in Eurasia and Africa precisely because humans had been hunting on these continents for hundreds of thousands of years. Hence

Table 5 Timing of extinction of the African Pleistocene megafauna

| Taxon | Common name | Last 100 ka | 100–50 ka | 50–16 ka | 16–11.5 ka | 11.5–0 ka | Reference |
|----------------------|----------------------|-------------|-----------|----------|------------|-----------|--------------------------------|
| Mammalia | | | | | | | |
| Proboscidea | | | | | | | |
| Elephantidae | | | | | | | |
| <i>Elephas</i> | Pleistocene elephant | X | | | | | Martin, 1984 |
| Perissodactyla | | | | | | | |
| Equidae | | | | | | | |
| <i>Hipparion</i> | Hipparion | X | | | | | Martin, 1984 |
| Artiodactyla | | | | | | | |
| Camelidae | | | | | | | |
| <i>Camelus</i> | Camel | X | | | | | Martin, 1984 |
| Cervidae | | | | | | | |
| <i>Megacerooides</i> | Giant deer | | | | | | Martin, 1984 |
| Bovidae | | | | | | | |
| <i>Megalotragus</i> | Haartebeest | | | | | X | Lee-Thorp <i>et al.</i> , 1995 |
| <i>Pelorovis</i> | Pleistocene buffalo | | | | | X | Klein, 1994 |
| <i>Parmularius</i> | Pleistocene bison | X | | | | | Martin, 1984 |
| <i>Bos</i> | Pleistocene bison | | | | | X | McKenna and Bell, 1997 |

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Table 6 Timing of extinction of the Eurasian Pleistocene megafauna

| Taxon | Common name | Last 100 ka | 100–50 ka | 50–16 ka | 16–11.5 ka | 11.5–0 ka | Reference |
|-----------------------|--------------------------|-------------|-----------|----------|------------|-----------|--------------|
| Mammalia | | | | | | | |
| Carnivora | | | | | | | |
| Hyaenidae | | | | | | | |
| <i>Crocuta</i> | Hyena | | | | X | | Stuart, 1991 |
| Proboscidea | | | | | | | |
| <i>Mammuthus</i> | Mammoth | | | | X | | Stuart, 1991 |
| <i>Palaeoloxodon</i> | Straight-tusked elephant | | X | | | | Stuart, 1991 |
| Perissodactyla | | | | | | | |
| Rhinocerotidae | | | | | | | |
| <i>Stephanorhinus</i> | Rhinoceros | | | X | | | Stuart, 1991 |
| <i>Coelodonta</i> | Woolly rhinoceros | | | | X | | Stuart, 1991 |
| Artiodactyla | | | | | | | |
| Hippopotamidae | | | | | | | |
| <i>Hippopotamus</i> | Hippopotamus | | X | | | | Stuart, 1991 |
| Camelidae | | | | | | | |
| <i>Camelus</i> | Camel | | | | ? | | Stuart, 1991 |
| Cervidae | | | | | | | |
| <i>Megaloceros</i> | Giant deer | | | | | X | Stuart, 1991 |
| Bovidae | | | | | | | |
| <i>Spirocerus</i> | Antelope | | | X | | | Stuart, 1991 |
| <i>Ovibos</i> | Musk ox | | | | | X | Stuart, 1991 |

After Barnowsky AD, Koch PL, Feranec RS, Wing SL, and Shabel AB (2004) Assessing the causes of Late Pleistocene extinctions on the continents. *Science* 306: 70–75.

the megafauna of Eurasia and Africa, wary of human predation, were not as easily killed.

Few subsequent authors have not really argued with Martin’s points 1, 2, 3, 5, 6, and 8. The chief arguments have been over points 4 and 7, which are the most controversial because the evidence concerning them is

so difficult to pin down. Let us deal with points 4 and 7 as best we can, in light of recent investigations.

The Environmental change Hypothesis

The suddenness of the extinction events has been called into question by a number of authors. Grayson (1987)

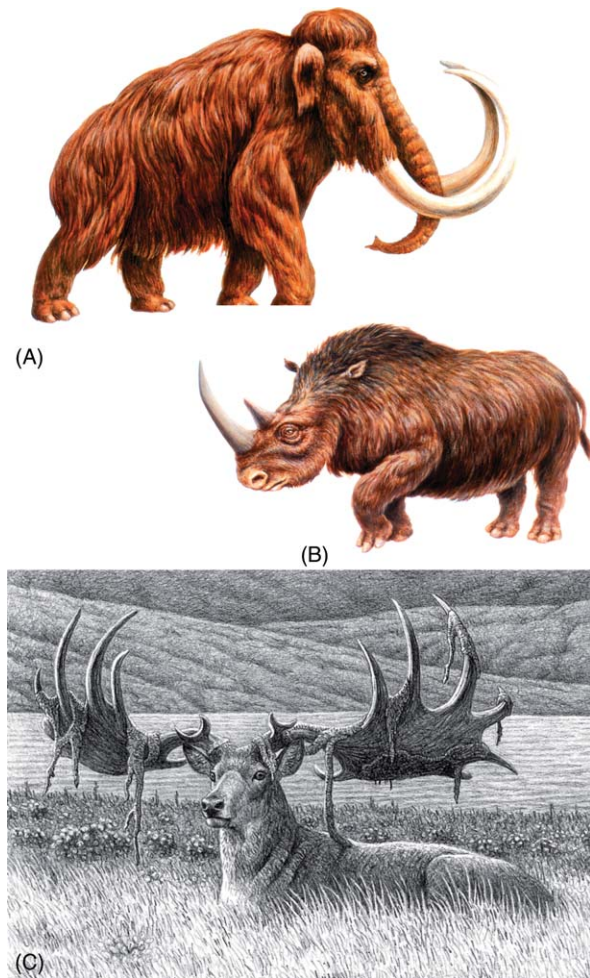


Figure 5 European megafaunal species that became extinct in the late Pleistocene or Holocene. (A) *Mamthus primigenius* from Lange (2002), p. 176; (B) *Coelodonta antiquatus* from Lange (2002), p. 136; (C) *Megaloceros giganteus* Art by Mauricio Anton (A, B) Reproduced from Lange IM (2002) *Ice Age Mammals of North America. A Guide to the Big, the Hairy, and the Bizarre*. Mountain Press Publishing Company; (C) image supplied courtesy of Mauricio Anton.

began his attack on the megafaunal overkill theory shortly after Martin's major work on the subject was published. Arguing from the North American data, he suggested that the numbers of individuals of megafaunal species may already have dwindled before 14 ka, and that many of the genera that have yet to be dated to terminal Wisconsin (last glacial) times may not have survived beyond 14 ka. In the almost 20 yr since this article was written, a considerable number of new radiocarbon ages have been established for last known examples of many North American megafaunal species. By the late 1990s, a suite of 140 AMS ^{14}C dates had been done on proteins extracted from fossil bones of North American megafaunal mammals that died near the end of the last glaciation. The results of that study were quite startling (Elias, 1999). It appears that the major

megafaunal extinction event took place at 13.3 ka (11.400 ^{14}C kyr BP). This event included the extinction of camels, horses, giant sloths, Pleistocene bison, and all other genera of megafaunal mammals that did not survive into the Holocene, with the exception of the proboscideans. Mammoths and mastodons persisted until about 12.85–12.83 ka (10.9–10.85 ^{14}C kyr BP). So it now appears that there were two distinct extinction episodes in North America. Each event took less than 100 yr.

The older event may have taken place before, during, or just after the first appearance of Clovis artifacts in the archeological record. The Clovis culture is the first widely accepted human occupation in the ice-free regions of North America. The most recent evaluation of the age of Clovis sites in North America (Taylor *et al.*, 1996) places the beginning of this culture about 13.5 ka (11.5 ^{14}C kyr BP). If the people who used Clovis tools arrived in North America at that time, then they overlapped only very briefly with the many megafaunal mammal species. Is there a cause and effect, here, or a coincidence? There is good evidence that Clovis hunters killed and butchered mammoth and mastodon, the megafaunal species that died out a few centuries later. Whether human predation was responsible for the proboscidean extinction remains an open question.

In their 2003 review of the topic, Grayson and Meltzer argue that Martin's overkill model does not work for North America, because there is virtually no evidence that supports it, and there is a large body of evidence that argues against it. The lack of archeological evidence for overkill is something that Martin himself predicted in point 8 of his overkill theory. He argued that the extinction event took place so rapidly that it would have left little or no trace on the landscape. Paleoindians were apparently nomadic people, and their wanderings left few permanent marks on the landscape in any case. It is difficult, at best, to argue from negative evidence, and Grayson and Meltzer (2003) castigate Martin for doing so, but Fiedel and Haynes (2003), in their response to Grayson and Meltzer's article, point out that large animal bones have rarely if ever been found in any North American archeological sites, spanning the past 12.5 radiocarbon kyr. Therefore if no Holocene 'big game hunting' sites can be found, one cannot expect the Pleistocene to be any better represented.

Another open-ended question that affects this debate concerns the time of arrival of humans in the Americas. The traditional 'Clovis-first' view was prevalent when Martin formulated his overkill theory. In the past 20 years, a number of candidate archeological sites have come to light that indicate a pre-Clovis occupation of the Americas, the strongest of which is the Monte Verde site in Chile (Dillehay, 1997). Evidence from this site

unequivocally places people in South America by 15 cal kyr BP. *Bona fide* pre-Clovis sites have been more difficult to document in North America. Sites such as Meadowcroft, Pennsylvania (Adovasio and Carlisle, 1984), Cactus Hill, Virginia, and Mud Lake, Wisconsin (Falk, 2004) offer tantalizing, if controversial, evidence that people may have been in North America 15–20 ka. If these claims can be substantiated, then Martin's theory would be considerably weakened, as one of its principal tenets ('extinction followed in man's footsteps') would be invalidated.

Meanwhile, in Australia, the debate about Pleistocene overkill likewise rages on. In 1999, Miller *et al.* discussed evidence for the extinction of the large, flightless bird, *Genyornis*, dating this extinction to 50 ka, based on ages from fossil eggshells. They argued that people had arrived in Australia by this time, and that humans were either directly responsible for the demise of *Genyornis* and other Australian megafauna, or indirectly responsible. The latter argument asserts that the early human inhabitants of Australia set fire to large tracts of grassland, in order to boost grassland productivity at the expense of trees and shrubs, and that this caused the collapse of long-established elements of the ecosystem, including the demise of browsers that relied on tree and shrub vegetation for food. In the Miller *et al.* (1999) argument, the demise of megafaunal predators followed the extinction of their large herbivore prey. Roberts *et al.* (2001) also discussed evidence from 27 sites that a continent-wide extinction event took place in Australia, about 46 ka.

However, the environmental change camp also has its champions in Australia. Wroe *et al.* (2004) argued that no megafaunal kill sites have been found in Australia, and that it is probable that early human populations were too small to bring about rapid extinctions of large mammals. They also argued that more recent evidence from the Cuddie Springs site indicates that *Genyornis* did not die out there until 40 ka. Johnson (2005) takes the middle ground between the two extreme views when he argues that, despite evidence for younger ages of extinctions in various parts of Australia, 'the evidence supports overkill, not climate change, as the cause of the extinctions.' For obvious reasons, he rejects the 'blitzkrieg' model of extinction, but supports humans as the cause, albeit on a slower timescale.

The Hyperdisease Theory

An alternative theory for megafaunal extinction has been proposed by MacPhee and Marx (1997). In their theory, a particularly virulent strain of an unknown, deadly disease was able to make the

jump from one mammal species to another, becoming a hyperdisease that wiped out the megafauna. In the hyperdisease theory, humans may have carried the source of infection from one continent to another as they spread across the world. If the pathogen was able to infect immunologically vulnerable populations of mammals, it would have caused rapid population crashes, possibly leading to extinction. Humans were not necessarily the carriers of such a disease. The carriers could have varied from place to place, following in the footsteps of human colonization. MacPhee and Marx include rats or fleas, or parasites of rats and fleas on their list of potential disease vectors. As of this writing, no firm evidence has been found to support this theory.

Can We find the Smoking Gun?

The indisputable evidence for human-caused extinction of megafauna during the Late Pleistocene, the so-called 'smoking gun' (or perhaps 'blood-dripping spear' would be a better metaphor), will probably never be found. There are several reasons for this:

- (1) Both the faunal and archeological evidence are fragmentary in nature. We will never have a complete picture of what happened. This will always leave room for debate.
- (2) The dating of events will never be exact. Radiometric dating is the only way to date most paleontological or archeological sites, and all radiometric dates come with uncertainties. In this sense, they are not true ages, as one would get from counting back annually layered sediments or tree rings. They remain age estimates, plus or minus centuries of time (when dealing with ages that are tens of thousands of years before present).
- (3) The early peoples of all the inhabited continents were hunter-gatherers who were mostly nomadic in lifestyle. They left pitifully little evidence of their occupation in the first place; what remains *in situ* after tens of thousands of years of decomposition, erosion, reworking of sediments, etc., will always be just a tiny fraction of the original material, be it mammal bones or human artifacts.

One scenario that would seem to fit the most facts, might be a *coup de grâce* model. In this model, human predation contributes to the demise of the Pleistocene megafauna, to some degree. Science has yet to determine the extent of human influence on megafaunal extinction, but it seems most likely that humans played a larger role in some regions than in others. The modeling efforts of Alroy (2001) and Brook and Bowman (2002) were at least more dispassionate attempts to deal with the data in hand. In

the coming decades, we may begin to approach a consensus, but it seems very doubtful that the definitive answers will ever be obtained.

See also: Vertebrate Overview. Vertebrate Records: Late Pleistocene of Africa; Late Pleistocene of North America; Late Pleistocene of Northern Asia; Late Pleistocene of South America; Late Pleistocene of Southeast Asia.

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Mid-Pleistocene of Africa

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The mammalian fauna of the African continent has undergone many changes during the Neogene. Most of these occurred by the end of the Pliocene and the beginning of the Pleistocene, when the African predator guild attained its modern composition and structure, driven principally by the extinction of saber-toothed cats on the continent and the disappearance

of the more archaic hyenas (Turner, 1990, 1995a; Turner and Antón, 1999). Other archaic elements of the African megafauna, such as the deinotheres, gomphotheres, and chalicotheres, also disappeared at approximately the same time. While the hominin genus *Paranthropus* went extinct, ungulates such as pigs and giraffes became less diverse and the three-toed hipparion horses became rare (Turner and Wood, 1993; Turner and Antón, 2004). In contrast, Migrants to Africa in the Pliocene and more recently thrived, adding more variety to the indigenous fauna. African faunas thus appear more modern at a much earlier date, in contrast to the situation in Eurasia and the New World, where archaic forms survived until the Holocene and the appearance of modern faunas is a very recent phenomenon. The living African mammal fauna can thus be considered largely a Pliocene relict.

Nevertheless, at the beginning of the Pleistocene the structure and composition of faunas still differed in several important ways from the pan-African fauna of today (Turner and Antón, 2004). Werdelin and Lewis (2005) suggested that this difference may have been even more marked than previously thought, at least with regard to the Carnivora. They argued that extant taxa such as the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and spotted hyena (*Crocuta crocuta*) can only be traced back to the Pliocene at the genus level at best, at least in eastern Africa, instead of at the species level as previously argued by Turner (1990). They also cast doubt on previous arguments for the extinction of the machairodont cats at approximately 1.5 Ma as proposed by Turner and Antón (1999, 2004) and for the interpretations of turnover in the guild of larger Carnivora also proposed by these authors. These differences in viewpoint stem in part from differences in the tendency to split rather than lump taxa, and they will always be a part of paleontological debate. However, arguments for the splitting of the genus *Crocuta* in particular are founded in large part on unpublished data (Werdelin and Lewis, 2005, p. 128) and are therefore difficult to address. They also do not take into account the South African record.

However this difference in viewpoints is resolved, it remains true that the nature and pattern of changes within the African Pleistocene have been poorly understood, largely because well-dated deposits such as those of eastern Africa that provide our picture of Pliocene events are relatively rare or information about them is unpublished. For these reasons, relatively little synthesis of Pleistocene faunal evolution has been attempted. Fortunately, this situation is now changing, and in recent years details of several sites have appeared or the material has been reanalyzed and deposits have