

NORTH AMERICAN URSID (MAMMALIA: URSIDAE) DEFAUNATION FROM PLEISTOCENE TO RECENT

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Abstract

North America had a large and varied biodiversity during the Quaternary, including the carnivore family Ursidae (Mammalia, Carnivora) that during the Pleistocene was quite varied, but by the Late Pleistocene into the Holocene, it went into a defaunation process. At least seven species occurred in Mexico and to the north, including two subfamilies, Tremarctinae and Ursinae. The first one had at least four species, including two within the short-faced bear *Arctodus*, one in the spectacled bear *Tremarctos*, and another undescribed, all of which are extinct but the Andean bear *Tremarctos ornatus* that presently lives in South America. Three ursine species are extant, but populations and distribution range have diminished. The polar bear *Ursus maritimus* now has a high extinction risk, along with the grizzly bear *U. arctos*. The black bear *U. americanus*, however, is increasing in some areas of its range. Extinction patterns are reviewed, with examples of some human-bear interactions.

Resumen

Norteamérica tuvo una gran y variada biodiversidad durante el Cuaternario, incluyendo la familia de carnívoros Ursidae (Mammalia, Carnivora) que durante el Pleistoceno fue más variada, pero en el Pleistoceno Tardío y el Holoceno, atravesó un proceso de defaunación. Hubo al menos siete especies que se distribuían de México hacia el norte, incluyendo dos subfamilias, Tremarctinae y Ursinae. La primera tuvo al menos cuatro especies, incluyendo dos dentro del oso de cara corta *Arctodus*, una de osos de anteojos *Tremarctos* y otra aún no descrita, de las cuáles todas se extinguieron con excepción del oso andino *Tremarctos ornatus* que sobrevive en Sudamérica. Las tres especies de ursinos aún existen, pero sus poblaciones y su amplitud distribucional ha disminuido, con el oso polar *Ursus maritimus* que se halla en gran riesgo de extinción, así como el oso gris *U. arctos*, mientras que el oso negro *U. americanus* tiene poblaciones que han aumentado en algunas regiones dentro de su distribución. Los patrones de extinción se revisan, con ejemplos de algunas interacciones humano-osos.

Samenvatting

Noord-Amerika bezat tijdens het Kwartair een grote biodiversiteit met onder meer de carnivore familie Ursidae (Mammalia, Carnivora). In het Pleistoceen was deze familie vrij gevarieerd, maar in het Laat-Pleistoceen en Holoceen vertoont ze een sterk afname. Er kwamen tenminste zeven soorten voor in en ten noorden van Mexico, bestaande uit twee subfamilies, Tremarctinae and Ursinae. De eerste bestond uit minstens vier soorten, waaronder twee in het geslacht kortsnuitbeer *Arctodus*, één brilbeer *Tremarctos* en verder een nog onbeschreven soort. Deze zijn allen uitgestorven met uitzondering van de brilbeer *Tremarctos ornatus* die tegenwoordig nog in Zuid-Amerika voorkomt. De subfamilie Ursinae kent momenteel drie soorten, maar het aantal en de verspreiding zijn sterk afgenomen. De ijsbeer *Ursus maritimus* wordt het meest bedreigd, net als de Grizzly beer *U. arctos*; alleen de zwarte beer *U. americanus* vertoont in bepaalde delen van zijn verspreidingsgebied een toename in aantal. Patronen van uitsterven worden besproken met enkele voorbeelden van interactie tussen beren en mensen.

INTRODUCTION

One of the most outstanding contributions in the past 25 years to biological studies is the proposal of the biodiversity concept. That concept states "...the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (UN Convention on Biological Diversity, 1992). Biodiversity

includes all life forms living on Earth through time, from microbes to higher vertebrate classes. The North American subcontinent has a high biodiversity that constitutes a unique biogeographic realm, the Nearctic. Furthermore, some countries, such as Mexico in North America, are named as megadiverse because they contain within their borders at least 70% of the world species diversity. In some cases, like Mexico, at least 10% of described species are known from that country (McNeely *et al.*, 1990).

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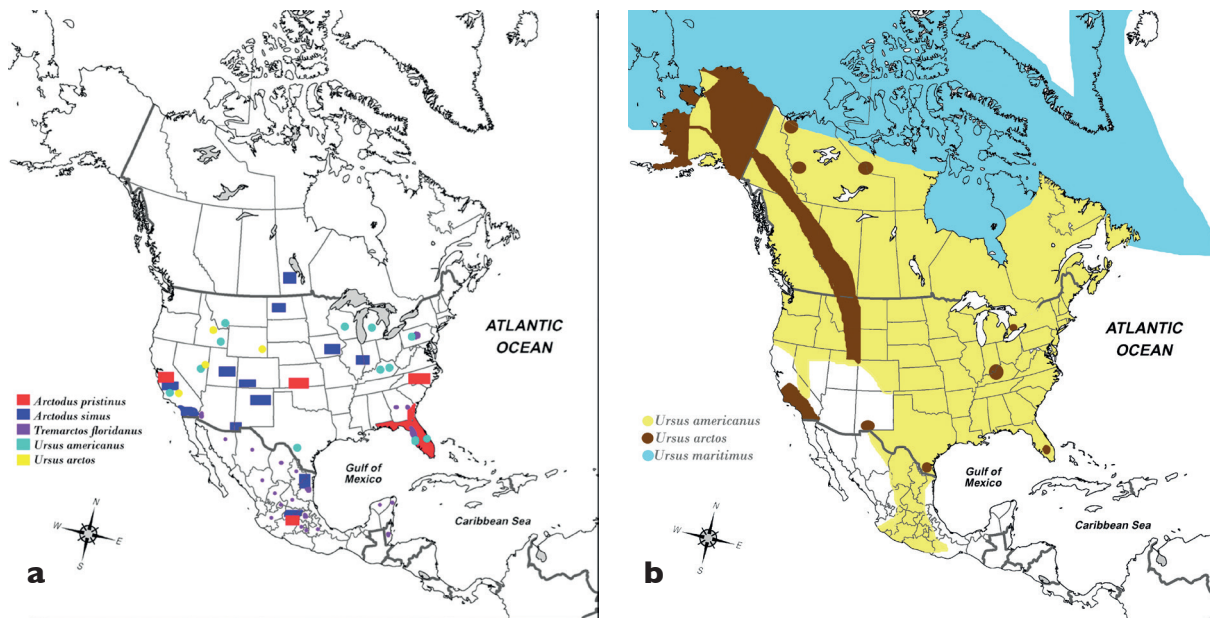


Figure 1: North American maps showing Quaternary (a) and current (b) ursid species distribution

Figuur 1: Kaarten van Noord-Amerika met verspreiding van kwartaire en recente berensoorten

That same pattern may have occurred in the past, at least in near geological times, such as the Pleistocene. Mexico had a quite diverse Quaternary fauna composed of 13 orders, 44 families, and 280 species (Ferrusquía-Villafranca *et al.*, 2010), while North America north of Mexico had 297 species (Kurtén & Anderson, 1980). That pattern most likely is due to both geophysical and historical factors. Geophysical factors include the highly diverse topography, climate, and vegetation. Historical factors include the Great American Biotic Interchange, Last Glacial Maximum, first entry of humans into the Americas, extinction-driven faunal changes, and European human-companion fauna in the latest Holocene (Kidwell, 2015).

In the past 500 years, humans have triggered a wave of extinction, threats, and local population declines that have been compared in both rate and magnitude with the five previous mass extinctions of Earth's history. Others are not convinced. Similar to other mass extinction events, the effects of this "sixth extinction wave" extend across taxonomic groups, but the extinction events also are selective, with some taxonomic groups and regions being particularly affected (Dirzo *et al.*, 2014). This claim adds to the anthropological models for explaining Late Pleistocene extinctions, especially the overkill hypothesis. Here, evidence is reviewed for one such group for the Americas, the ursids.

QUATERNARY BEAR FAUNA

The Family Ursidae (Mammalia, Carnivora) has occurred in North America from the Late Eocene (Chadronian) to the present, with perhaps its greatest diversity during the Late Pleistocene. In the past, four subfamilies inhabited the Americas, these being Amphicyonodontinae, Hemicyoninae, Tremarctinae, and Ursinae (McLellan & Reiner, 1994; Hunt, 1998). The first two, now raised to the family level (McKenna & Bell, 1997), are quite diverse in the Tertiary and are extinct now. The third one still survives in South America and the fourth in North America. The three living ursine bears represent only a fraction of the diversity that has been discovered in the North American fossil record (Hunt, 1998). Most of the fossil record is assigned to the tremarctine bears with at least four extinct genera (Fig. 1a, Table 1).

North American species today include the black bear, *Ursus americanus*, and the Grizzly or brown bear, *U. arctos*. Black bears have been known in North America for the last three million years (Kurtén & Anderson, 1980) whereas the

brown bear immigrated to North America sometime after 100 ka (Kurtén & Anderson, 1980; McLellan & Reiner, 1994). The polar bear, *U. maritimus*, has a circumpolar distribution, and only recently appeared in North America (sometime in the Late Pleistocene to early Holocene, i.e., most likely during the Younger Dryas Chronozone; Anderson, 1984; Vincent, 1989) (Fig. 1b). Some authors recognize the polar bear as the monotypic genus *Thalarchos* (McKenna & Bell, 1997).

American black bears are found throughout much of Canada, the United States, and the northern half of Mexico. Although they were extirpated from large portions of their historic range because of habitat loss and intentional overexploitation, their occupied range has been expanding in recent years (Pelton *et al.*, 1999; Williamson, 2002). The species, nevertheless, has been extirpated from large parts of its former range, especially in the Midwest of the United States, and in Mexico. American black bears presently occupy all provinces and territories of Canada, except Prince Edward Island (where they were extirpated in 1937), 41 U.S. states (with occasional sightings in at least three others), and 12 states of northern Mexico, as far south as the State of Hidalgo, to the northeast of Mexico City (Hall, 1981; Rojas-Martínez & Juárez-Casillas, 2013). A Late Pleistocene

Family Ursidae

Subfamily Tremarctinae (extinct)

Arctodus pristinus Leidy, 1854

Arctodus simus (Cope, 1879)

Tremarctos floridanus (Gidley, 1928)

Unnamed tremarctine

Subfamily Ursinae

Ursus americanus Pallas, 1780

Ursus arctos Linnaeus, 1758

Ursus maritimus Phipps, 1774

Table 1: Taxonomy of the North American Quaternary Bears

Tabel 1: Taxonomie van de Noord-Amerikaanse kwartaire beren



Figure 2: North American Quaternary Ursidae: (a) Pleistocene; (b) Holocene

Figuur 2: Noord-Amerikaanse kwartaire beren: (a) Pleistoceen; (b) Holoceen

record comes from Tlapacoya, State of Mexico (Álvarez, 1969), and a southernmost record was reported from Cerro Rabón, Oaxaca (Bitterli *et al.*, 1990). The species is endemic to North America and never has ranged outside of these three countries. During the past two decades, most American black bear populations have grown both numerically and geographically (Williamson, 2002). Fossil records in North America are known from the Middle Pleistocene into the Holocene (Kurtén and Anderson, 1980), and black bears are the most common of the Pleistocene bears (Graham & Lundelius, 1994; McLellan & Reiner, 1994). A major body size reduction in black bears occurs at the end of the Pleistocene and perhaps throughout the Holocene (Graham, 1991).

The brown bear is the most widely distributed ursid globally. Now greatly restricted from its former distribution range, it once ranged across a large portion of North America, including northern Mexico, south to central Durango (Ceballos & Oliva, 2005). An archaeological record places it in northern Jalisco during the Holocene (O. J. Polaco, personal communication 2009). It ranged throughout Europe, Asia,

the Middle East, and even across north Africa. It presently occupies approximately 5,000,000 km² of the northwestern portion of North America, 800,000 km² of Europe (excluding Russia), and much of northern Asia. The largest numbers exist in Russia, USA (Alaska), and Canada. Many populations in Europe, and the more southerly portions of Asia and North America are small and isolated (Servheen *et al.*, 1999; Swenson *et al.*, 2000). Extirpation from east of the Mississippi River occurs during the Pleistocene-Holocene transition (Graham & Lundelius, 1994). During the 20th century, brown bears are extirpated from Mexico and a large portion of the southwestern U.S. (Brown, 1985; Mattson & Merrill, 2002). Fossil records in North America are known from the Late Pleistocene (post 25,000 radiocarbon years BP) into the Holocene (Kurtén & Anderson, 1980).

Polar bears live throughout the ice-covered waters of the circumpolar Arctic, and their range is limited by the southern extent of sea ice (Schliebe *et al.*, 2008). Although some occur in the permanent multi-year pack ice of the central Arctic basin, they are most common in the annual ice over the

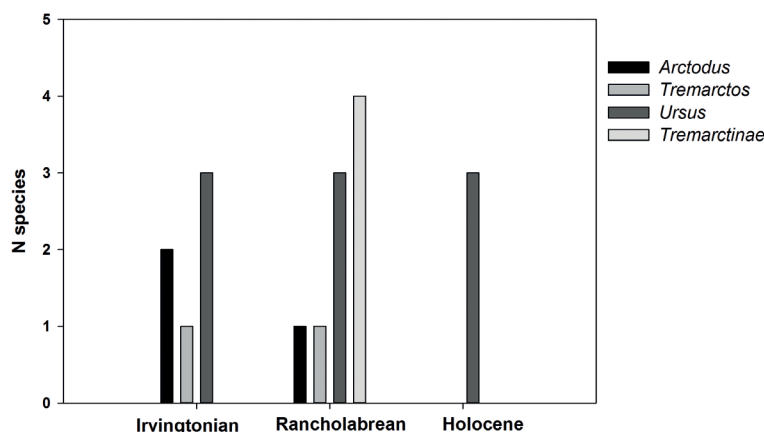


Figure 3: Quaternary defaunation of Ursidae in North America

Figuur 3: Kwartaire verdwijning van beerachtigen in Noord-Amerika

continental shelf and inter-island archipelagos that surround the polar basin. Polar bears that have continuous access to sea ice are able to hunt throughout the year. In those areas where the sea ice melts completely each summer, polar bears are forced to spend several months on land fasting on stored fat reserves until freeze-up (Schliebe *et al.*, 2008). North American fossil remains are very rare and the spotty record is primarily a Holocene one, with a very late Pleistocene record from Baillee Island in the western Northwest Territories of Canada (Anderson, 1984; Vincent, 1989).

In regard to the North American Quaternary Ursidae (*sensu stricto*), a rich bear fauna was formed by representatives from two of the three known subfamilies, the American-endemic Tremarctinae and the world-wide distributed Ursinae (Ailuropodinae was not represented). North American tremarctines included the Pleistocene spectacled bear, *Tremarctos floridanus* (known from Early to Late Pleistocene), and the short-faced bear *Arctodus* with two species, *A. pristinus* (known from Early to Middle Pleistocene; 2.6 to 0.5my) and *A. simus* (known from Middle to Late Pleistocene; 1.8my to 11ky). Both species were known from south to central Mexico (Ferrusquia *et al.*, 2010). These two species probably were the largest carnivores at their time, each weighing around 350 kg. *Arctodus simus* was a long-legged, short-bodied animal with a short face and broad muzzle, while *A. pristinus* was smaller, had shorter limbs, with a more elongated face (Kurtén & Anderson, 1980; Anderson, 1984). *Arctodus*, like the polar bear, was dominantly carnivorous in contrast to the omnivorous habits of spectacled bears. *Arctodus simus* was considered an active predator, being the most powerful predator of the American Pleistocene (Kurtén & Anderson, 1980; Anderson, 1984). Stable isotopic evidence, however, indicated it was more a scavenger with a meat diet from diverse species (Matheus *et al.*, 2003; Pérez-Crespo *et al.*, this volume). *Arctodus* went extinct at the end of the Pleistocene.

Tremarctos floridanus was a widespread species that may have survived until the early Holocene (Devil's Den, Florida; Kurtén & Anderson, 1980). Today, *Tremarctos* survives as the spectacled bear, *T. ornatus*, in South America, leaving North and Central America lacking this subfamily. The extinct species is distinguished from the extant species by much larger size and heavier proportions, with a tendency towards a general reduction of the premolars and elongation of the back molars (Anderson, 1984).

A juvenile skeleton of a spectacled bear, identified as *Tremarctos floridanus*, comes from Cebada Cave, Belize (Czaplewski *et al.*, 2003). The record points to a narrowing of its distribution at the very end of the Pleistocene. More recently, bear specimens have been recorded from Hoyo Negro cenote (a deep natural pit, or sinkhole, resulting from the collapse of a doline or limestone bedrock that exposes groundwater underneath) in Yucatan Peninsula (Chatters *et al.*, 2014). Although initially referred to the genus *Tremarc-*

tos, further study is warranted to determine their correct taxonomical position (B. Schubert, personal communication, 2015).

Overall, at least seven bear species occur in the North American Pleistocene (Figure 2a), while presently only three are extant (Figure 2b). These three are in the subfamily Ursinae, and considered endangered or threatened (Figure 3). The extinct species are in the subfamily Tremarctinae. Currently, this subfamily is represented by a unique species from the South American Andean region.

The extinction and extirpation of species as well as body size shifts may be due to several factors. These factors include the depletion in number of large herbivores, diminishing of nutritional quality of plants during climate change, and competition with early peoples for food resources. Despite these factors, bears from the subfamily Ursinae have survived to the present.

HUMAN UTILIZATION

Few records are available for the possible use of bear by Late Pleistocene peoples. In Mexico, black bear remains appear to be associated with early peoples in central Mexico (Tlapacoya, State of Mexico; Álvarez, 1969). Records of tremarctinae bear for some cenotes are found in the Yucatan Peninsula, and in particular Hoyo Negro, has a possible association with early human remains (Chatters *et al.*, 2014).

More direct interaction between early peoples and bears is documented at the Lubbock Lake Landmark (Texas, USA) during the Late Pleistocene. Lubbock Lake is on the Southern High Plains of western Texas in a now dry stream valley within the upper Brazos River basin. This multi-component site is well-stratified, and the Late Pleistocene activity area from which short-faced bear (*Arctodus simus*) remains came (Clovis culture) is dated at 11,100 radiocarbon years BP (Johnson, 1987). The short-faced bear remains exhibit two categories of human modification that indicate very different uses of the bear carcass. Butchery marks compose the first category and consist of pry marks and two types of cut marks. Cut marks (narrow, single-stroke) on the metacarpals indicate skinning. Cut marks (narrow, single-stroke and wide, deep, multiple-stroke) on the radius indicate defleshing. Pry marks on the proximal articular surface of the radius indicate disarticulation. The wide, deep, multiple-stroke marks indicate some resistance in the tissues and suggest that the carcass was stiff. The carcass most likely was a found one, scavenged by people (Johnson, 1987; Johnson & Bement, 2009).

The second category is that of fracture-based utilitarian technology. This technology employs a high velocity impact technique (dynamic fracturing) as the fracturing method, focused on intact fresh long bones (Johnson, 1985). Various

production paths can be taken using this technique depending on the animal-size group. For large to medium sized ungulates, the major production paths are marrow processing and bone expediency tools. Expedient tool use was the objective with the short-faced bear radius at the Lubbock Lake Landmark. Dynamic fracturing of the radius created two major portions (distal and proximal), each exhibiting a helical fracture surface. Without further modification, the proximal radius was used as a butchering tool, the tool bit being the apex of the helical fracture. Use-wear evidence is a combination of edge flaking, differential polish, and worn and rounded surfaces all along the apex. Scanning electron microscopy analysis confirms the localized wear polishing, edge rounding, and striae of the microsurface on the apex (Johnson, 1990).

The fracture characteristics exhibited by the bear's radius indicated the bone was fractured while fresh. The bear remains, then, may represent a human scavenging event of a found, stiffened carcass of perhaps no more than a day or two dead. People viewed the carcass in terms of subsistence (meat procurement) and technology (raw material resource for tool production), much the same as they viewed mammoth carcasses at this time (Johnson, 2005).

Currently, the only other known human-bear interaction is for black bear (*Ursus americanus*) at Lehner Ranch (Arizona, USA). Lehner Ranch is in southeastern Arizona within the San Pedro River Valley, along Curry Draw that is one of its tributaries. Numerous known Clovis-age sites are found in this valley, primarily with a focus on mammoth (*Mammuthus columbi*) and ancient bison (*Bison antiquus*) procurement (Haynes & Huckell 2007). Lehner Ranch is a Clovis-age site with different activity areas. Partially calcined teeth of a 3-month old bear cub come from a roasting pit. The context suggests the bear cub was eaten (Saunders, 1977:51). Dated charcoal from the surrounding occupation surface average 10,940 radiocarbon years BP (Taylor *et al.*, 1996).

Native Americans increasingly utilized black bears during the Holocene, particularly in the late Holocene upper Midwest, e.g., Hopewell and Mississippian cultures (Styles, 2011). Despite this increased usage, black bears thrived throughout their range. Human impact came in the form of Euro-American settlement that brought habitat loss and hunting pressures to dramatically reduce their range and overall population.

CONCLUDING REMARKS

In general, late Pleistocene humans and the more carnivorous bears may have been competitors for the same game animals. The timing of carcass utilization or scavenging, however, most likely would have been different to avoid direct conflict. Furthermore, people also ate short-faced bear and black bear and utilized bones of the short-faced bear for creating expedient butchering tools. Estimated weight ranges for adult male short-faced bears (*Arctodus simus*) are between 350 to 375 kg and adult females between 150-270 kg (Kurtén, 1967). Modern adult male black bears typically weigh between 57-250 kg and adult females between 41-170 kg (Hunter, 2011). Late Pleistocene black bears are larger than their modern counterpart and could be considered a very large carnivore. Short-faced bear, however, is a megacarnivore. Both bears would have been dangerous prey. Bear hunting may not have been common during the late Pleistocene, particularly with bears the size of *Arctodus* or the black bear, but hunting or scavenging carcasses did occur occasionally. That occasional activity, however, would not have had an impact on bear populations.

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