

BUILDING BIODIVERSITY: MAMMALIAN IMMIGRATION AND THE ORIGIN OF THE NORTH AMERICAN PLEISTOCENE MAMMALIAN FAUNA

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Summary

Throughout the Cenozoic, the diversity of the mammalian fauna of North America was influenced not only by in situ evolution resulting in endemic taxa but also by its position between Eurasia to the west and South America to the south. Changing sea levels and plate tectonics permitted the dispersal of taxa originating on these other two continents into North America, resulting in an increased diversity of its mammalian fauna over time. In the Paleogene, the primary source area for these new taxa or exotics was from Eurasia and faunal interchange between North America and Eurasia continued into the Neogene. In the late Neogene, the taxonomic diversity of North American fauna was further increased with a series of dispersals of taxa originating in South America and taxa of North American origin entering South America, an event known as the Great American Biotic Interchange. The successful integration of these new taxa into the North American mammalian fauna and their ability to ecologically compete with endemic taxa, whether herbivores or carnivores, is also demonstrated by the survival of some of these taxa until the Pleistocene extinction event as well as their presence in the modern fauna.

Samenvatting

Gedurende het Cenozoïcum is de diversiteit van de zoogdierfauna van Noord-Amerika beïnvloed door zowel de evolutie van inheemse taxa ter plaatse als door migraties vanuit Eurazië en Zuid-Amerika. Veranderingen in de zeespiegel en plaattektoniek maakten de verspreiding van zoogdiertaxa vanuit deze twee continenten naar Noord-Amerika mogelijk, wat zorgde voor een toename in de diversiteit van de zoogdierfauna. In het Paleogeen was Eurazië de voornaamste bron van nieuwe taxa of exotica en deze uitwisseling tussen Noord-Amerika en Eurazië bleef ook tijdens het Neogeen plaatsvinden. In het late Neogeen nam de taxonomische diversiteit van de Noord-Amerikaanse fauna verder toe door een aantal migraties van en naar Zuid-Amerika. Dit proces wordt ook wel de "Great American Biotic Interchange" genoemd. De succesvolle integratie van deze nieuwe taxa in de Noord-Amerikaanse zoogdierfauna en hun ecologische aanpassingsvermogen om te concurreren met de inheemse soorten, zowel de herbivoren als de carnivoren, wordt geïllustreerd door het feit dat vele soorten overleefden tot de pleistocene massa-extinctie of zelfs tegenwoordig nog voorkomen.





Close-up of Fig. 2 North American interglacial fauna.
Close-up van Fig. 2 Noord-Amerikaanse interglaciale fauna.

PROBOSCIDEANS

Proboscideans first appear in North America in the middle Miocene (Barstovian) with the Eurasian genus *Gomphotherium*. While there is a diversification of gomphotheres during the Miocene and Pliocene, only one genus which originated in North America is present in the Pleistocene: *Cuvieronius*. The genus first appears in the early Blancan but does not become common until the Pleistocene. It is a Neotropical genus with a range from the southern United States and in the late Blancan or early Irvingtonian it entered South America where it is a common member of the South American fauna.

The second genus to enter North America was *Mammut*, first appearing in the early late Miocene (Clarendonian) and surviving into the Pleistocene. The terminal Pleistocene species is *M. americanum* which was widespread from coast to coast and ranged from the Yukon south into Mexico with some limited records in Central America. Before it became extinct at the end of the Pleistocene, it disappeared from the northern part of its range in eastern Beringia at the end of the Sangamon Interglacial (Zazula et al., 2014). Analysis of undigested plant remains found in the ribcages of some specimens revealed twigs and cones of conifers, leaves, coarse grasses, swamp plants, and mosses, suggesting a preferred habitat of open spruce woodlands and spruce forests. Mastodons were not confined to this habitat, as they inhabited Florida, Texas, and the Great Plains, where they probably lived in valleys, lowlands, and swamps.

The last proboscidean to enter North America is the mammoth, *Mammuthus*. Its appearance is used to define the beginning of the North American Land Mammal age, the Irvingtonian. Multiple species have been described but the best known is *M. columbi*. The species survived until the Pleistocene extinction event and the species is present in multiple kill sites associated with the Clovis culture, suggesting its extinction may have resulted from hunting by paleoindians. In the latest Pleistocene a second species, *M. primigenius*, entered North America. Its primary distribution was in the northern part of the continent and near the margin of the continental ice sheets as they moved south, while *M. columbi* was more southern in its distribution including records in Central America (McDonald & Dávila, 2017). Relict populations of *Mammuthus* survived into the Holocene on the Pribilof Islands off the coast of Alaska. The youngest date is $7,908 \pm 100$ years B.P. based on a small upper third molar found on St. Paul Island compared to the youngest radiocarbon date for the species on the Alaskan mainland at $11,500 \pm 150$ years B.P. (Guthrie, 2004).

RODENTS

The genus *Castor* originates in Eurasia and appears in North America in the late Miocene (Hemphillian). The beaver is the largest rodent in the North American fauna today but was greatly exceeded in size by an extinct taxon, *Castoroides*. *Castoroides* is in a separate subfamily which has a long history in North America since the early Miocene (Arikarean). It is the terminal genus surviving until the end of the Pleistocene. It is also the largest member of the subfamily with an estimated body mass of 60–100 kg (Reynolds, 2002).

Analysis of the vegetation associated with a giant beaver in Indiana by Swinehart & Richards (2001) indicates that the site was a mineral-rich wet meadow, dominated by bulrushes. The surrounding forest was dominated by white spruce, balsam fir, and tamarack. Plint et al. (2019) examined the stable carbon and nitrogen isotopes from the giant beaver confirming *Castoroides*' diet consisted predominantly of submerged aquatic macrophytes and the giant beaver did not consume trees or woody plants, so did not share the same behaviors of tree-cutting and harvesting as *Castor*.

Following the formation of the isthmus of Panama, some South American rodents dispersed northward. Among these is the prehensile-tailed porcupine, *Coendou*, which still survives in southern Mexico and Central America. The range of *Coendou* extended into the United States during the Pliocene and Pleistocene and gave rise to the endemic North American genus, *Erethizon* (Sussman et al., 2016). The preferred habitats of the two genera are mutually exclusive, with *Coendou* inhabiting tropical rain forest and *Erethizon* preferring more northern temperate habitat with a range that extends to the northern tree line in Canada and Alaska.

The other rodents of South American origin in the Pleistocene of North America are capybaras, an extinct genus *Nechoerus* and the extant *Hydrochoerus*. Both are restricted in their distribution to primarily the southeastern United States south into Mexico. *Nechoerus* first appears in North America in the Pliocene (Blancan), becoming extinct at the end of the Pleistocene. *Hydrochoerus* appears later in the Rancholabrean but its range became reduced after the Pleistocene, so the northernmost record today is central Panama.

PERISSODACTYLA

Originating in North America with later dispersals into Eurasia, *Equus* is one of the more common members of the North American Pleistocene fauna. While common, the species taxonomy has not been resolved, with multiple species described often based on isolated teeth and other nondiagnostic specimens making most of them invalid. This reflects the conservative nature of the skeleton of horses and limited diagnostic features. It is possible some of the North American species of *Equus* are conspecific with taxa in Eurasia especially in Beringia. Consequently, their disappearance from North America may merely be a range contraction rather than extinction. Recently the recovery of DNA from a stilt-legged form has resulted in the recognition of a new genus, *Haringtonhippus* (Heintzman et al., 2017). Although becoming extinct in North America at the end of the Pleistocene, the genus survived in Eurasia and Africa represented by multiple species. Given the difficulty of determining species, many of the radiocarbon dates for *Equus* are only to genus. *E. conversidens*, recovered from the Wally Beach site in southwestern Alberta, dated to $11,330 \pm 70$ B.P. and is believed to have been hunted by Clovis people based on the recovery of *Equus* protein residue on two of three Clovis points found at the site.

The other perissodactyl in the North American Pleistocene fauna is *Tapirus*, which also originated in North America with subsequent dispersal into South America and Southeast

Asia. Four species are currently recognized, a large and a small, with one of each on either side of the North American continent. Ecologically they are considered to have been generally like the living species in their ecology and habitat preferences. Generally, their Pleistocene distribution is restricted to the southern United States south through Mexico into Central America. Today the northernmost record is at the isthmus of Tehuantepec in Mexico.

ARTIODACTYLA

The North American Pleistocene fauna included many taxa from endemic artiodactyl families. These include Tayassuidae (peccaries), Camelidae (camels and llamas) and Antilocapridae (pronghorn antelope). These families were later complemented by the appearance of the Cervidae and Bovidae from Eurasia.

Extant peccaries today are represented by three taxa, but only one, *Pecari tajacu*, the collared peccary is present in North America. The collared peccary is rare as a fossil and during the Pleistocene the common taxa are two extinct genera, *Platygonus* and *Mylohyus*. *Platygonus* is the more common of the two and ranged as far north as the Yukon and south into Mexico. While it extended from coast to coast it is more common in the central and eastern parts of the United States and relatively uncommon in the west. Like modern peccaries, it was a herd animal with many sites containing multiple individuals of different ages (Finch et al., 1972). *Mylohyus* had a more restricted distribution with most records from the southeastern United States. Unlike *Platygonus*, which was more gregarious, *Mylohyus* was probably solitary and apparently did not often seek shelter in caves, where *Platygonus* remains are commonly encountered.

While the Camelidae originated in North America, all members of the family became extinct here at the end of the Pleistocene and the only surviving taxa are in South America, represented by llamas, and Asia (Bactrian camels) and the Middle East (Dromedary camels). While quite diverse during most of the Tertiary, in the North American Pleistocene, one camelid, *Camelops*, and two llamas, *Hemiauchenia* and *Palaeloma*, are the only representatives of the family. *Camelops* is primarily found from the Great Plains westward but ranged as far north as the Yukon. It became extirpated from the Yukon at the beginning of the last glaciation (Zazula et al., 2011). *Hemiauchenia* is the more common of the two extinct llamas. It is widespread and known from sites from Florida to California. *Palaeloma* is not as common and found primarily in the western United States south into South America. It has been proposed that *Palaeloma* originated in South America and then redispersed back into North America as its first appearance is in the Middle Pleistocene (Irvingtonian) (Webb, 1974).

The Antilocapridae is another North American group that was more diverse in the Tertiary than in the Quaternary. Represented today by a single species, *Antilocapra*, which is relatively uncommon in the Pleistocene, the family is better represented by three extinct genera, *Stockoceros*, *Tetrameryx* and *Capromeryx*. In the early Pleistocene *Capromeryx* had a

range that extended into Florida but by the late Pleistocene its range had contracted to the western United States and overlapped with the other two genera. *Capromeryx furcifer* is the smallest of the three extinct genera and stood about 560 mm at the shoulder with a body mass estimated at about 10 kg so it was about two-thirds the size of living pronghorn. *Stockoceros* was originally described as a subgenus of *Tetrameryx* but is now considered a separate genus. Both genera are represented by large samples.

The dispersal of the Cervidae and Bovidae from Eurasia into North America marks a major change in the ecological composition of the North American mammalian fauna. Today the majority of large-bodied ungulate herbivores in North America are members of these two families and overshadow the native groups. The first appearance of *Bison* south of 55° N latitude in North America is used as the definition of the Rancholabrean North American Land Mammal Age (Bell et al., 2004). While *Bison priscus* is found in Beringia and Eurasia, other species such as *B. latifrons*, with a two-meter horn span, are endemic to North America. The surviving species, *B. bison* evolved in North America. The living muskox, *Ovibos*, has a circumpolar distribution which includes parts of northern Alaska and Canada into Greenland. Fossils of *Ovibos* are known from the northern United States and as a cold-adapted species its southernmost distribution parallels the southern margins of the continental ice sheets (McDonald & Davis, 1989). An extinct muskox, *Bootherium*, is often referred to as the woodland muskox as it appears to be closely associated with coniferous habitat. It ranged from Alaska, where naturally freeze-dried carcasses have been recovered from the permafrost, south to the mid-continental United States. The presence of two skull morphs indicates it was distinctly sexually dimorphic including a significant difference in size between the two sexes. Two other bovids, *Euceratherium* and *Preptoceros*, are found in the southwestern United States and are referred to as shrub-ox reflecting their adaptation to more arid environments. Dung of the shrub-ox recovered from dry caves on the Colorado Plateau indicates it was a browser and its diet included *Artemisia*, *Acacia* and *Chrysothamnus*.

Other extant bovids in North America include *Ovis* and *Oreamnos*. Pleistocene *Oreamnos* is represented by an extinct species with a distribution south of the living species. Its remains have been found in dry caves in the southwestern United States that have preserved horn sheaths and dung of the animal. The living Saiga antelope was present in Alaska and the Yukon but by the end of the Pleistocene its distribution had decreased so that it is now limited to the Asian continent.

The Cervidae are well represented in the modern fauna of North America including *Odocoileus*, *Rangifer*, *Alces*, *Cervus*, *Mazama* and one extinct genus, *Cervalces*. These genera are known from the temperate part of North America, except *Mazama* which is known from southern Mexico and Central America into South America. While *Rangifer* is known from numerous records in the southern 48 states, today its modern range has contracted northward into Canada and Alaska. *Cervalces* is similar in size to *Alces* but lacks the retracted nasals suggesting a nose morphology



Figure 2. The fauna of the North American Mammoth Steppe. Two taxa from Eurasia, the extant muskox, *Ovibos moschatus*, on the left and woolly mammoth, *Mammuthus primigenius*, to the right, and in the center, Lambe's horse, *Equus lambei*, a North American endemic taxa.

De fauna van de Noord-Amerikaanse mammoetsteppe. Twee taxa uit Eurazië, de nog bestaande muskusos, *Ovibos moschatus*, links en de wolharige mammoet, *Mammuthus primigenius*, rechts, met in het midden wilde paarden van Yukon, *Equus lambei*, een Noord-Amerikaanse inheemse soort.



Figure 1. North American interglacial fauna. Jefferson's ground sloth, *Megalonyx jeffersonii*, an endemic North American sloth with a South American origin, faces off with a flat-headed peccary, *Platygonus compressus*, a North American endemic. Left background, western camels, *Camelops hesternus*, a North American endemic and center background, American mastodon, *Mammut americanum*, of Eurasian origin.

Noord-Amerikaanse interglaciale fauna. Jefferson's grondluiaard, *Megalonyx jeffersonii*, een endemische Noord-Amerikaanse luiaard van Zuid-Amerikaanse origine, doet stoer tegenover een reuzenpekari, *Platygonus compressus*, een Noord-Amerikaanse inheemse soort. Links op de achtergrond staan twee andere Noord-Amerikaanse inheemse soorten, de uitgestorven westelijke kameel, *Camelops hesternus*, en in het midden op de achtergrond zien we een Amerikaanse mastodont, *Mammut americanum*, van Euraziatische origine.



North and Central American Origin Carnivora	Eurasian Origin Carnivora	South American Origin Marsupialia
† <i>Canis</i> (<i>Aenocyon</i>) <i>dirus</i>	† <i>Xenocyon</i>	<i>Didelphis</i>
<i>Puma concolor</i>	<i>Cuon</i>	
† <i>Miracinonyx</i>	<i>Canis lupus</i>	Chiroptera
† <i>Smilodon</i>	† <i>Panthera atrox</i>	† <i>Desmodus stocki</i>
<i>Tremarctos</i>	† <i>Panthera spelaea</i>	
† <i>Arctodus</i>	<i>Panthera onca</i>	Rodentia
<i>Ursus</i>	<i>Lynx</i> spp.	<i>Coendou</i>
	† <i>Homotherium</i>	† <i>Neochoeerus</i>
Rodentia	<i>Ursus</i>	<i>Hydrochoerus</i>
<i>Erethizon</i> * SA		
† <i>Castoroides</i>	Rodentia	Xenarthra
	<i>Castor</i>	† <i>Megalonyx</i> * SA
Perissodactyla		† <i>Meizonyx</i> * SA
<i>Tapirus</i> spp.	Artiodactyla	† <i>Nohochichak</i> * SA
<i>Equus</i> spp.	<i>Odocoileus</i> *	† <i>Xibalbaonyx</i> * SA
† <i>Haringtonhippus</i>	<i>Rangifer</i>	† <i>Nothrotheriops</i> * SA
	† <i>Cervalces</i>	† <i>Paramylodon</i> * SA
Artiodactyla	<i>Cervus</i>	† <i>Eremotherium</i>
† <i>Platygonus</i>	<i>Alces</i>	<i>Myrmecophaga</i>
† <i>Mylohyus</i>	<i>Mazama</i> *	<i>Dasyus</i>
<i>Pecari</i>	<i>Bison</i>	† <i>Holmesina</i>
† <i>Palaeolama</i>	† <i>Bootherium</i> * EA	† <i>Pampatherium</i>
† <i>Hemiauchenia</i>	<i>Ovibos</i>	† <i>Glyptotherium</i> * SA
† <i>Camelops</i>	† <i>Euceratherium</i> * EA	† <i>Pachyarmatherium</i>
† <i>Capromeryx</i>	† <i>Preptoceros</i> * EA	
† <i>Stockoceros</i>	<i>Oreamnos</i> * EA	Notoungulata
† <i>Tetrameryx</i>	<i>Ovis</i>	† <i>Mixotoxodon</i>
<i>Antilocapra</i>	<i>Saiga</i>	
	Proboscidea	
	† <i>Cuvierionius</i> * EA	
	† <i>Mammut</i>	
	† <i>Mammuthus</i>	

Table 1. Examples of genera present in the late Pleistocene of North American including Central America and the continent from which the lineage was derived. *) Genus known only from North America but derived from a non-North American lineage; EA – Eurasia, SA – South America. †) An extinct taxon.

Voorbeelden van aanwezige genera in het late Pleistoceen van Noord-Amerika, inclusief Midden-Amerika, en het continent van origine. *) Genus is alleen bekend uit Noord-Amerika, maar afkomstig uit een niet Noord-Amerikaanse evolutielijn; EA - Eurazië, SA - Zuid-Amerika. †) Een uitgestorven taxon.



Figure 3. The dirk-toothed cat, *Homotherium serum*, with a saiga antelope, *Saiga tatarica*; two taxa of Eurasian ancestry in the North American Pleistocene fauna.

De sabeltandkat, *Homotherium serum*, met een saiga, *Saiga tatarica*; twee taxa van Euraziatische herkomst in de Noord-Amerikaanse pleistocene fauna.

more like that of *Cervus*. It is closely associated with boreal vegetation. Currently there is no absolute terminal date for *Cervalces*, but the numerous postglacial occurrences, many based on shed antlers, probably date from the Wisconsinan glacial retreat, between 15,000 and 10,000 years B.P. None of the current radiocarbon dates for the species indicates it survived past the Younger Dryas and into the Holocene.

SOUTH AMERICAN ORIGIN

The number of taxa originating in South America present in the North American Pleistocene is not as great as those from Eurasia. Likewise, only a small subset survived the Pleistocene extinction and is part of the modern fauna. The most distinctive of these are the opossum, *Didelphis*, armadillo, *Dasypus*, porcupine, *Erethizon* and vampire bat, *Desmodus*. This is in marked contrast to the Pleistocene fauna which included seven genera of sloth, two glyptodonts, two pampatheres (giant armadillos) and the giant anteater. While the distribution of the vampire bat today is limited from Mexico south into South America, in the Pleistocene an extinct species which was slightly larger is known from sites in the southern United States. Likewise, the armadillo, *Dasypus*, is represented by an extinct species, but was almost twice the size of the living species. The giant anteater, *Myrmecophaga*, is present in Central America today but during the Middle Pleistocene (Irvingtonian) its range extended as far north as Sonora Mexico (Shaw & McDonald, 1987). The two glyptodonts are restricted to the southern United States, with a decrease in the range of *Glyptotherium* from the Blancan to Rancholabrean prior to its extinction. *Pachyarmatherium* is only present in North America during the Blancan and early Irvingtonian but may have survived in South America until the end of the Pleistocene. The sloths were present in a variety of habitats in North America from temperate forest and grassland to tropical.

The one ungulate in the North American fauna from South America is *Mixotoxodon*. The genus is present in northern South America and common in Central America. Recently it has been identified from a tooth preserved in late Pleistocene sediments in east Texas (Lundelius et al., 2013). Pollen directly associated with the toxodont tooth indicates a mesic grassland with abundant sedges suggesting the presence of seeps or springs.

CARNIVORANS

The most distinctive of the endemic North American carnivorans includes four extinct taxa: the sabertooth, *Smilodon*, short-faced bear, *Arctodus*, North American cheetah, *Miracinonyx*, and dire wolf, *Canis* (*Aenocyon*) *dirus*.

While sabertooth morphology is present in other true felids as well as non-felids, the genus *Smilodon* originated in North America probably from a Eurasian ancestor and later dispersed into South America after the formation of the isthmus of Panama. The genus is best known from the large number of individuals recovered from the tar deposits of Rancho La Brea. The Eurasian cave lion, *Panthera spelaea*, has been identified from eastern Beringia based on aDNA, while south of the continental ice sheet, a distinct species, *P.*

atrox, is present. Barnett et al. (2009) considered them subspecies of the extant *Panthera leo*. The dirk toothed cat, *Homotherium*, is another taxon of Eurasian origin that has a deep history in North America and survived until the Pleistocene extinction. While not as common as *Smilodon*, it had a wider distribution from eastern Beringia south into Venezuela (Rincón et al., 2011). Both taxa co-occur in several faunas. Friesenhahn Cave, Texas appears to have been used as a den site based on the presence of both adults and juveniles. They were associated with the remains of multiple juvenile mammoths suggesting they were the primary prey. The North American cheetah, *Miracinonyx*, is convergent with the modern cheetah and is more closely related to the North American mountain lion, *Puma concolor*. Although relatively uncommon, complete skeletons of this species have been recovered from Natural Trap Cave, Wyoming (Martin et al., 1977).

Arctodus also is known only from North America, although a closely related genus, *Arctotherium*, is known from South America. While the earlier species of *Arctodus* is small, the late Pleistocene species is among the largest known bears with the mass of a large male estimated around 700-800 kg (Christiansen, 1999). The range of *Arctodus* extended from Alaska south into Mexico. An extinct species of *Tremarctos*, larger than the extant species, is also present in the North America Pleistocene fauna. Black bears have a long history in North America while the brown or grizzly bear, *Ursus arctos*, only entered North America from Eurasia in the latest part of the Rancholabrean (Davison et al., 2011).

The dire wolf lineage has a deep history in North America with the terminal species, *Canis dirus*, being the largest. An aDNA study of the dire wolf by Perri et al. (2021) proposed that the lineage is highly divergent and split from living canids around 5.7 million years ago. Based on this study it was proposed that the dire wolf should be considered a distinct genus, *Aenocyon* and not a member of *Canis*. The dire wolf was widespread across North America south of the continental ice sheets and is the most abundant carnivore present at Rancho La Brea. The Eurasian gray wolf, *Canis lupus*, entered North America during the late Pleistocene. Whether this resulted in ecological competition resulting in the extinction of the dire wolf has not yet been determined. The presence of *Cuon* in North America is based on specimens from a single locality, San Josecito Cave, Mexico.

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