Late Quaternary biogeography and extinction of Proboscideans in North America

R.Wm. Graham

Department of Earth and Space Sciences, Denver Museum of Nature and Science, Denver, USA - Rgraham@dmns.org

North America supported one of the highest diversities of proboscideans in one of the smallest areas during the late Pleistocene (10-20 ka). There were at least four different genera (*Mammut, Mammuthus, Haplomastodon,* and *Cuvieronius*). All of these genera were monospecific except for *Mammuthus* with four different species (*M. columbi, M. jeffersonii, M. primigenius*, and *M. exilis*). None of these proboscideans had a continental wide distribution at the end of the Pleistocene. In fact, during full glacial times when continental ice covered most of northern North America, all four proboscidean genera inhabited areas south of the ice sheet that were smaller than the geographic range of either of the living elephant genera (*Loxodonta* and *Elephas*).

Based upon geographic distribution, dental morphology, isotopic analyses, and associated paleoenvironmental indicators, all of these proboscideans probably had preferred habitats. *M. primigenius* (woolly mammoth) was the northern most taxon and it was a late Eurasian immigrant, appearing in North America some time after 200 ka. It occurred in Alaska, the upper midwestern and northeastern United States (US) and along the northern Atlantic coastal plain. The woolly mammoth preferred arctic or mammoth steppe, "tundra", and the forest/woodland ecotone between these two "biomes." *M. jeffersonii* (Jefferson's mammoth) evolved in North America and it is convergent with the woolly mammoth by having a large number of plates and thin enamel. Jefferson's mammoth occupied the upper midwestern US at the end of the Pleistocene and overlapped temporally and geographically with the woolly mammoth with which it may have been a potential competitor.

The most widespread (latitudinally, longitudinally, and altitudinally) North American proboscidean at the end of the Pleistocene was *M. columbi* (Columbian mammoth). It dominated the US west of the Mississippi River and south of the continental ice sheets. It ranged well into Mexico. The Columbian mammoth also occurred in Florida between 10-20 ka where it may have been isolated from the western populations. Columbian mammoths are known from coastal sites to more than 3000 m (10000 feet) above sea level. This species of mammoth is predominantly associated with grazing mammals like camels (*Camelops*), horses (*Equus*), bison (*Bison*), and big headed llamas (*Hemiauchenia*); it appears to have preferred a steppe/savanna/parkland environment.

Mammut americanum (American mastodont) has been in North America for at least the last five million years. During the late Pleistocene (10-20 ka), the American mastodont inhabited most of the eastern US and southeastern Canada south of the ice sheet and ranged into Mexico. Some of the richest and latest finds of *Mammut* occur in the Great Lakes region of the US and Canada, the Mississippi River valley, and Florida. There are a few isolated terminal Pleistocene records in the western US. Its distribution is almost a mirror image of the distribution of the Columbian mammoth. Also, in well-stratified sites in the midwestern US, mammoth and American mastodont almost

never co-occur at a site suggesting habitat exclusion. The American mastodont preferred woodland to forest habitats, especially the late Pleistocene boreal forest. It is frequently found with browsing mammals like giant beaver (Castoroides), stagmoose (*Cervalces*), woodland musk ox (*Bootherium*), and stout-legged llama (*Palaeolama*).

Haplomastodon and *Cuvieronius* are two New World genera with pre-Quaternary origins in North America but they primarily inhabited southern North America, Central America, and South America during the late Quaternary. At the end of the Pleistocene, *Haplomastodon* and *Cuvieronius* only extended as far north as Mexico. There may have been an isolated population of *Cuvieronius* in Florida. These two mastodonts were geographically sympatric with *Mammut* and *Mammuthus* in central Mexico in the terminal Pleistocene, although their temporal and ecological overlaps are poorly known. The molar teeth of *Haplomastodon* and *Cuvieronius* have similar morphology and they both presumably preferred open woodland habitat as well as mesic tropical lowland habitats farther to the south.

Mammuthus exilis had the smallest geographic distribution of any of the North American proboscideans as it was restricted to the Channel Islands off the coast of California. It was presumably derived from the Columbian mammoth.

All of these proboscideans became extinct sometime after the last glacial maximum (18 ka) and it appears that most, if not all, survived until the terminal Pleistocene (10-12 ka). Extensive dating of *M. columbi* and *M. americanum* remains indicate that both of these taxa survived until 10.8 ka while most other large Pleistocene mammals were extinct by 11 ka. These data suggest that the Keystone Species Model of Pleistocene extinction may not be valid for these taxa since they were the last, rather than the first, to go extinct. These dates are concordant with a Clovis model of extinction but they are also in agreement with a major climate trigger, the Younger Dryas.

Several factors probably contributed to proboscidean extinction and these same factors are critical to the survival of modern elephants. Geographic range reduction was probably the dominant factor. The pre-Wisconsin distribution for all North American proboscideans, except for *M. exilis*, demonstrates that their ranges were reduced throughout the Quaternary. Among mammals in general, it is believed that the probability of extinction increases exponentially with reduction in geographic range. Futhermore, the size of the home range of a mammal species is a direct function of its body size. As the largest ungulates, proboscideans would have required the largest geographic ranges. As already documented, the inclusive geographic range of all of these proboscideans during the late Quaternary was less than the range of either of the living elephant species historically.

Habitat destruction was probably another contributing factor. The Pleistocene proboscideans had preferred habitats as documented by their geographic ranges, dental morphology, isotopic composition of their tooth enamel, and association with other environmental proxies. The extinction of proboscideans and other megafauna is highly correlated with the disappearance of certain Pleistocene habitat types (open boreal forest, parkland, and savanna).

One of the challenges for environmental models of extinction is the question: What was unique about the end of the Pleistocene environmental change? If geographic range reduction was one of the major drivers, as proposed here, then the environmental change does not need to be unique but must simply serve as a trigger once a threshold has been reached. For geographic range reduction, the threshold is critical minimum population size or critical minimum size for geographic range. Until these limits are reached, environmental change will not cause extinction but once these limits are exceeded then extinction will be triggered.

The environmental change does not need to be unique but merely drive populations and geographic ranges below viable limits.

Human involvement in proboscidean extinction in North America is hard to evaluate. Evidence for human association with late Quaternary North American proboscideans has only been found for *M. columbi, M. americanum*, and *Haplomastodon*. In these cases, humans may have been involved in their demise. However, the actual impact of humans is not really known because it is hard to estimate predation pressure and population sizes for proboscideans and humans.

Finally, the extinction of North American late Quaternary proboscideans underscores the significance of geographic range and habitat for the survival of the modern elephant species.