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Reconciling phylogenetic and morphological trends in North American *Mammuthus*

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ABSTRACT

The morphology of mammoth upper third permanent molars (M3) is used to address regional- and continental-scale patterns in the structure of mammoth populations. Recent refinements to the understanding of *Mammuthus* phylogenetic diversity south of the Laurentide ice show extensive overlap between regional populations. We assess the underlying geographic structure in *Mammuthus* tooth morphology in light of these new genetic data. Comparison of regional trends in dental morphology show a single, morphologically variable, population of *Mammuthus* was present in North America during the Wisconsin glaciation. Within this population, there are no significant differences in degree of hypsodonty or molar shape however, there is a geographic pattern of lower enamel:dentin ratios in *Mammuthus* from the Channel Islands, West Coast, and Southwest/Mexico as measured by the number of molar lamellae and the standardized thickness of lamellae. These results contrast with historical perspectives of *Mammuthus* population structure suggesting at least four species of North American mammoths but are consistent with recent phylogeographic analyses of mitochondrial ancient DNA.

1. Introduction

As a popularizer and promoter of mammoth science, Larry Agenbroad had few parallels. Through sustained and innovative research, and with the Mammoth Site as a hub for research and training of future generations, Larry contributed to an understanding of extinct proboscideans that is far greater than the typical reach of a single individual. The dataset we present here directly benefits from the many overviews and updates of research on North American *Mammuthus* he published through the years (Agenbroad, 2005, 1994, 1984; Agenbroad and Mead, 1996). Like Larry, we see biogeographic variability as key to understanding the evolution and ecology of North American *Mammuthus*. Our goal in this contribution is to explore the biogeography of *Mammuthus* tooth morphology in reference to recent genomic research (Enk et al., 2011, 2016).

The genus *Mammuthus* has undergone significant taxonomic pruning over the last century. Radiating out of Africa ~3 ma and arriving in North America by 1.5–1.3 ma (Agenbroad, 2005; Bell et al., 2004; Lister and Sher, 2015), the evolutionary history of *Mammuthus* at the sub-generic level has been the subject of much debate. Henry Fairfield Osborn, perhaps the most prolific of proboscidean taxonomists, noted three genera (*Archidiskodon*, *Parelephas*, *Mammonteus*) of North American mammoths and as many as 16 species-level taxa (Osborn, 1942). Subsequent revisions reduced this number to four species of *Mammuthus* (*Mammonteus*): *M. meridionalis*, *M. columbi* (including the early *M. imperator* morphotype), *M. primigenius*, and *M. exilis* (Agenbroad, 2005, 1984; Graham, 1986; Maglio, 1973). Some researchers also recognize a variant of *M. columbi* as the separate taxon, *M. jeffersonii* (Kurtén and Anderson, 1980; Saunders et al., 2010). Although the number of recognized taxa has remained relatively steady in the last few decades, they have been subject to extensive morphological redefinition or conflation of morpho-species and chrono-species (Kurtén and Anderson, 1980; Madden, 1981). As Agenbroad aptly stated, the "classification of mammoths in the New World has been, and unfortunately remains, confused" (Agenbroad, 1984:91). Although there have been significant advances in our

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understanding of the ecology and extinction of mammoths over the last few decades, relatively few large-scale studies of North American mammoth dental morphology have clarified these taxonomic issues (Lister and Sher, 2015). Three issues make up most of the differences in opinion: 1) the timing and biogeography of the earliest North American *Mammuthus*, 2) the morphological definition of late Pleistocene (i.e., Wisconsin) mammoths and their biogeographic distributions, and finally, 3) a concern for the evolutionary relationships between different mammoth species.

Maglio (1973) summed up his perspective on evolutionary relationships within *Mammuthus* by saying that different mammoth species were arbitrarily defined “segments along a phyletic continuum” where “the more complete the record of transitional populations, the more arbitrary become the species limits” (Maglio, 1973:61–62). Despite the four decades that have passed since Maglio made this statement, we believe this remains an excellent characterization of current perspectives on North American mammoth taxonomy. In recent years, a wealth of new data and the re-analysis of old collections illustrate the difficulty in separating different species of North American mammoths on the basis of morphological characters alone (Barnosky, 1988; Saunders et al., 2010). New analytical tools allow the identification of temporal patterns (Feranec and Kozlowski, 2016; MacDonald et al., 2012) and opened new avenues for exploring genetic relatedness (Barnes et al., 2007; Enk et al., 2011, 2016). Increasingly, speciation in *Mammuthus* and other large herbivore taxa is seen as both a phyletic and ecological continuum, where different populations are capable of interbreeding and introgressing in sustained and complex ways (Debruyne et al., 2008; Shapiro et al., 2004; Wilson et al., 2008).

As noted by Agenbroad (1984), the only way to address this confused taxonomy is through large-scale, systematic reanalysis of museum collections to better understand variability in the morphology of North American *Mammuthus*, and how these patterns relate to chronological and biogeographic trends. Through just such a specimen-by-specimen analysis, Lister and Sher (2015) recently reduced the number of taxa within North American *Mammuthus* to two morphologically variable lineages, *M. columbi* and *M. primigenius*. As sample sizes and mammoth geographic ranges increase for the last glacial interval (i.e., Wisconsin glaciation), geographic patterns in dental morphology also become more complex, a pattern that is shared with Eurasia (Lister and Sher, 2001, 2015).

Mitochondrial genomes of mammoths throughout the Midwest, Great Plains, Great Basin, and West Coast show relatively minor phylogeographic differences, suggesting all temperate North American mammoth species share a common matriline (Enk et al., 2011, 2016). These authors distinguished between two Clade 1 groups: haplogroup C (Yukon, Great Lakes, East Coast) and haplogroup F (Great Plains, Great Basin). Partial mitogenomes from the West Coast (mainland and coastal islands) were basal within their phylogenetic tree.

This presents two scenarios for the phylogenetic history of North American *Mammuthus* that are not mutually exclusive. The first possibility suggests the emigration of a single Eurasian taxon (*M. trogontherii*) to temperate North America followed subsequently by *M. primigenius* (also viewed as a descendant of Asian *M. trogontherii*) during the late Pleistocene. This would have resulted in a complex, geographically-structured, meta-population of late Pleistocene *Mammuthus*, including introgressing populations of *M. primigenius* and *M. columbi* in the Midwest (Lister and Sher, 2015). The second possibility is that the single matriline indicates extensive interbreeding with Beringian *M. primigenius* populations during the late Wisconsin, to the point of complete replacement of the founding *M. columbi* matrilines.

Here we attempt to more comprehensively document mammoth morphological characteristics across North America. We find that there is broad agreement in the geographic distribution of genetic haplotypes and molar morphology. However, regional variability in mammoth dental morphology was likely influenced by historic and ecological conditions affecting different groups within a single, continental, meta-population.

2. Methods and materials

Mammoths were a common element of late Pleistocene landscapes in North America. As possible keystone megafauna (Owen-Smith, 1987), their remains are well-represented in museums and research collections across the continent. Similar to previous studies of dental morphology in *Mammuthus* (Agenbroad, 1994; Lister and Sher, 2001, 2015; Saunders et al., 2010; Whitmore et al., 1967), we focus on last permanent molars, here referred to as the M3 (permanent, upper 3rd molar) following the nomenclature of Osborn (1942).

We analyzed two samples of mammoth teeth in this study. The first sample consists of measurements on 39 mammoth dentitions that are associated with a recent study of mitochondrial phylogenetics in *Mammuthus* from temperate North America (Enk et al., 2016). Due to the opportunistic nature of genetic preservation, these dentitions are from both male and female mammoths, lower and upper dentitions, and of widely varying ages (Table S1).

Our second dataset consists of 278 M3s from 40 repositories (Table 1; Table 2; Table S2; Fig. 1). These include published measurements from the desert Southwest and High Plains (Saunders, 1970, 1999), as well as relevant specimens in the recent dataset published by Lister and Sher (2015). To these published data, we add new measurements on mammoth dentitions from west coast, eastern Great Plains, and midcontinent (~25%). Published measurements on pre-Wisconsin *M. columbi* from North America ($N = 33$) and Eurasian samples ($N = 49$; *M. primigenius* and *M. trogontherii*) were included to explore potential clinal variation. The remainder of the dataset encompasses 196 specimens from known or presumed Wisconsin-aged deposits from throughout North America, including representatives of all late Pleistocene mammoth taxa: *M. columbi*, *M. exilis*, *M. jeffersonii*, and *M. primigenius*.

All molars were assigned to species on the basis of plate number and overall shape (Agenbroad, 1984; Maglio, 1973; Osborn, 1942; Saunders et al., 2010). Localities were also aggregated into five regional samples: Eastern US, Great Plains and Rocky Mountains, Southwest and Mexico, West Coast, and Channel Islands. Published samples of *M. primigenius* (Eurasian and Beringian), early *M. columbi*, and *M. trogontherii* were included for comparison (Lister and Sher, 2015).

Mammoth teeth show a high degree of morphological variability and a number of measurements have been proposed to document this variability. These measurements likely reflect a range of biologically and environmentally determined variables. In the past, researchers have assumed that the number of enamel ridge-plates (i.e., lamellae) in a molar, or the relative degree of antero-posterior compression of plates was genetically predetermined, therefore reflecting “species-level” morphological variability (Maglio, 1973; Osborn, 1942). Although this remains a possibility, other researchers (e.g., Foronova, 2007; Lister, 2001) have noted variable scaling-factors or life history influences on these metrics, limiting their use in taxonomic studies. Lister and Sher (2015) addressed these limitations by correcting for size in lamellar measurements. At this time, it is difficult to account for “fabricational noise” in elephant dentitions (Roth, 1989) therefore we have not included specimens that show abnormal intra-tooth