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The effects of dental wear on impairing mammoth taxonomy: A reappraisal of the Newton mammoth, Bradford County, northeastern Pennsylvania



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ABSTRACT

A mammoth skeleton found at the Newton Site, a kettle lake 15 km southeast of Towanda, Pennsylvania, has been referred to *Mammuthus columbi* on the basis of its high, narrow skull. However, the specimen's thin enamel (1.3–1.8 mm) and moderately high lamellar frequency (8–8.75 lophs/dm) resemble some specimens of *Mammuthus primigenius*. Prehistoric range maps show that a Columbian mammoth inhabiting the Towanda area would be a significant outlier from this species' range; however, its location would align well with the range of *M. primigenius*. To better ascertain the Newton mammoth's identification, we examine herein the effects of dental wear on the morphology of mammoth molars. As mammoth molars wear, the enamel lophs become more broadly spaced and the enamel ridges thicken towards the base of the crown. Thus, an older *M. primigenius* with extensively worn molars might display thicker enamel and a lower lamellar frequency, and might therefore appear to be a Columbian mammoth on the basis of dental morphology alone. Our results show that the molars of the Newton mammoth are well-worn and are characterized by an enamel thickness and lamellar frequency that aligns better with *M. primigenius* than with *M. columbi*. We conclude that one must take into account the effects of dental wear when classifying mammoth species using solely molars.

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1. Introduction

Mammoths (*Mammuthus* spp.), an iconic mammal for the Ice Age, were widely distributed throughout the northern hemisphere during the Pleistocene. Because of the durability of their bones, and especially their teeth, they are common fossils throughout North America. During the late Pleistocene there were two species of mammoths in North America (Lister and Sher, 2015). In the 48 contiguous United States, the Columbian mammoth (*Mammuthus columbi*) generally lived west of the Mississippi River and from Texas along the Gulf coastal plain and into Florida (Neotoma Paleocological Database). This species also extended well into Mexico and further south (Arroyo-Cabrales et al., 2007). Conversely, the woolly mammoth, *M. primigenius*, had migrated across the Bering Land Bridge from Siberia in the late Pleistocene

and inhabited Alaska and northwest Canada as well as an area along the ice front in the upper Midwest, Great Lakes region, and Northeast United States (Agenbroad, 2005).

The two species were adapted for distinctive and disparate ecological roles, although we know a great deal more about the woolly mammoth's soft-tissue anatomy due to discoveries of frozen carcasses of *M. primigenius* in Siberia and Alaska (e.g., Guthrie, 1990; Rountrey et al., 2012; Fisher et al., 2012). With a layer of thick, insulating fur underlying a pelage of coarse guard hairs and a subcutaneous layer of fat up to nine cm thick, *M. primigenius* was well-adapted to the colder steppe environment just south of the ice sheets (Kubiak, 1982; Tridico et al., 2014). Isotopic (Bocherens et al., 1996; Fox-Dobbs et al., 2008; Metcalfe et al., 2013; Drucker et al., 2015) and dental microwear analyses (Rivals et al., 2010, 2012) suggest *M. primigenius* from the Mammoth Steppe and Beringia consumed tougher foods most often associated with an open grassland environment, including sedges, grasses, and herbaceous plant species. *M. columbi* was likely adapted to warmer climates, with remains of this taxon found well south of the terminal Wisconsin moraine in areas surrounding the Great Lakes, Great Plains,

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Gulf Coastal Plain, American Southwest, and Florida. Coprolite remains from Arizona suggest a diet originating from a mixed environment, perhaps from a large, dry area interspersed with rivers where wetland plants could grow (Mead et al., 1986; Mead and Agenbroad, 1992); the preference for a mixed environment was corroborated by stable carbon isotopic studies of *M. columbi* from Mexico documenting a population with a mixed C₃/C₄ diet (Pérez-Crespo et al., 2012). *Mammuthus columbi* from California were found to be highly depleted in ¹³C, indicative of a more heavily wooded environment (Trayler et al., 2015), while individuals from two late Pleistocene sites in Florida show mixed C₃/C₄ to pure C₄ diets (Yann and DeSantis, 2014). In general, *M. primigenius* preferred the arctic steppe, tundra, and forest/woodland ecotone, while *M. columbi* likely preferred a “steppe/savanna/parkland” habitat (Graham, 2001, p. 707).

The discovery of the most complete mammoth skeleton yet known from Pennsylvania by Walter Newton in 1983 raises some interesting questions regarding the differences between *M. primigenius* and *M. columbi*. The site is a kettle lake, Spring Lake, near Towanda and it was preserved in glacial drift that marks the terminus of the Wisconsin Ice Sheet in northeastern PA (Barnosky et al., 1988). Excavations and coring by the Carnegie Museum of Natural History yielded plant macrofossils, pollen, and insect remains that contribute to the reconstruction of the paleoenvironment inhabited by the Newton mammoth (Barnosky et al., 1988).

Dental parameters (plate number, enamel thickness, and lamellar frequency) of the upper third molar (M³) have most often been used to differentiate mammoth species (Maglio, 1973, p. 9). Barnosky et al. (1988) measurements of the Newton mammoth's teeth (M³ and m₃) placed the specimen within the range of overlap of dental attributes for both *M. columbi* and *M. primigenius*. However, on the basis of its high, narrow skull Barnosky et al. (1988) referred the Newton specimen to *M. columbi*. The authors recognized the tenuous nature of the identification, citing adaptive convergence for the striking similarities between the Newton mammoth and some specimens of *M. primigenius*.

Clearly, the taxonomic assignment of a specimen to a taxon should be based on morphological attributes and not geographic distribution (Bell et al., 2010). However, the identification of a Columbian mammoth from northeastern Pennsylvania placed it well outside of the normal geographic range of this species (Fig. 1, red circles). The eastern periphery of current *M. columbi* remains begins in southwestern Canada (Hills and Harington, 2003), trending southeasterly through the Hot Springs Mammoth Site in South Dakota, through Colorado, Oklahoma, all of Texas, and staying along the Gulf coast into Florida. *Mammuthus jeffersonii*, an apparent clinal variant of *M. columbi* (Pasenko and Schubert, 2004), is found abundantly throughout the Great Lakes region, but no remains have been found east of Lake Michigan. On the other hand, *M. primigenius* remains are well-known from Alaska, the Yukon, and the Great Lakes Region (Fig. 1, blue triangles). Recoveries of *M. primigenius* from the Hiscock Site in New York (Laub et al., 1988; Steadman, 1988) and the Scarborough Site in Maine (Hoyle et al., 2004) support the interpretation that the taxon was living in the northeastern United States, just south of the terminal moraine during the Wisconsin glaciation. Spring Lake therefore lies within the known range of *M. primigenius* but more distal to the known range of *M. columbi*.

In addition, the environmental reconstruction of spruce-herb parkland with some tundra (Barnosky et al., 1988, p. 181) is more characteristic of the environment of *M. primigenius* than it is of *M. columbi*. Barnosky et al. (1988) recognized this dilemma and based upon Agenbroad (1984) distribution map for North American mammoths suggested that the Newton mammoth probably lived close to an ecological tension zone that fluctuated through time and

caused subsequent shifts in the geographic distribution of both mammoth species. If *M. primigenius* did not inhabit Spring Lake at the time the Newton mammoth lived, then convergence of dental characters between the two species might be expected, rather than character displacement.

One aspect that was not considered in the Barnosky et al. (1988) study is the effect dental wear has on the morphologically defining attributes (enamel thickness and lamellar frequency) for mammoth species. Because of the dynamics of tooth development (Rountrey et al., 2012), and intraspecific variability, the morphology of a mammoth's third molar is never static. Although the enamel lophs continue from the surface of the crown to the base, they tend to be wider apart towards the base, and the enamel tends to thicken (Graham, 1986; Lister and Sher, 2015). In theory, this should increase the measured value of the enamel thickness and decrease the lamellar frequency as the tooth matures. Thus, although *M. columbi* molars tend to have thicker enamel and more widespread enamel lophs than their woolly relatives, an older *M. primigenius* specimen might exhibit worn molars that appear more similar to young Columbian mammoth teeth.

If the Newton mammoth is indeed a Columbian mammoth, it would be a unique record of the taxa in cold spruce environments with arctic climate signatures, and would support the assertion by Agenbroad (1984) that the periphery of the two species' ranges overlapped in the northeastern United States, although this region is not well-constrained due to the paucity of remains of *M. columbi* in the region. However, if the Newton mammoth were in reality a woolly mammoth, it would fit in the ecological province and suggest that dental wear must be taken into account when taxonomically identifying mammoth molar material. Thus, we set out to test the hypothesis that the effects of dental wear sufficiently altered the enamel thickness and lamellar frequency of the Newton mammoth and led to confusion in its taxonomic assignment.

To test our hypothesis, we measured lamellar frequency, enamel thickness, and relative age (using wear stages of African elephant molars (Laws, 1966)) of *M. primigenius* and *M. columbi* molars from the American Museum of Natural History (AMNH) and the U. S. National Museum (USNM) at the Smithsonian Institution. To ascertain how well our sample aligned with current taxonomic practices, we compared it with the sample of *M. primigenius* and *M. columbi* molars used by Vincent Maglio (1973) to diagnose mammoth species. We then measured the same attributes of the Newton mammoth specimens housed at the Carnegie Museum of Natural History (CMNH). We sought to highlight the overlap in dental characters for both species and determine with which group the Newton mammoth aligned when the effects of dental wear are taken into account.

2. Determining individual age of a mammoth at time of death

In order to assess the effects of dental wear on the diagnostic characters for mammoth molars, it is essential to assign specimens either relative or annular ages. In previous studies determining the individual age of fossil proboscideans at the time of death, paleobiologists (e.g., Saunders, 1977; Harington, 1980; Haynes, 1985; Graham, 1986; Kirillova et al., 2012) relied on a study of aging of modern African elephants (*Loxodonta africana*) from Murchison Falls, Uganda by Laws (1966). The terminology and numbering of teeth in the eruption sequence of elephants, mammoths and mastodons varies because of uncertainties of homologies of teeth. In this study, we refer to the first three teeth in the eruption sequence as deciduous premolars (dP_{2–4} for lower teeth or DP_{2–4} for upper teeth) and the final three teeth as permanent molars (M_{1–3} or M^{1–3} for lowers and uppers, respectively). Others like Laws (1966) numbered the teeth sequentially from 1 to 6. Using dental

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