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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 (Traylor 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 (dP₂₋₄ for lower teeth or DP₂₋₄ for upper teeth) and the final three teeth as permanent molars (M₁₋₃ or M¹⁻³ for lowers and uppers, respectively). Others like Laws (1966) numbered the teeth sequentially from 1 to 6. Using dental

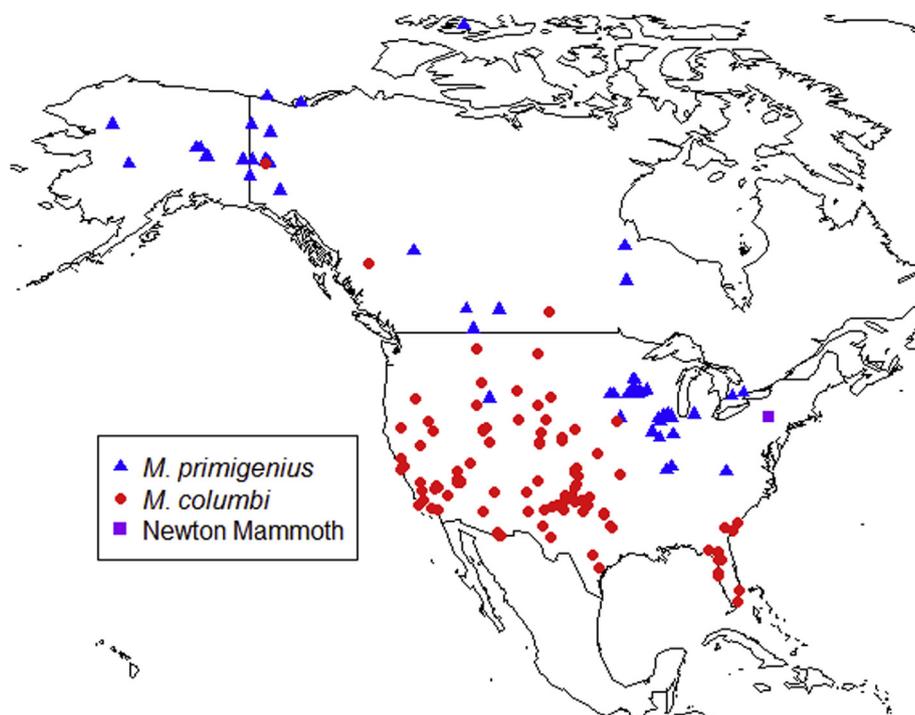


Fig. 1. Map of Late Pleistocene Mammoth Occurrences Map of North American Late Pleistocene (<300,000 years B.P.) *Mammuthus* occurrences. Data downloaded from the Neotoma database (<http://www.neotomadb.org>) in March 2016. Note the Newton mammoth; the purple square in the northeastern United States. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

eruption and wear stages on molars, Laws (1966) grouped a series of 385 lower jaws into thirty relative age groups with broad estimates of annular years. However, other schemes of age-determination in elephants, both *Loxodonta africana* (Sikes, 1968; Jachmann, 1985, 1988) and *Elephas maximus* (Roth and Shoshani, 1988), were proposed and showed that the Laws (1966) method can lead to under- or over-estimates of the annular age of jaws and isolated teeth. Furthermore, Rountrey et al. (2012) documented inconsistencies in age estimates between tusk growth increments and cheek teeth wear stages.

Age determination by tooth eruption sequence and tooth wear stages can further be complicated by the fact that tooth plates in the various taxa of Elephantidae can form at different rates (Dirks et al., 2012; Metcalfe and Longstaffe, 2012) which may explain the mismatch between tusks and cheek teeth. Differential rate formation also limits the use of modern elephant molars as analogs for annular aging of mammoths and other fossil Proboscidea. Additionally, rates of eruption and attrition vary considerably in elephantids, along with broad scale phenotypic variation within a population (Roth, 1989, 1992). In African elephants (*Loxodonta africana*), the third molar may persist in occlusion for up to 35 years (Laws, 1966), while tooth eruption is typically on the order of 20–25 years (Asher and Lehmann, 2008). This relationship between occlusion (and thus attrition) and eruption might result in varied and hard-to-predict morphologies for proboscidean teeth of known ages.

Recognizing that none of the existing methods are perfect for determining the individual age for African elephants, let alone extrapolation to mammoths, we have adapted the Laws (1966) method. As Jachmann (1988) points out, for individuals older than Laws' relative age group XVIII, which includes all the *Mammuthus* molars in this study, there is negligible difference between his technique and that of Laws. Thus, Laws (1966) method should provide a reasonable estimate of age for this study.

The molars of the Newton mammoth were extensively worn (Fig. 2). The anterior portions of the molars are mostly worn away and the newly exposed enamel lophs are among the most posterior ones. This stage of wear would place the Newton mammoth between Laws (1966) wear stages XXVI and XXVII. An African elephant with these wear stages would be about 51 ± 4 years old (Laws, 1966). Assuming the differences in rate of wear and/or dental plate formation lie within the error bars of age estimates obtained by Laws, the Newton mammoth molars would have been in occlusion for about 15 years.

3. Material and methods

The dental parameters of the Newton mammoth (re-measured for this study to retain an element of consistency and limit observer error) were compared to three separate "populations" of *M. columbi* and one of *M. primigenius*. All four of these mammoth samples represent end members in the extremes for the different morphotypes, so they serve as excellent reference populations. To corroborate their usefulness, we compare these "reference populations" with the populations of *M. primigenius* and *M. columbi* measured by Maglio (1973), which have served as the effective taxonomic standards for diagnosing mammoth species despite Maglio emphasizing that his work was not "a detailed study of North American collections" (Maglio, 1973, p. 62). Maglio's reference specimens of *M. primigenius* and *M. columbi*, which detailed the characters he believed to be the most indicative in defining the taxa, are not explicitly denoted in his volume, but rather are said to have come from "many localities" throughout North America (Maglio, 1973, p. 63). Similar to Maglio's intent, it is not the purpose of this study to assess the complete variation in mammoth populations throughout North America. Our goal, rather, is to better resolve the extent to which dental wear is capable of altering dental morphologies.



Fig. 2. Teeth of the Newton Mammoth The mandible (top row) and upper right M3 (bottom row) of the Newton mammoth, originally excavated in 1983 and originally referred to *M. columbi* (Barnosky et al., 1988). Note the advanced wear stage as evidenced by a high crown:root ratio in the molars and substantial wear to the occlusal surface.

For the sample of *M. columbi*, we measured 36 M representing three geographically disparate late Pleistocene populations from: 1) Lamb Spring, Colorado, 2) Florida, and 3) the Great Lakes region (Table 1). The Lamb Spring samples were selected for three reasons. First, the Lamb Spring population is located along the front range of the Rocky Mountains just south of Denver, Colorado. To date, the “typical” morphology of *M. primigenius* has not been found in this population or anywhere in Colorado. Second, this population represents a death assemblage that accumulated over a short period of time (≤ 2500 years) (Rancier et al., 1982; Mandryk, 1998), so extensive temporal and environmental variations are limited. Third, the geologic age of the Lamb Spring sample is late Pleistocene in age, which is close to the minimum age for the Newton mammoth (ca. 14,000 years B.P.). The Florida sample of *M. columbi* is from a variety of localities but to date the “typical” morphology for *M. primigenius* is not recorded for any mammoth specimens from Florida. Although the precise ages of the Florida specimens are not known, they likely represent late Pleistocene localities (Webb, 1972). Previous paleoecological work characterized late Pleistocene Florida as predominately supporting *M. columbi* in two distinct stages of pine-dominated forest (during the LGM) and oak forest/scrub and prairie (post-LGM) (Koch et al., 1998), although there are documented discrepancies between northern and southern Floridian environments. The Great Lakes sample is a little more problematic in that both *M. columbi*, or its clinal variant

M. jeffersonii, and *M. primigenius* morphologies were found in this area (Saunders et al., 2010). The specimens chosen for this paper were all originally referred to *M. columbi*, and many of these specimens are dated and can be referred to the latest Pleistocene (14–10,000 years B.P.).

For the woolly mammoth comparative sample, we measured 58 M of *M. primigenius* collected in the summer of 1933 by Charles Frick and the Frick Expedition during their tour around the deposits outside of Fairbanks, Alaska (Table 1). The fossils were among thousands of specimens recovered from the outwash of perpetually frozen Pleistocene silt cliffs, which were being removed by giant hydraulic rams to expose the gold-rich gravels they overlaid (Galusha, 1975). Although it is difficult to ascribe individual specimens to an exact geographic locale due to the relative paucity of field reports from the Frick expeditions, Péwé (1975) noted that “... all taxa reported from the perennially frozen silt in the Fairbanks area are represented in silt of Wisconsinan age.” This is due to the observation that most fossil material recovered around Fairbanks comes from retransported valley-bottom silt and organic material of Wisconsinan age, which was deposited after the vertebrate-bearing loess facies of Illinoian age was predominantly removed (Péwé, 1975; Péwé and Reger, 1989). Without direct radiocarbon dates, an exact date cannot be reported for the molars used in this study; however, Guthrie (2006) reported dates on *Mammuthus* from the same area ranging from 14,023 \pm 98 years BP to

Table 1

Localities, stratigraphic information, age, species and number of molar specimens (N) from each population utilized in this study.

Site	Calibrated Age (reference)	Species	N	Depositional Environment or Stratigraphic Setting (reference)
Fairbanks, AL	14–49,000 years BP (Guthrie, 2006)	<i>Mammuthus primigenius</i>	58	Perennially-frozen loess alluvium indicative of a cold, steppe tundra environment (Péwé and Reger, 1989; Péwé, 1975)
Lamb Spring, CO	11–14,000 years BP (Rancier et al., 1982)	<i>Mammuthus columbi</i>	19	Reworked channel fill from an inactive spring peripheral to an alpine tundra environment (Mandryk, 1998)
Florida Sites	Late Pleistocene (Webb, 1972)	<i>Mammuthus columbi</i>	7	Pine forest mixed with broad-leaved upland habitats during the LGM; oak forest/scrub and prairie post-LGM (Koch et al., 1998)
Great Lakes Sites	13–21,000 years BP (Saunders et al., 2010)	<i>Mammuthus columbi</i>	10	Spruce dominated open woodland (Saunders et al., 2010)
Spring Lake	12–17,000 years BP (Barnosky et al., 1988)	<i>Mammuthus primigenius</i>	4	Spruce-herb parkland (Barnosky et al., 1988)

46,348 ± 2712 years BP, further suggesting a Wisconsinan or post-Wisconsinan date for the specimens in our study.

A pair of Yuasa digital calipers was used to measure the specimens. The exact values of the measured variables for our samples are presented in [Supplemental Table S1](#). The length of the molar was measured from the anterior end of the occlusal surface to the posterior end of the crown. The width of the molar was measured at the widest point of the occlusal surface. We did not include broken samples or teeth that experienced damage that would interfere with our measurements. We used these measurements to separate and select for only third molars in this study, which can be distinguished from other molars by their length, width, and numbers of plates ([Saunders, 1970](#)).

To remain consistent, lamellar frequency measurements were taken at four locations: the buccal base, buccal apex, lingual base, and lingual apex of the molar. We then reported the average value of these four measurements. This was done to account for sources of error of lamellar frequency in elephant molars due to the curvature of the teeth and the non-parallel arrangement of molar plates in both the horizontal and vertical planes (see [Maglio, 1973](#), pp. 12–13 for discussion).

Following [Aguirre \(1969\)](#), we reported enamel thickness as the average (±one standard deviation) of between 3 and 5 measurements along the crown as well as the maximum range of variation for each molar. This was done to account for the large range of enamel thicknesses occurring along the occlusal surface. The number of measurements varied based on visual assessment of enamel thickness (i.e., we took more measurements on teeth exhibiting a greater variety of thickness). Observed variation in enamel thickness arises from two conditions. First, the thickness of a singular enamel loph is not constant on the occlusal surface, as it locally pinches out in spots and is generally thicker at the peripheries than in the center. Second, newly-erupted plates generally expose either amalgamated sheaths (increasing the measured enamel thickness) or the thinner vertical apices of the sheaths (decreasing enamel thickness), while highly-worn anterior lophs may be conjoined or too eroded to return accurate enamel thickness values. As a result, enamel thicknesses tend to be more highly variable than lamellar frequencies.

We fit a linear regression to our plots to understand how co-dependent the two characters under observation were, then ran a Spearman's rank correlation coefficient as a nonparametric measure of statistical dependence between the two. We then ran a non-metric multidimensional scaling (NMDS) ordination on all numerical data using a Bray–Curtis dissimilarity index, which included the following metrics: length, width, lamellar frequency, enamel thickness minimum/maximum/average, and wear stage. We chose to report the variable loadings on the first two dimensions of the NMDS, which had stress values of 0.0150 and 0.0162, respectively. We overlaid convex hulls (polygons) representing the three species to the ordination using the function 'ordihull' (R package 'vegan'). The degree to which these polygons overlap provides a visual indication of the extent to which the Newton mammoth aligns with either the Woolly mammoth or the Columbian mammoth populations when all metrics are considered together. We evaluated the statistical validity of these polygons using the function 'ordiellipse' (R package 'vegan'), which draws 95% confidence intervals around class centroids as ellipses. If the ellipses do not overlap, they are outside of the assigned level of confidence, and the polygons are therefore considered significantly different.

4. Results

Length of molars of *M. columbi* ranged from a minimum of 212.8 mm to a maximum of 385.3 mm, with an average value of

271.1 mm (n = 36) ([Supplemental Table S1](#)). Length of molars of *M. primigenius* ranged from a minimum of 171.0 mm to a maximum of 345.0 mm, with an average value of 263.7 mm (n = 58). The width of molars of *M. columbi* ranged from a minimum of 72.4 mm to a maximum of 114 mm, with an average value of 92.8 mm. The width of molars of *M. primigenius* ranged from a minimum of 69.2 mm to a maximum of 119.7 mm, with an average value of 91.8 mm.

Specimens of *Mammuthus columbi* adhered well to the expected values outlined by [Maglio \(1973\)](#), with 32 of the 36 (~89%) molars characterized by a lamellar frequency of 5–9 plates/dm and an enamel thickness of 1.5–3.0 mm ([Fig. 3A](#)). The outliers all had enamel thicknesses of greater than 3.0 mm and a lamellar frequency of between 5 and 7 plates/dm; additionally, each of these molars was either wear stage XXVII or XXVIII, indicating teeth with a high degree of wear.

Specimens of *Mammuthus primigenius* did notably worse at adhering to Maglio's range of values, with only 28 of the 58 (~48%) molars characterized by a lamellar frequency of 7–12 plates/dm and an enamel thickness of 1.0–2.0 mm ([Fig. 3B](#)). The great majority of these outliers had an enamel thickness value that was too large (n = 27); only one outlier had a lamellar frequency that was too low (5.5 plates/dm). While some of these outliers fell outside the range of what Maglio found for either species of mammoth, 22 of the molars (~38% of *M. primigenius* teeth sampled) fell within the range of values expected only for *M. columbi*. Many of these molars were characterized by a late wear stage of XXVII or XXVIII.

The molars of the Newton mammoth retain an estimated 18 to 25 enamel-sheathed plates, a number which agrees with the estimate provided in the original examination ([Barnosky et al., 1988](#)). Whereas [Barnosky](#) obtained a width of 97 and 99 mm for the right and left M³, respectively, we obtained a width of 85 and 87 mm for the lower teeth. Likewise, we obtained length estimates of between 216 and 278.5 mm for the right and left m₃ versus their more constrained range of 235–255 mm. All of these estimates fall within the expected range of values for *M. columbi* and *M. primigenius* obtained by [Graham \(1986\)](#) and [Harington and Ashworth \(1986\)](#). Additionally, they fall within the range of values observed for the samples in this study.

We obtained lamellar frequencies of between 8 and 8.75 plates/dm on the four molars of the Newton mammoth based on an average of measurements taken at the four locations described above. While [Barnosky](#) reported a value of 9 plates/dm, this difference likely arises from the observation that plates space out towards the base of the crown ([Graham, 1986](#)), which served to lower our estimates. Our enamel thickness measurements ranged from a minimum of 1.0 mm to a maximum of 2.2 mm, with average values of 1.3–1.8 mm for the four teeth. This aligns closely with [Barnosky et al.](#)'s report of an enamel thickness of 1.5 mm. Both lamellar frequency and enamel thickness lie within the range of morphologic overlap expected *sensu* [Maglio \(1973\)](#) and reported by [Barnosky et al. \(1988\)](#).

Lamellar frequency and enamel thickness are indirectly proportional in both *M. columbi* ($\rho = -0.515$) and *M. primigenius* ($\rho = -0.561$) ([Fig. 4](#)). This indicates a significant ($p = 1.319e-3$; $p = 4.717e-6$) weak negative correlation ($R^2 = 0.304$; $R^2 = 0.256$) between the thickness and the spacing of the enamel lophs on the occlusal surface. Low R^2 values indicate that the data are more non-linear than a linear regression allow, a result of abundant intra-specific variation in molar characters. In [Fig. 4](#), it is apparent that the Newton mammoth clusters within the other *M. primigenius* and at the periphery of the *M. columbi*. It is also clear from the two regression lines that there is a great deal of overlap in these characters for the two species as originally discussed by [Barnosky et al. \(1988\)](#).

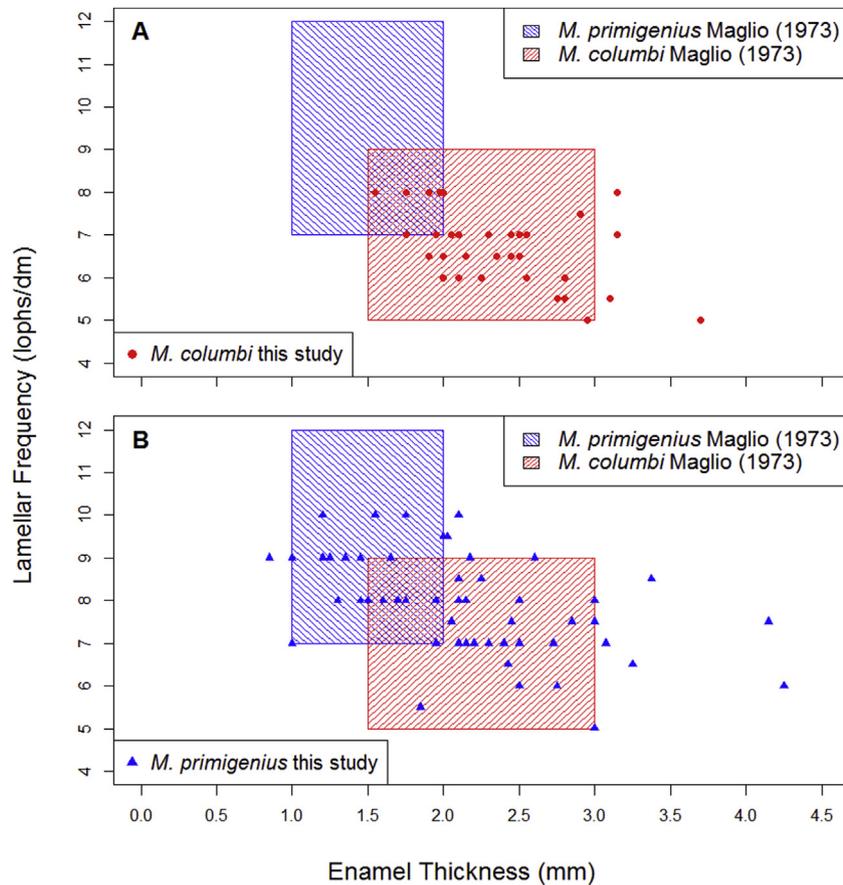


Fig. 3. Comparison of Expected Range of Characters (Maglio, 1973) and Measured Specimen Characters The range of lamellar frequency and enamel thickness measurements as outlined by Maglio (1973) and compared with *M. columbi* and *M. primigenius*. A) Overlay of *M. columbi* measurements with 89% (32/36) adherence. B) Overlay of *M. primigenius* measurements with 48% (28/58) adherence.

The Newton mammoth aligns better with the populations of *M. primigenius* than *M. columbi* in both lamellar frequency (Fig. 5) and enamel thickness (Fig. 6). For such a high wear stage, the mammoth retains a low enamel thickness and high lamellar frequency. Extrapolating back, the mammoth's molars should have, at the point of eruption, been characterized by an even lower enamel thickness and higher lamellar frequency. It would be against the observed trend for the molars to have had a higher enamel thickness and lower lamellar frequency at the point of eruption. Thus, although the Newton mammoth molars lie within the range of overlap of the two species, given the effects of dental wear we infer that they are better classified as the teeth of *M. primigenius*.

Additional support for the Newton mammoth as *M. primigenius* comes from a multivariate ordination using NMDS (Figs. 7 and 8). When considering all numerical metrics of the individual molars, the molars of the Newton mammoth lay within the ordination space of *M. primigenius* but outside of *M. columbi*. While this lends support for classifying the Newton mammoth as a woolly, one might also observe that nearly all Columbian molars lie within the range of *M. primigenius*. Therefore, there is no statistical difference between the two species when employing NMDS on molar characters alone, despite *a priori* knowledge of the two populations being different taxa. Because of this, molar characteristics alone are probably not the best means to classify species of *Mammuthus*.

5. Discussion

The summation of our results suggests that the Newton

mammoth is better classified as a woolly mammoth, *M. primigenius*, than a Columbian mammoth, *M. columbi*. Bivariate relationships between enamel thickness, lamellar frequency, and wear stage (Figs. 4–6) all highlight that the Newton mammoth falls peripheral to or outside of the cluster in *M. columbi* molars we examined, while falling well within the *M. primigenius* cluster. This is further highlighted by the multivariate ordination, which shows apparent disparity between *M. columbi* and the Newton mammoth (Figs. 7 and 8). Also evident from this study is the large morphological variation found in the sample of *M. primigenius*, which is perhaps a result of higher lamellar frequencies and thinner enamel in newly erupted molars coupled with ontogenetic changes in the surfaces of well-occluded teeth.

Despite the variation in values, the negative relationship between lamellar frequency and enamel thickness (Fig. 4) implies the following scenario: shortly after eruption, the enamel lophs exposed on the surface are tightly packed together, and the enamel ridges that make the plates up are thinner to allow for the lack of space. As the mammoth ages and the tooth wears down, the lophs pinch out and the space between lophs widens, and the larger gap between lophs (Fig. 5) is compensated for by thickening the enamel (Fig. 6). Our data indicate that across populations, both within species and between species, this relationship holds true.

The effects of dental wear may help to explain why *M. primigenius* molars can be found with lamellar frequency and enamel thickness values expected of *M. columbi*, but not vice versa (Fig. 3). None of the 36 *M. columbi* molars that we measured had a lamellar frequency above 9 plates/dm or an enamel thickness

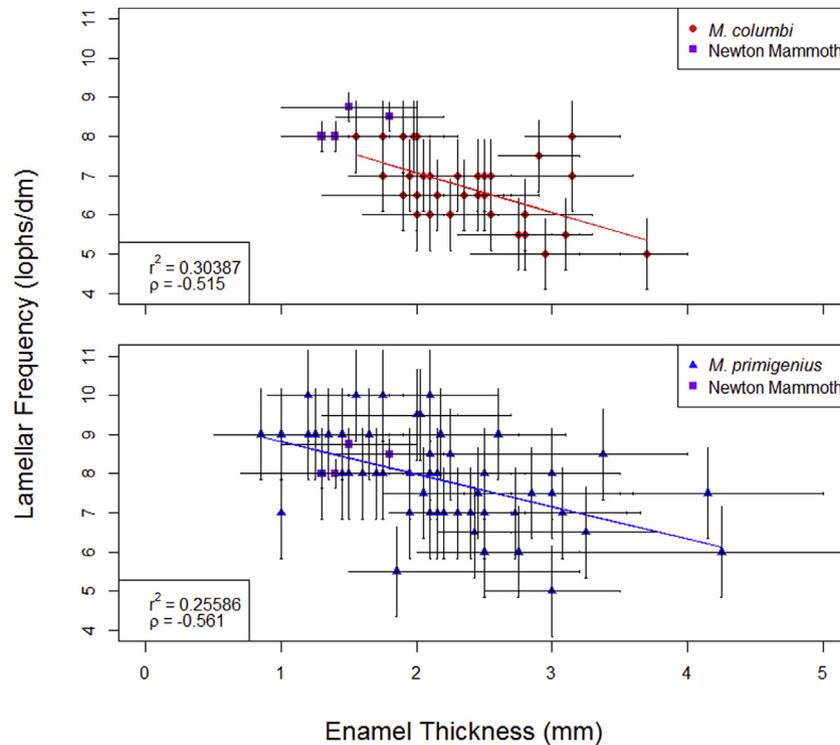


Fig. 4. Lamellar Frequency vs. Enamel Thickness Bivariate plots of enamel thickness and lamellar frequency for *M. columbi* (red circles) and *M. primigenius* (blue triangles), with the Newton mammoth (purple squares) for reference. Both species display an inverse relationship between the two variables, with lamellar frequency decreasing as the enamel plates of the occlusal surface increase in thickness. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

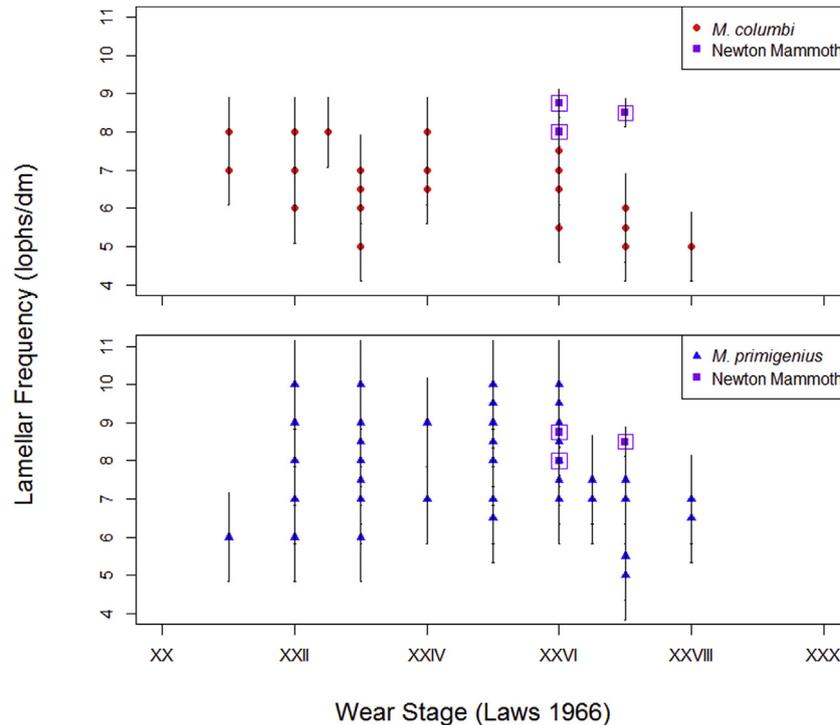


Fig. 5. Lamellar Frequency vs. Wear Stage Lamellar frequency as a function of wear stage (following Laws, 1966). Both taxa display a great deal of variance in the spacing between adjacent lophi; however, the Newton mammoth appears to align more appropriately with *M. primigenius*.

below 1.5 mm (Fig. 3A). Thus none of the *M. columbi* molars lie within the range of characters expected only for *M. primigenius*. This makes intuitive sense – if the upper range of *M. columbi* dental

characters is a lamellar frequency of 9 plates/dm and an enamel thickness of 1.5 mm, subsequent wear will only decrease the former value and increase the latter. We did, in fact, observe *M. columbi*

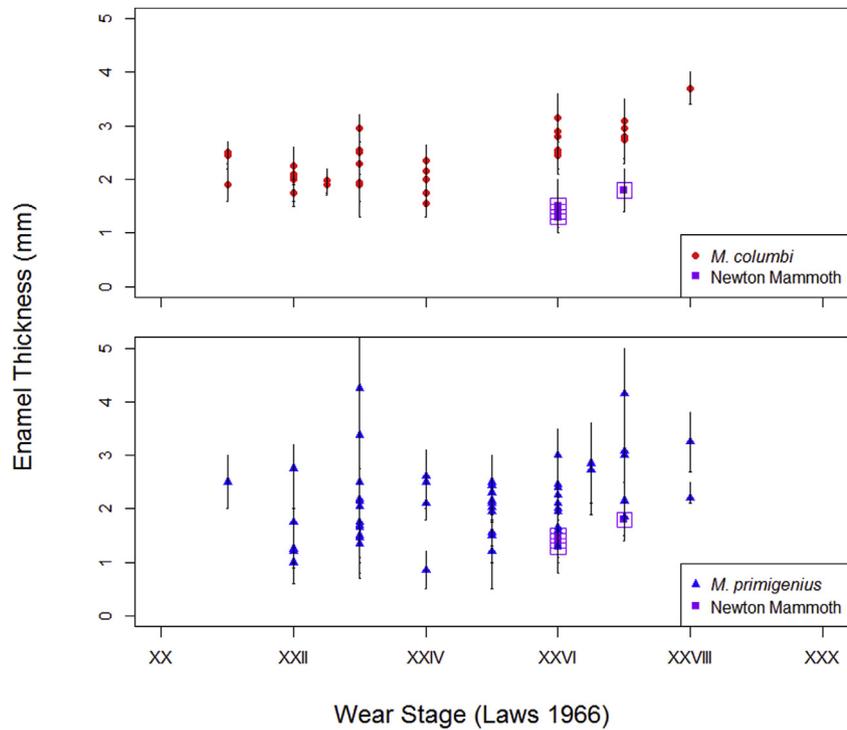


Fig. 6. Enamel Thickness vs. Wear Stage Enamel thickness as a function of wear stage (following Laws, 1966). *M. primigenius* (blue triangles) molars display more variable enamel thicknesses and cluster with the molars of the Newton Mammoth (purple squares). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

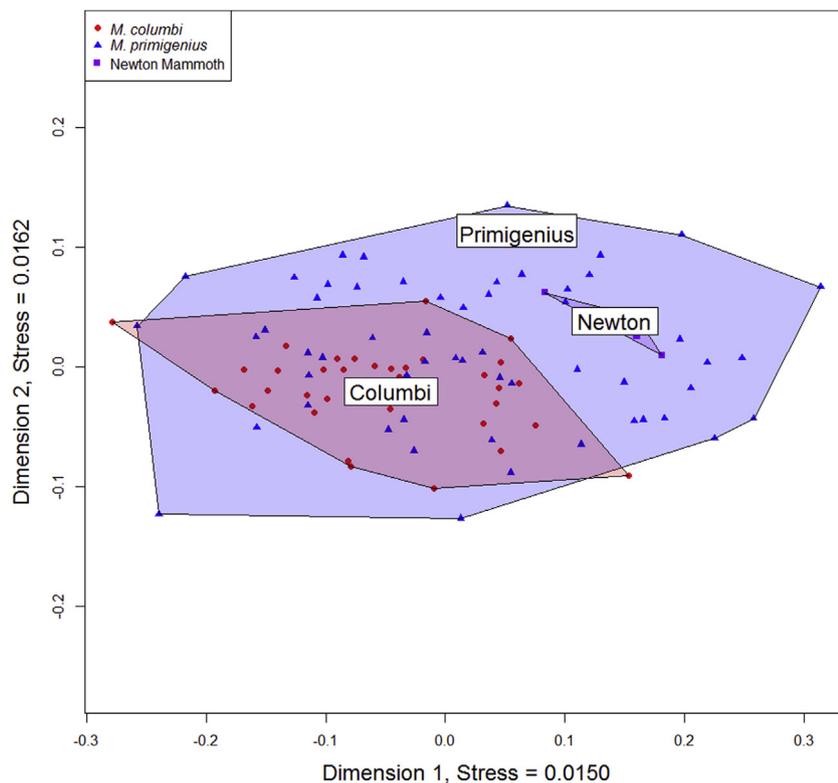


Fig. 7. Ordination of Molar Characters NMDS ordination of the following quantitative characters in mammoth molars: length, width, lamellar frequency, enamel thickness minimum/maximum/average, and wear stage. Polygons overlain on points to evaluate taxonomic segregation. *M. primigenius* displays sufficient variance to encompass both *M. columbi* and the Newton mammoth; however, the Newton mammoth and *M. columbi* do not overlap.

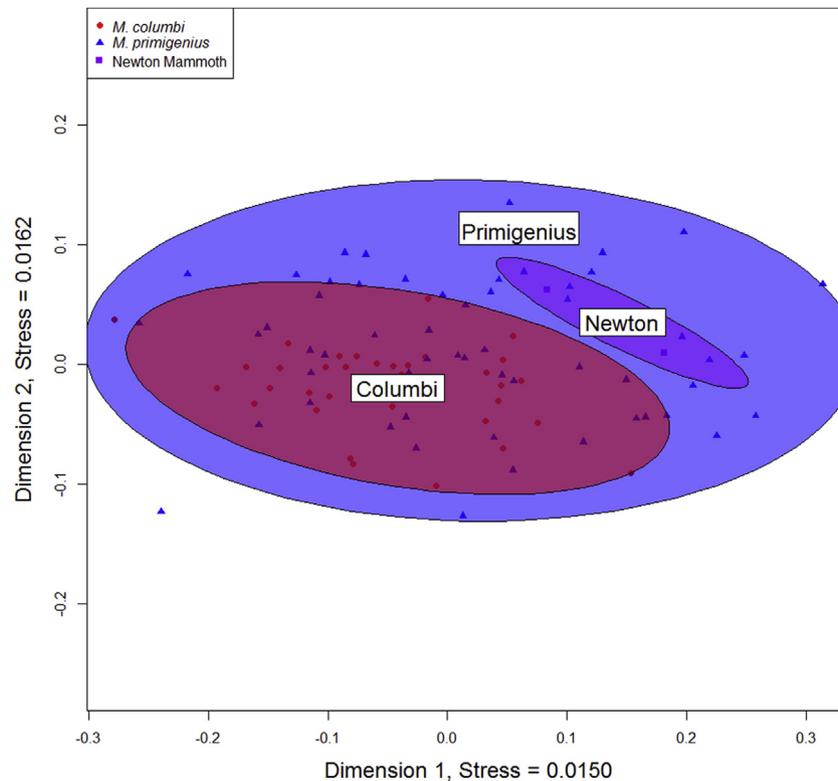


Fig. 8. Confidence Ellipses of Molar Characters 95% confidence ellipses overlain on the NMSD ordination. The lack of overlap between the Newton mammoth and *M. columbi* suggest the teeth are more disparate in quantitative characters than would be expected by chance.

teeth with a lamellar frequency of 5 plates/dm and an enamel thickness as high as 3.7 mm. On the other hand, *M. primigenius* lamellar frequency values ranged between 5.5 and 10 plates/dm and enamel thicknesses of above 4 mm were recorded (Fig. 3B), consistent with the inferred effects of dental wear.

Dental wear does not help to explain why the cranium length-to-width in the Newton mammoth is larger than average for *M. primigenius*. Barnosky et al. (1988) reported a ratio of 1.32 for the Newton mammoth, where his observed specimens of *M. columbi* gave a range of 1.11–1.72 and *M. primigenius* gave 0.7 to 1.08. It may be that woolly mammoths exhibited a larger range of length-width ratios than previously suggested. On the other hand, Barnosky et al. (1988) note that the Newton mammoth differs from other specimens of *M. columbi* “in its small size and its wide M3s” (Barnosky et al., 1988, p. 177). Classifying the Newton mammoth as *M. primigenius* does help to explain its wider-than-average third molars (85–101 mm), which fall well within the range of *M. primigenius* (69–119 mm, this study; 68–113 mm, Harington and Ashworth, 1986, p. 912) and at the upper limit of *M. columbi* (72–114 mm, this study; 70–100 mm, Graham, 1986, Fig. A2.2). The small size of the Newton mammoth skull is also consistent with skulls of *M. primigenius*, as pointed out originally by Barnosky et al. (1988).

Recent studies in mammoth taxonomy do not clarify taxonomic uncertainty in the group. Lister and Sher (2015) did a quantitative study of mammoth molars from the Holarctic where they recognized only two mammoth species, *M. columbi* and *M. primigenius*, in North America but they also documented overlap in dental attributes. Another taxon, *M. jeffersonii*, was recognized by other authors (Saunders et al., 2010). *Mammuthus jeffersonii* was differentiated from *M. columbi* by a third molar with a high plate count (24–30 plates), relatively thin enamel (1.5–2.0 mm), and a

high lamellar frequency (7–9) (Maglio, 1973, p. 62). Based upon the morphological attributes discussed above, *M. jeffersonii* teeth are difficult to differentiate from *M. primigenius* (e.g., Maglio, 1973; Saunders, 1988; Lister and Sher, 2015). Osborn (1942) also characterized *M. jeffersonii* teeth as having short length, broad width and crimped enamel in comparison to *M. columbi*. Saunders et al. (2010, p. 176) used these characters to identify *M. primigenius* from Sugar Creek, Illinois.

Recent ancient DNA (aDNA) studies of North American *M. primigenius* and *M. columbi* indicate that the breeding dynamics and morphological attributes of these two species is much more complex than it has previously been assumed. Late Pleistocene *M. primigenius* specimens from North America and latest Pleistocene (ca. 11,000 years B.P.) and *M. columbi* from both Utah (Huntington Mammoth) and Wyoming (Union Pacific Mammoth) share a mitochondrial haplotype (Enk et al., 2011). Therefore, it appears that there was gene flow between these geographically disparate populations. Furthermore, it suggests that *M. jeffersonii* may be a hybrid of the other two species (Enk et al., 2011). Much more aDNA work is needed to determine the precise dynamics between North American mammoths.

Our study suggests that the Newton mammoth is best categorized as a woolly mammoth, *M. primigenius*. However, given certain characters, primarily the skull size, it is possible that it could represent a hybrid between *M. columbi* and *M. primigenius*. One test for this hypothesis would be aDNA analysis of the Newton mammoth. In the absence of aDNA testing, examination and analysis of previous specimens from the area assigned to *M. columbi* and mapped by Agenbroad (1984) would be beneficial. It is possible that some or all of those specimens do not actually represent *M. columbi*, perhaps belonging instead to *M. primigenius* since the effects of dental wear were not taken into account at the time of

identification.

5.1. Environments and mammoth tooth morphology

Another interesting question with regards to the variability and morphology of late Pleistocene mammoth teeth is the role environment might play in the selection for morphology (i.e., phenotypic plasticity). As discussed above, most *M. columbi* are associated with vegetation indicative of warmer climates than those of *M. primigenius*. *Mammuthus columbi* is frequently found with other grazing animals including horses (*Equus* sp.), bison (*Bison* sp.), camels (*Camelops* sp.), and grazing sloth (*Paramylodon harlani*) (McDonald and Pelikan, 2006). Although *M. columbi* is found in a variety of environments from Washington to Florida, it appears to have preferred parkland- or savanna-like environments. On the other hand, *M. primigenius* is frequently associated with pollen records reflecting tundra-like environments or open spruce (*Picea*) forest (Saunders et al., 2010).

Spring Lake, the location where the Newton Mammoth was discovered, lies 16 km southeast of Towanda, in Bradford County, Pennsylvania. Spring Lake is a kettle lake that lies about 50 km south of the Valley Heads Moraine, which records a late Wisconsin series of fluctuations in the southern terminus of the ice sheets occurring between 15,000 and 12,600 years B.P. (Mickelson et al., 1983). About 50 km south of Spring Lake is the Olean drift border, a feature thought to represent the maximum advance of late Wisconsin ice between ca. 20,000 and 12,700 years B.P. (Mickelson et al., 1983, p. 24). The Newton mammoth, like other *M. primigenius* and *M. jeffersonii*, was in close association with the glacial front.

Pollen cores obtained from the center of Spring Lake and dating to the same time interval and lithological unit as the mammoth skeleton show an assemblage dominated by *Picea* and less abundantly by *Pinus*, Cyperaceae, and Poaceae, leading to the conclusion that the area surrounding Spring Lake at the time the mammoth lived was an open spruce parkland environment with tundra-like areas (Barnosky et al., 1988). The assemblage of fossil insects recovered from the 12,080-year stratum support an interpretation that the environment was mostly treeless. Additionally, they indicate that the environment surrounding Spring Lake experienced similar climatic and thermal conditions as the present Arctic tree line (Barnosky et al., 1988). This environment is more closely associated with *M. primigenius* rather than *M. columbi*.

Radiocarbon dates from an organic-rich silt encasing the recovered mammoth bones place the age of the mammoth between 12,080 ± 100 and 15,910 ± 160 yr BP (WIS-1925) (12,152 ± 272 and 17,144 ± 244 Cal BC), consistent with a date on the bone of 14,240 ± 150 yr BP (15,504 ± 272 Cal BC) (WIS-1935) (Barnosky et al., 1988). Calibrated dates for the Newton site are reported here using the calibration curve CalPal2007_hulu. However, recent advances in both methodology and technology for deriving ¹⁴C dates suggest that these are actually minimum ages. First, it has been shown that bone dates on collagen gel, whether done by the conventional beta counting method or the AMS method, are frequently younger than dates based upon individual amino acids or purified collagen (Stafford et al., 1991). Secondly, Grimm et al. (2009) have shown that bulk sediment dates from pollen cores are also frequently too young when compared with AMS dates on organic remains like seeds, wood, needles, etc. from the same horizons. Thus, new ¹⁴C dates on the mammoth bone may be required to determine its precise geological age. If it is older than 14,000–15,000 years B.P., and we hypothesize that to be the case, then the regional environmental reconstruction indicating low vegetation cover on a cold, dry landscape (e.g., Williams et al., 2004) is consistent with our taxonomic identification.

Others suggested that late Pleistocene mammoths in the Midwest (Joyce, 2006; Saunders et al., 2010) and New York State (Feranec and Kozłowski, 2016) may have occupied forested environment. Upon first consideration, this might suggest a degree of behavioral and/or dietary flexibility in mammoths that was previously unappreciated. Indeed, all of these sites do have pollen spectra indicative of forested environments; however, with closer examination of the records, it appears that all of the mammoths are associated with a tundra-like or a spruce-tundra-like environment characteristic of the woolly mammoth. (Johnson, 1997; Feranec and Kozłowski, 2016).

This raises the possibility that a dentition more similar to that of *M. primigenius* is better adapted to the vegetation of these cold, dry, and perhaps dusty environments whereas the dentition of *M. columbi* is better for warmer environments with more grass (e.g., grassy parkland- and savanna-like vegetation). Thus, vegetation type may have more to do with mammoth tooth morphology than its genotype. The mix of *M. columbi*-type and *M. primigenius*-type aDNA in the Utah and Wyoming populations (Enk et al., 2011, 2016) may reflect this aspect of dental adaptation. Both of these mammoths exhibit a typical *M. columbi* tooth morphology although they are genetic hybrids. Neither exhibit intermediate dentitions. Clearly, if this is the case, then there is a need to re-evaluate mammoth taxonomy based on dentition. It may be less useful for North American paleontologists to recognize individual species of mammoth in the late Pleistocene, but rather to refer to clinal variants of *Mammuthus* along environmental gradients. Future work on the relationship of genotype and phenotype should evaluate mammoth populations across a broad geographic area in order to examine the relationship between inferred genotypes and dental parameters.

6. Conclusions

Based on the effects of dental wear, the Newton mammoth is better classified as *Mammuthus primigenius*. Our analyses show that once dental wear is considered, the Newton mammoth third molars must have had a higher lamellar frequency and lower enamel thickness than is observed on the worn molars today, placing them within the range of *M. primigenius*. Other characteristics of the Newton mammoth noted by Barnosky et al. (1988), such as a smaller skull and short wide molars, are more congruent with *M. primigenius* than *M. columbi*. Finally, even though geography and environments cannot be used to infer taxonomic grouping, the tundra-like and spruce parkland-like environments reconstructed for the Newton mammoth are more consistent with *M. primigenius* than *M. columbi*.

There are still many questions that remain with regards to the Newton mammoth, in particular, and mammoth taxonomy, in general. Re-dating of the specimen will allow us to test our hypothesis that the Newton mammoth is older than indicated by the existing ¹⁴C dates. Analysis of aDNA, if preserved, will further test our taxonomic interpretation. Re-examination of mammoth teeth assigned to *M. columbi* in other areas of the northeast would be beneficial in light of our observations of dental wear and taxonomy. Most important, however, is to obtain a better understanding of the relationships between genotypic and phenotypic selection in determining the morphology of mammoth teeth.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2017.01.030>.

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