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Research Article

Taxonomic, biogeographic, and biological implications of mammoth teeth from a dynamic Pleistocene landscape in Alberta, Canada

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Abstract

Continental-scale patterns of morphological and biological change represent broad time- and spatially averaged interpretations. Conversely, regionally focused studies of morphological variability offer an opportunity to consider patterns of biological change at more refined spatial scales, where nuanced histories may be identified. That approach is particularly applicable for areas known to have dynamic biogeographic and glacial landscapes (e.g., western Canada). We studied proboscideans from Alberta, Canada, an area thought to represent a zone of sympatry between extinct forms of mammoth (i.e., *Mammuthus columbi*, *Mammuthus primigenius*) in order to test existing taxonomic hypotheses and chronologically contextualize the regional record of mammoths through the Late Pleistocene. Morphometric analysis of sixth molars of mammoths from Alberta (n = 17) support identification of three distinct morphologies that we assign to *M. columbi*, *M. primigenius*, and intermediates of those taxa. The presence of intermediate forms is perhaps unsurprising, given both the recognition of hybridization in *M. columbi* and *M. primigenius* and the previously documented occurrence of both taxa in Alberta. Some records of *M. columbi* may document a broader northern geographic incursion for that taxon than previously recognized, but could also represent a much deeper time component to the history of *Mammuthus* in Alberta (i.e., *Mammuthus trogontherii*).

Keywords: Proboscidean, Elephantidae, *Mammuthus*, biological turnover, teeth, biogeography, morphometrics, megafauna

Introduction

Mammuthus is one of several iconic extinct Ice Age genera that define both scientific and popular reconstructions of Late Pleistocene North American landscapes. Our understanding of the paleontological record of species of *Mammuthus* is largely a reflection of our understanding of dental morphology, and the relationship of that morphology to taxonomy. Variation and morphological patterns in mammoth teeth are mostly considered at continental scales (e.g., Lister and Sher, 2015; Lister, 2017), but regional studies highlight the significance of evaluating geographically restricted samples in order test broad hypotheses of change in proboscidean populations in North America (e.g., Saunders et al., 2010). Here, we summarize morphometric features of isolated mammoth teeth from Alberta, Canada, a geographic region with documented biogeographic fluidity thought to preserve the remains of both woolly and Columbian mammoths (Harington and Shackleton, 1978; Burns and Young, 1994; Burns et al., 2003; Hills and Harington, 2003; Jass and Barrón-Ortiz, 2017). We use those morphometric data, morphometric data from the literature (Lister and Sher, 2015; Widga et al., 2017), and both new and previously published radiocarbon data to establish an understanding of and context for quantitative morphological variation in mammoth teeth from Alberta. Finally, we discuss the significance of our observations for existing taxonomic hypotheses of *Mammuthus* from Alberta.

Taxonomic context

The taxonomy of non-insular North American species of *Mammuthus* has changed considerably since Osborn's (1942) seminal work, where 15 species of *Mammuthus* were recognized. Subsequent work vastly reduced the number of recognized species, with most studies identifying between two and four valid species occurring in the Late Pleistocene (*Mammuthus columbi*, *Mammuthus exilis*, *Mammuthus jeffersonii*, and *Mammuthus primigenius*; e.g., Maglio, 1973; Kurtén and Anderson, 1980; Madden, 1981; Agenbroad, 1984, 1994, 2005; Graham, 1986; Saunders et al., 2010; Lister and Sher, 2015; Lister, 2017; Lucas et al., 2017; Widga et al., 2017). For Late Pleistocene faunas of western North America, most authors now restrict morphological identifications to *M. primigenius* (woolly mammoth) and *M. columbi* (Columbian mammoth), with the former distributed in "northern" latitudes and the latter in "southern" latitudes.

Dental remains have always played a prominent role in the taxonomy of mammoths. Not only are teeth durable, facilitating their preservation and recovery, but they possess characters used by researchers since the 1800s in order to establish and recognize different mammoth species (Osborn, 1942; Maglio, 1973; Madden, 1981; Lister, 2017). The total number of lamellae (enamel plates), relative spacing of lamellae, and relative enamel thickness of the

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last permanent molars are some of the characters used to distinguish mammoth species (e.g., Lister and Sher, 2015; Lister, 2017; Widga et al., 2017). In recent years, genomic (Enk et al., 2016; Chang et al., 2017; Palkopoulou et al., 2018; van der Valk et al., 2021) and morphological (Lister and Sher, 2015; Lister, 2017; Widga et al., 2017) studies documented evidence of hybridization and introgression between *M. primigenius* and *M. columbi*, suggesting possible further complexity for our understanding of morphological variation in mammoth dentitions. Minimally, those studies illustrate the need for comprehensive descriptions of morphometric and statistical data for teeth at a regional level in order to understand morphological variability across time and space.

Among the most widely utilized dental characters in mammoth taxonomy are: (1) the total number of lamellae in an unworn molar; (2) the relative crown height (i.e., degree of hypsodonty) in an unworn molar; (3) the relative spacing between lamellae; and (4) the relative thickness of occlusal enamel bands (Osborn, 1942; Maglio, 1973; Madden, 1981; Lister and Sher, 2015). These traits can be studied in any of the upper (M) or lower (m) molars produced within the lifespan of an individual, but most researchers place special emphasis on the upper and lower M6—the last molar to form and erupt into the oral cavity (= M3 of some authors). Of particular relevance to our work is the distinction between *M. primigenius* and *M. columbi*. Although relative crown height is not particularly different between the two taxa, molars of *M. primigenius* possess on average a greater number of lamellae, narrower relative spacing between lamellae, and narrower enamel thickness than molars of *M. columbi* (Lister and Sher, 2015). We note that molars of *M. trogontherii*, an Early to Middle Pleistocene Eurasian and Beringian species which is considered by some researchers to have given rise to both *M. columbi* and *M. primigenius* (Lister and Sher, 2015; Lister, 2017; van der Valk et al., 2021), has dental characters that closely resemble those observed in *M. columbi* (Lister and Sher, 2015; Lister, 2017). Pending further morphological and molecular analyses, the retention of *M. columbi* and *M. trogontherii* as "separate species names [is] largely a pragmatic decision based on long historical usage in North America and Eurasia, respectively." (Lister, 2017, p. 27). Morphological and molecular analyses of Early to Middle Pleistocene mammoth specimens will likely continue to clarify that interpretation (e.g., van der Valk et al., 2021).

The published late Quaternary record of mammoths in Alberta was recently summarized along with tentative species identifications for many previously unreported isolated mammoth teeth from Alberta (Jass and Barrón-Ortiz, 2017). Those identifications were based on preliminary observations of enamel thickness and lamellar frequency (Jass and Barrón-Ortiz, 2017). Teeth retaining characters deemed consistent with *M. columbi* and *M. primigenius* were both reported, along with specimens that appeared to show intermediate morphologies, with the caveat that future analyses would permit further evaluation of those taxonomic hypotheses.

Mammoths, megafauna, and a dynamic landscape

Most records of mammoth in Alberta represent isolated data points consisting of single specimens, including isolated teeth (Burns et al., 2003; Jass and Barrón-Ortiz, 2017). Those records, and other records of megafauna, come mostly from uncertain stratigraphic positions in alluvium, in both primary and secondary depositional settings that may include Quaternary vertebrate remains representing a range of Pleistocene ages (e.g., Hills and Wilson, 2003). As a result, records of Quaternary megafauna in Alberta are sometimes viewed through the lens of broad time bins (e.g., Jass et al., 2011). As increasing numbers of individual specimens are directly dated or evaluated in other ways (e.g., aDNA), more specific biological patterns may emerge for individual taxa.

Recent work examining aDNA of separate series of the isolated records of *Bison* and *Mammut* has shown that for at least some megafauna, the Quaternary vertebrate record preserved in Alberta is biogeographically complex (Heintzman et al., 2016; Karpinski et al., 2020). For mastodons, in particular, genetic data indicate the presence of different clades at discrete time intervals through the Pleistocene, reflecting possibly distinct temporal dispersals (Karpinski et al., 2020). Such patterns likely correspond with the significant environmental and geologic fluctuations documented for the Pleistocene in western Canada (e.g., Dyke et al., 2003; Dyke, 2004, 2005; Dalton et al., 2020). However, our understanding of the interrelationship of environmental and geologic fluctuations with biogeographic patterns of individual taxa, and the relationship between those biogeographic patterns and morphological patterns preserved in the regional fossil record, remains limited for most taxa (e.g., mammoths).

Some researchers suggested that *M. columbi* and *M. primigenius* were allopatric (e.g., Maglio, 1973), but more recent work suggests time-averaged sympatry in the distributions, at least at the margins of the ranges at mid-latitudes (Agenbroad et al., 1994; Enk et al., 2016; Smith and Graham, 2017; Widga et al., 2017). Modern elephants can range over vast geographic spaces within a lifetime, with estimated ranges from hundreds to thousands of square kilometers (e.g., Lindeque and Lindeque, 1991; Douglas-Hamilton et al., 2005; Ngene et al., 2017), and recent work on *M. primigenius* suggests that similar scales of mobility occurred in *Mammuthus* (Wooler et al., 2021). Given sympatric records elsewhere, the mobility of elephantids, and evidence for introgression among mammoths (e.g., Enk et al., 2016), the presence of sympatric populations seems a reasonable inference for Alberta, where mammals with northern and southern evolutionary origins are inferred as co-occurring over broad time scales (e.g., Burns, 2010; Jass et al., 2011).

Given that context and the tentative taxonomic identifications proposed by Jass and Barrón-Ortiz (2017), we predicted that mammoth teeth recovered from Upper Pleistocene deposits in Alberta would show a particularly large range of quantitative variation, ranging from "typical" *M. primigenius* to "typical" *M. columbi* morphologies, and including specimens with intermediate morphologies (see "Materials and Methods" for delimitation of "typical" and intermediate morphologies). Given the currently documented biogeographic distributions of those taxa and rare documentation of *M. columbi* in northern North America (see Smith and Graham, 2017), we also predicted that *M. primigenius* would be more prevalent in our samples.

Materials and methods

Following the dental nomenclature of Agenbroad (1994), the sixth upper molars (M6) and sixth lower molars (m6) are the last molars to form, erupt, and come into occlusion in *Mammuthus*; they are referred to by some researchers as the permanent M3/m3 molars (e.g., Lister and Sher, 2015; Widga et al., 2017). We studied the sixth molars (M6/m6) of *Mammuthus* recovered from Pleistocene deposits in Alberta, Canada (Tables 1a, b and

Table 1a. Data for M6 of *Mammuthus* recovered from Alberta, Canada. All measurements in millimeters.

Number	Locality	Side	PF	P	min P	L	W	W′	C	H
RAM P84.5.1	Pit 48	Left	x21-	22		294.84	86.57 (l2)	80.32 (l2)	6.25 (3.5 + 2.75)^{a}	178.41 (l12)
RAM P02.8.70	Twin Bridges Gravel Pit 4	Right?	-23p			250.00	104.97 (l′5)	96.71 (l′5)	8.26 (4.13 + 4.13)^{b}	149.12 (l′15)
RAM P80.14.1	Elm Jay Industrial Park	Left	∞25p	25		272.91	96.93 (l3-4)	91.33 (l3-4)	5.6 (2.08 + 3.52)^{a}	144.38 (l10)
RAM P91.10.4	Pit 45	Right?	x17-	21		225.95	93.57 (l5-6)	90.23 (l5-6)	3.34 (1.67 + 1.67)^{a}	192.43 (l5)
RAM P81.3.5	Undocumented gravel pit, Alberta	Right	∞12-			142.92	120.93 (l′7)	115.17 (l′7)	5.76 (2.88 + 2.88)^{a}	127.67 (l′11; advanced wear)
RAM P97.8.1	Schultz Resort Site	Right	-14-			195.96	93.29 (l′2-3)	88.29 (l′2-3)	5.0^{c}	151.16 (l′7)
RAM P88.7.1	North Saskatchewan River	Left?	-13- (l′6,i,l′7,i, l′8)			203.68	97.91 (l′4)	92.61 (l′4)	5.3 (2.65 + 2.65)^{a}	200.24 (l′7)
RAM P94.4.3	Pit 46	Left	∞18p			276.88	109.59 (l′7)	104.59 (l′7)	5.0^{c}	148.51 (l′13; minimum, plate worn)
ROM 28983	Villeneuve	?					113.0			210
ROM IBW.83	Medicine Hat	?	x16-				102.0		5.0^{c}	180

Key: PF, Plate Formula; ∞, anterior loss through wear; -, anterior loss through breakage; x, anterior talon; p, posterior platelet; i, "accessory" lamellae; P, observed or reconstructed complete lamellar number excluding x and p; L, length of the preserved tooth crown perpendicular to the average orientation of lamellae; W, width of the tooth crown at the widest preserved lamella including cementum; W′, width of the tooth crown at the widest preserved lamella excluding cementum; l and l′, lamella (or lamellae) where measurements were taken (the lamellae are numbered in an anterior–posterior direction [excluding the talon]; l indicates lamella(e) of teeth in which the anterior end of the crown is preserved or reliably estimated; l′ indicates that the anterior portion of the crown is broken or worn and the lamellae are numbered from the anterior end of the preserved crown); C, cementum thickness (estimated based on measurements of cementum preserved on medial and/or lateral sides); H, tooth crown height at the highest unworn, preserved lamella, measurements for worn lamellae are noted. All data are from this study, with the exception of ROM 28983 and ROM IBW.83 (from Lister and Sher, 2015).

[a] Cementum measured on occlusal surface.

[b] Based on cementum measurement from posterior portion of tooth.

[c] Estimated.

Table 1b. Additional data for M6 of *Mammuthus* recovered from Alberta, Canada. All measurements in millimeters.

Number	Locality	LF	LFcalc	LL	LL′	ET	100*LL/W (LLI)	100*LL′/W′ (LLI′)	100*ET/W (ETI)	100*ET/W′ (ETI′)
RAM P84.5.1	Pit 48	7.03	7.12	14.22	14.04	2.28	16.43	17.48	2.63	2.84
RAM P02.8.70	Twin Bridges Gravel Pit 4	9.3	9.20	10.75	10.87	2.16	12.42	11.24	2.06	2.23
RAM P80.14.1	Elm Jay Industrial Park	9.92	9.16	10.08	10.92	2.03	11.64	11.95	2.10	2.22
RAM P91.10.4	Pit 45	7.81	7.52	12.80	13.29	2.12	14.79	14.73	2.27	2.35
RAM P81.3.5	Undocumented gravel pit, Alberta	7.33	8.40	13.64	11.91	1.99	15.76	10.34	1.65	1.73
RAM P97.8.1	Schultz Resort Site	7.43	7.14	13.46	14.00	2.34	15.55	15.85	2.50	2.64
RAM P88.7.1	North Saskatchewan River	6.28	6.38	15.92	15.67	2.35	18.39	16.92	2.40	2.53
RAM P94.4.3	Pit 46	6.08	6.50	16.45	15.38	2.78	19.00	14.71	2.53	2.66
ROM 28983	Villeneuve	8.60		11.63		1.6	13.43		1.42	
ROM IBW.83	Medicine Hat	6.88		14.53		2.0	16.79		1.96	

Key: LF, lamellar frequency; LFcalc, calculated lamellar frequency; LL, lamella length calculated using LF; LL′, lamella length calculated using LFcalc; ET, enamel thickness; LLI, ETI and LLI′, ETI′ are variables standardized to a crown width (W and W′, respectively) of 100 mm (see "Materials and Methods"). All data are from this study, with the exception of ROM 28983 and ROM IBW.83 (from Lister and Sher, 2015).

2a, b, Fig. 1). Our study sample (n = 17) was limited to teeth that did not show advanced stages of wear as this can confound the taxonomic identification of mammoth molars (Smith and Graham, 2017). Additionally, teeth in our sample were complete enough and in a state of preservation that permitted measurement of at least three variables: tooth width, lamellar frequency, and enamel thickness (Tables 1a, b and 2a, b). We directly measured 14 specimens housed at the Royal Alberta Museum (RAM) in

Table 2a. Measurements of m6s of *Mammuthus* recovered from Alberta, Canada. All measurements in millimeters.

Number	Locality	Side	PF	P	min P	L	W	C	H
RAM P99.3.164	Pit 48	Left	xx25p	25		331.96	83.86 (l6)	7.43 (4.18 + 3.25)[e]	140.08 (l10; minimum, plate worn)
RAM P97.10.144	Island Bluff	Left	x21-			288.94[b]	110.59 (l′15)	6.5 (3.25 + 3.25)[f]	158.92 (l13)
RAM P97.10.143	Island Bluff	Right	xx12-				110.24 (l11)	6.5 (3.25 + 3.25)[f]	167.16 (l9; starting to come into wear)
RAM P18.319.4	Empress Pit	Right	-11p				108.70 (l′2)	8.68 (4.34 + 4.34)[e]	116.44 (l′9; minimum, plate worn)
RAM P97.11.1b	Riverview Pit	Left	∞22-[a]		24	245.97[c]	99.63 (l′10)	4.12 (2.06 + 2.06)[g]	120.95 (l′16)
RAM P97.11.1b	Riverview Pit	Left	∞22-[a]		24	245.97[c]	99.63 (l′10)	4.12 (2.06 + 2.06)[g]	120.95 (l′16)
RAM P21.391.1	Schwengler Mammoth	Right	x21-	~24		301.17[b]	96.18 (l9)	4.28 (2.14 + 2.14)[h]	158.48 (l14)
CMN 17845	Bindloss	Right	-8-				107.3[d]	5.8	120

Key: PF, Plate Formula; ∞, anterior loss through wear; -, anterior loss through breakage; x, anterior talonid; p, posterior platelet; P, observed or reconstructed complete lamellar number excluding x and p; ~, approximately; L, length of the preserved tooth crown perpendicular to the average orientation of lamellae; W, width of the tooth crown at the widest preserved lamella including cementum; l and l′, lamella (or lamellae) where measurements were taken (the lamellae are numbered in an anterior–posterior direction [excluding the talonid]; l indicates lamella(e) of teeth in which the anterior end of the crown is preserved or reliably estimated; l′ indicates that the anterior portion of the crown is broken or worn and the lamellae are numbered from the anterior end of the preserved crown); C, cementum thickness (estimated based on measurements of cementum preserved on medial and/or lateral sides); H, tooth crown height at the highest unworn, preserved lamella, measurements for worn lamellae are noted. All data are from this study, with the exception of CMN 17845 (from Churcher, 1972).

[a] Embedded in jaw; posterior end not visible.

[b] Missing plates at the end.

[c] To last measurable plate [l′20].

[d] Cementum thickness of 5.8 mm added to reported width (Churcher, 1972) based on average cementum width of the other Alberta teeth studied.

[e] Cementum measured on occlusal surface.

[f] Cementum measured on occlusal surface, anterior position of specimen P97.10.143.

[g] Based on cementum measured in area where it was sectioned.

[h] Cementum measured on occlusal surface, anterior portion.

Table 2b. Additional measurements of m6s of *Mammuthus* recovered from Alberta, Canada. All measurements in millimeters.

Number	Locality	LFB	LLB	ET	100*LLB/W (LLBI)	100*ET/W (ETI)
RAM P99.3.164	Pit 48	7.50	13.33	1.85	15.90	2.21
RAM P97.10.144	Island Bluff	6.30	15.87	2.36	14.35	2.13
RAM P97.10.143	Island Bluff	7.10	14.08	2.35	12.78	2.13
RAM P18.319.4	Empress Pit	5.10	19.61	2.64	18.04	2.43
RAM P97.11.1b	Riverview Pit	5.44[a]	18.38[a]	1.77	18.45[a]	1.78
RAM P97.11.1b	Riverview Pit	5.59[b]	17.89[b]	1.77	17.96[b]	1.78
RAM P21.391.1	Schwengler Mammoth	5.85	17.09	2.25	17.77	2.34
CMN 17845	Bindloss	5	20.00	3	18.64	2.80

Key: LFB, basal lamellar frequency; LLB, basal lamella length; ET, enamel thickness; LLBI and ETI are variables standardized to a crown width (W) of 100 mm (see "Materials and Methods"). All data are from this study, with the exception of CMN 17845 (from Churcher, 1972).

[a] LFB, LLB, and LLBI is for medial side (the buccal side is embedded in the jaw).

[b] LFB, LLB, and LLBI estimated by calculating the average ratio between lamellar frequency of medial and lateral sides in other m6 specimens from RAM (see "Materials and Methods"); these values are presumably closer to the actual LFB, LLB, and LLBI for this specimen.

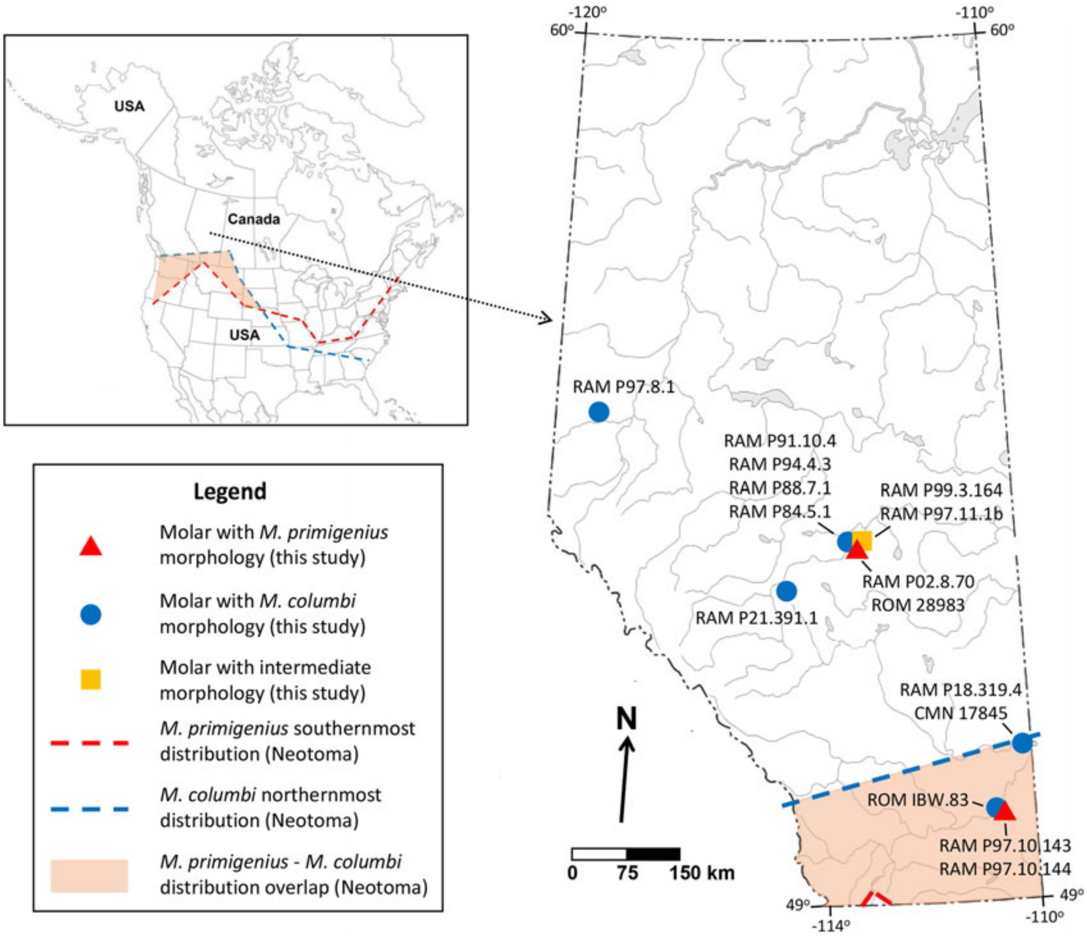

Figure 1. Locality map for specimens of *Mammuthus* included in this study. Inset map includes known northern margins for distribution of *M. columbi* and known southern margins for distribution of *M. primigenius*. Zone of geographic overlap is illustrated by shaded area. Distributional boundaries based on records in Neotoma Paleoecology Database (Williams et al., 2018). Requests for more specific locality information should be directed to the Royal Alberta Museum.

Edmonton, Alberta, Canada (Figs. 2 and 3), and added published measurements of specimens housed at the Canadian Museum of Nature (CMN; Ottawa, Ontario, Canada) and Royal Ontario Museum (ROM; Toronto, Ontario, Canada). We note that RAM P94.4.3 was reported as a lower left m6 and P97.10.144 as an upper left M6 (Jass and Barrón-Ortiz, 2017), but we here identify them as an upper left M6 and a lower left m6, respectively (Tables 1a, b). We also revise the identifications of RAM P81.3.5 and P97.8.1, which were previously questionably identified as sixth molars (Jass and Barrón-Ortiz, 2017) (Tables 1a, b).

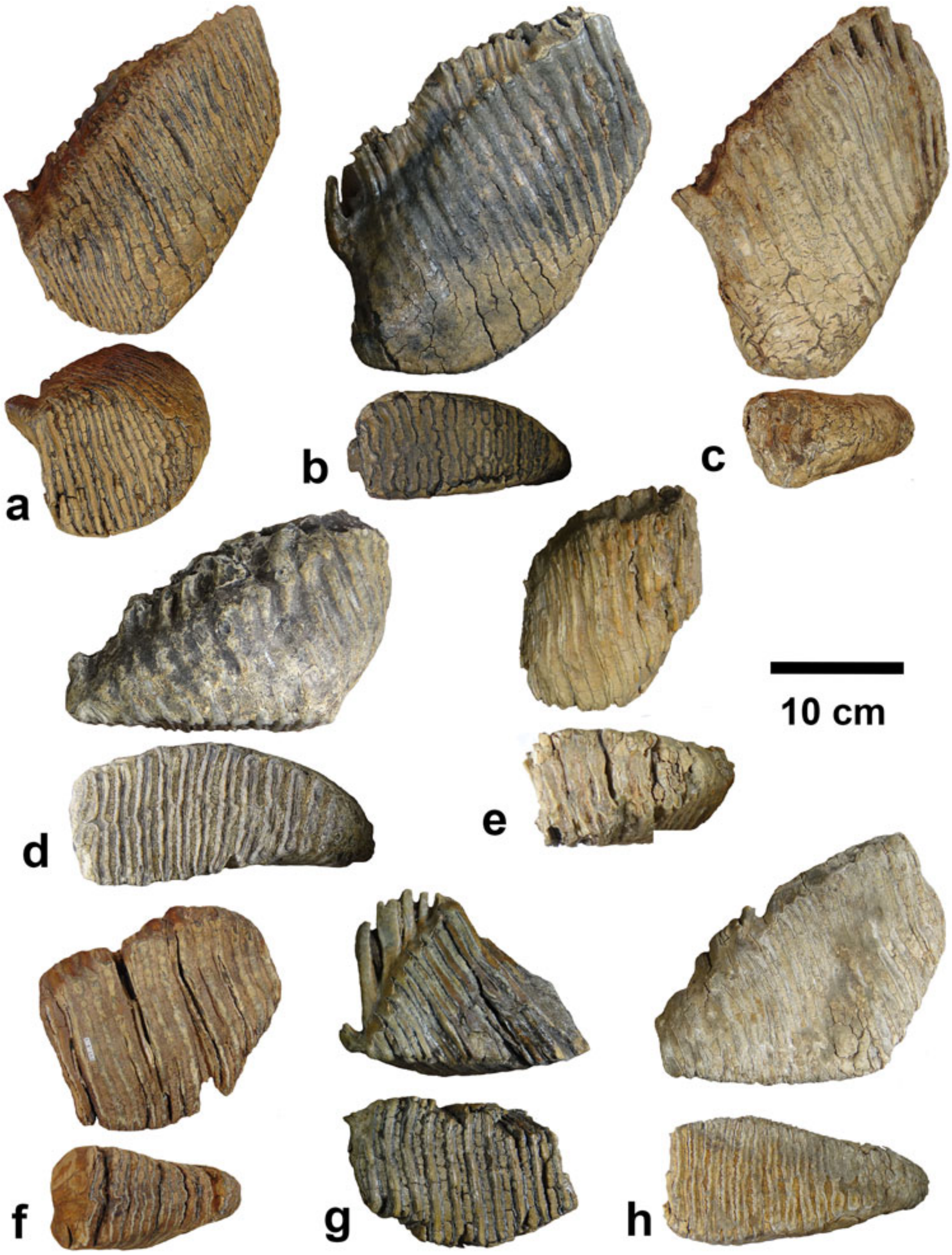

Figure 2. Upper sixth molars (M6) of *Mammuthus* from Alberta. (a) RAM P80.14.1, lateral and occlusal views. (b) RAM P84.5.1, lateral and occlusal views. (c) RAM P91.10.4, medial? and occlusal views. (d) RAM P94.4.3, lateral and occlusal views. (e) RAM P88.7.1, lateral? and occlusal views. (f) RAM P97.8.1, medial and occlusal views. (g) RAM P81.3.5, medial and occlusal views. (h) RAM P02.8.70, medial? and occlusal views. Anterior side of all teeth located to the left.

Radiocarbon dating

Radiocarbon data for four specimens (CMN 17845, RAM P94.4.3, P02.8.70, and P97.11.1b) were compiled from published sources (Hills and Harington, 2003; Jass and Barrón-Ortiz, 2017). We sampled nine additional specimens (RAM P84.5.1, P91.10.4, P97.8.1, P97.10.143, P97.10.144, P97.11.1T, P99.3.164, P18.319.4, and P21.391.1) for radiocarbon analysis. P97.11.1 is inferred to represent multiple elements of a single individual. Both the original radiocarbon age assigned to the dentary and teeth (see Metcalfe et al., 2016) and our reassessed age come from a bone fragment assigned to that specimen (P97.11.1T). All samples were collected using a Dremel 100-N/7 rotary tool fitted with a cutting disc made of a hard abrasive. The samples were sent to the A. E. Lalonde AMS Laboratory at the University of Ottawa, Ottawa, Ontario, Canada (UOC), or the W. M. Keck Carbon Cycle Accelerator Facility at the University of California, Irvine, United States (UCIAMS). Pretreatment methods (ultrafiltration) and processing for samples sent to Lalonde were described in Crann et al. (2017). Equipment used for sample preparation was summarized in St-Jean et al. (2017). Samples submitted to the Keck Carbon Cycle AMS Facility (UCIAMS) were decalcified in 0.5N HCl, gelatinized at 60°C and pH 2, and ultrafiltered to select a high molecular weight fraction (>30 kDA; John Southon, personal communication). Radiocarbon dates were calibrated in OxCal v.4.4.4 using the IntCal 20 calibration curve (Reimer et al., 2020; Bronk Ramsey, 2021).

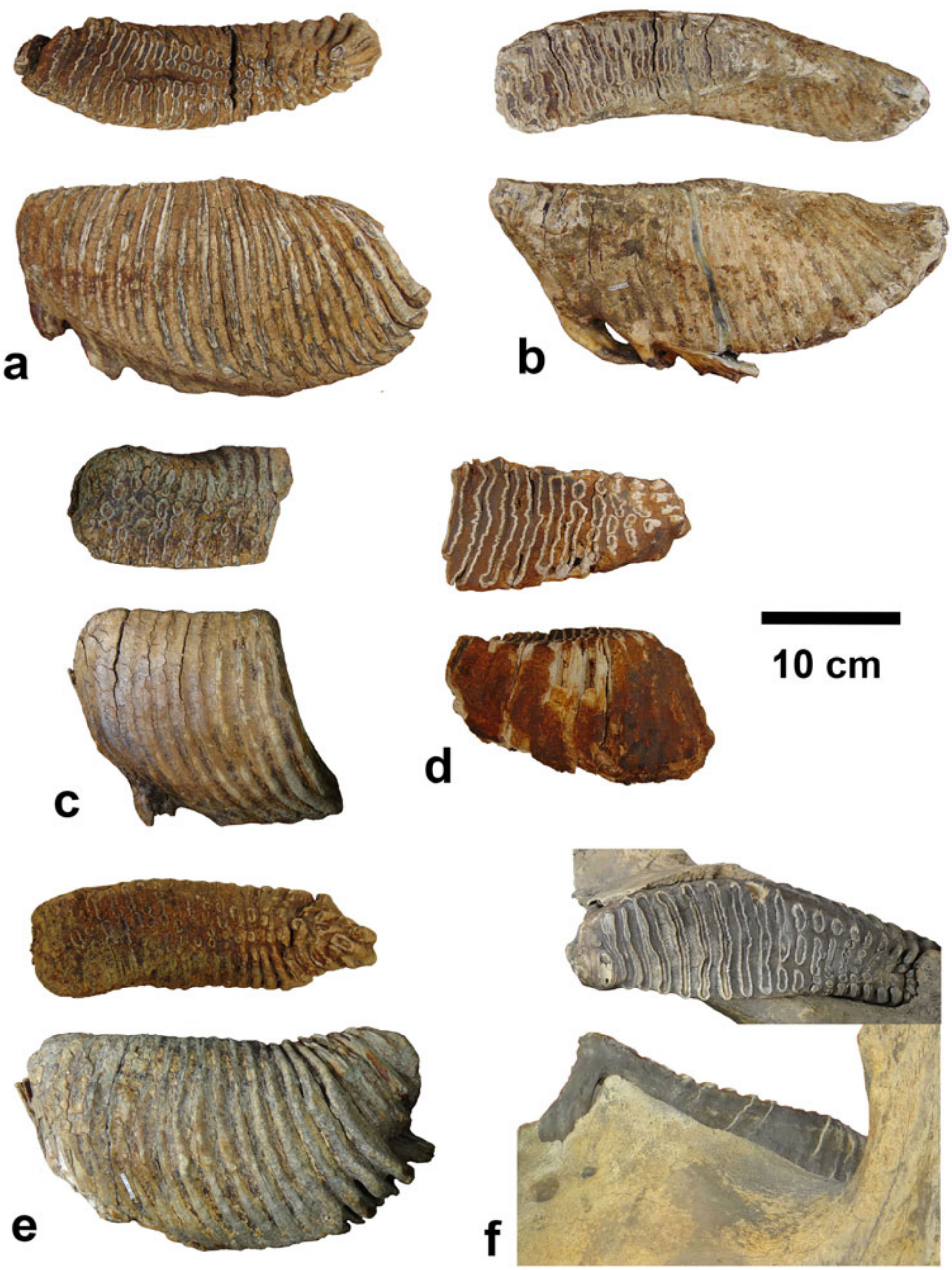

Figure 3. Lower sixth molars (m6) of *Mammuthus* from Alberta. (a) RAM P21.391.1, occlusal and medial views. (b) RAM P99.3.164, occlusal and lateral views. (c) RAM P97.10.143, occlusal and medial views. (d) RAM P18.319.4, occlusal and medial views. (e) RAM P97.10.144, occlusal and lateral views. (f) RAM P97.11.1b, occlusal and lateral views. Anterior side of all teeth located to the left.

Morphometric analysis of mammoth teeth

For measurements, we followed the methodology of Lister and Sher (2015) and Widga et al. (2017) and a subset of their comparative data sets (Supplementary Tables 1–3). See Lister and Sher (2015, figs. 2E and D) for illustration of location of measurements. All measurements (except for the estimated total number of lamellae) are in millimeters and were taken using Mitutoyo digital calipers to the nearest 0.01 mm. Collected dental data and calculated indices are as follows:

(1) Total number of lamellae in an unworn molar (P). We estimated this value for sufficiently complete specimens following the methodology of Lister and Sher (2015). This number excludes talons, talonids, and platelets.

(2) Length (L) of the preserved tooth crown perpendicular to the average orientation of lamellae. In other words, we measured perpendicular to the most prevalent orientation of lamellae in occlusion.

(3) Width (W) of the tooth crown at the widest preserved lamella (measured with calipers held parallel to the lamella) including cementum. If cementum was weathered or missing in one or both sides of the tooth, we estimated the amount of cementum missing (C) based on measurements of cementum present in other areas of the tooth or in other teeth from the same sample (following Lister and Sher, 2015).

(4) Width (W′) of the tooth crown at the widest preserved lamella (measured with calipers held parallel to the lamella) excluding cementum. If cementum was present, we subtracted its estimated width (following Widga et al., 2017). We took this measurement only in upper M6 for comparisons with the data set of Widga et al. (2017).
(5) Height (H) of the tooth crown measured from the base of the crown to the apex of the highest unworn, preserved lamella.
(6) Enamel thickness (ET). We measured enamel thickness parallel to the growth axis of the lamella. We took this measurement at up to 10 points on the occlusal surface and we calculated the average of those values.
(7) Enamel index (EI and EI′). We calculated EI with the formula $EI = 100 \times ET/W$. For upper molars, we also obtained EI′, which was calculated in the same manner as EI, but using W′ instead of W. This variable measures enamel thickness with the tooth standardized to a width of 100 mm.
(8) Lamellar frequency (LF) and basal lamellar frequency (LFB). We measured LF and LFB following Lister and Sher (2015). In this methodology, lamellar frequency is obtained with the formula $LF = 100 \times p/l$; l = length of a portion of the tooth, and p = number of enamel plate–cementum intervals occupying that length. In the upper molars, lamellar frequency (LF) was measured at the top and base of the crown, on both the medial and lateral sides, and the average of these four measurements was calculated. In the lower molars, lamellar frequency was only measured at the base of the tooth crown (LFB) on both the medial and lateral sides and the average of the two measurements was calculated. Lamellae in the lower molars tend to converge towards the top of the crown, making the top measurements less consistent due to differences in tooth wear among individuals (Lister and Sher, 2015).
(9) Calculated lamellar frequency (LFcalc). We obtained LFcalc for the upper molars in our sample following Widga et al. (2017). These authors calculate lamellar frequency using the formula $LFcalc = 100 \times P'/L$; P′ = number of preserved lamellae in the tooth.
(10) Lamella length (LL, LL′, and LLB). We calculated the average length of one lamella-cementum interval using the formulae $LL = 100/LF$ and $LLB = 100/LFB$ for the upper and lower molars, respectively (Lister, 2017); LL = lamella length and LLB = basal lamella length. For upper molars, we also obtained LL′, which was calculated in the same manner as LL, but using LFcalc instead of LF.
(11) Lamellar length index (LLI, LLI′, and LLBI). We calculated LLI and LLBI for upper and lower molars, respectively, using the formulae $LLI = 100 \times LL/W$ and $LLBI = 100 \times LLB/W$; LLI = lamella length index and LLBI = basal lamella length index. For upper molars, we also obtained LLI′, which was calculated in the same manner as LLI, but using LL′ and W′ instead of LL and W. This variable measures lamella length and basal lamella length with the tooth standardized to a width of 100 mm.

Given the state of preservation for many teeth in our sample, our study focused especially on the analysis of two variables: lamellar length index and enamel index (measurements 7 and 11 above). Other than the total number of lamellae (enamel plates P), these two variables are documented as most relevant for discriminating North American mammoth teeth (Lister and Sher, 2015; Lister, 2017; Widga et al., 2017). Using bivariate scatter plots, we compared lamellar length index and enamel index for the specimens we measured and specimens from Alberta reported in the literature (Churcher, 1972; Lister and Sher, 2015; Widga et al., 2017) with a subset of the comparative data sets of Lister and Sher (2015) and Widga et al. (2017) (Supplementary Tables 1–3).

Two of the specimens we studied (RAM P88.7.1 and P97.11.1b) preserved a specific morphology that necessitates a more detailed description of how data were collected. RAM P88.7.1 (Fig. 4) preserves what appear to be “accessory” lamellae between plates 6 and 7 and between plates 7 and 8. The “accessory” lamellae do not reach the occlusal surface, but rather terminate at approximately the midsection of the tooth crown. We excluded the “accessory” lamellae from our measurement and calculation of lamellar frequency. A second specimen, RAM P97.11.1b, is embedded in a partial dentary with most of the medial side of the tooth exposed, but the posterior and lateral sides of the tooth are obscured by the dentary. Thus, we were unable to quantify the total number of lamellae (enamel plates, P) and we could only measure the basal lamellar frequency (LFB) of the medial side. We estimated LFB for the lateral side of the tooth by calculating the mean LFB lateral/LFB medial ratio in the other m6 specimens we measured (mean ratio = 1.0546 ± 0.05; n = 5) and using this value to estimate LFB of the lateral side (RAM P97.11.1b LFB medial = 5.44; estimated LFB lateral = 5.74). This allowed us to estimate the average LFB of this specimen (estimated average LFB = 5.59). Tables 1a and b show both the LFB of the medial side and the estimated average LFB along with the respective indices we calculated (LLB and LLBI). We plot both the LLBI calculated for the medial side and the estimated LLBI in relevant figures (see “Results”).

Figure 4. RAM P88.7.1. Arrows point to “accessory” enamel plates between plates 6 and 7 and between plates 7 and 8.

Delimiting "typical" morphologies of M. primigenius *and* M. columbi

We used the distribution in morphospace of specimens traditionally identified as *M. primigenius* and *M. columbi* to delimit "typical" morphologies of these taxa. Late Pleistocene *Mammuthus* fossils from Beringia have traditionally been identified as *M. primigenius* (e.g., Maglio, 1973; Agenbroad, 1984, 2005; Harington, 2011; Lister and Sher, 2015; Lister, 2017). Late Pleistocene *Mammuthus* fossils from the southern United States and Mexico (and further south into Central America) have traditionally been identified as *M. columbi* (e.g., Maglio, 1973; Agenbroad, 1984, 2005; Arroyo-Cabrales et al., 2010; Lucas and Alvarado, 2010; Lister and Sher, 2015; Lister, 2017). These two subgroups tend to occupy distinct areas of morphospace in bivariate scatter plots of lamellar length index versus enamel index (e.g., Fig. 5), but they overlap to some degree. We identified specimens that plot below the zone of overlap (in the lower-left area of the graph) as specimens with "typical" *M. primigenius* morphology. Specimens that plot above the zone of overlap (in the upper-right area of the graph) were considered specimens with "typical" *M. columbi* morphology. Specimens that plot in the zone of overlap (shaded area) were treated as individuals with "intermediate" or overlapping *M. columbi–M. primigenius* morphology (see "Results" and "Discussion" for further considerations regarding specimens with "intermediate" morphology). We note one exception to the delimitation of these morphological groups. Early Pleistocene specimens from Beringia primarily plot in the morphospace region with "typical" *M. columbi* morphology, but they are instead identified as *M. trogontherii*. As mentioned in the introduction, molars of *M. trogontherii*, an Early to Middle Pleistocene Eurasian and Beringian species, have dental characters that closely resemble those observed in *M. columbi* (Lister and Sher, 2015; Lister, 2017).

For further comparison, we subdivided the data sets of Lister and Sher (2015) and Widga et al. (2017) chronologically and geographically (Supplementary Tables 1–3). The subgroups we identified are: (1) Early Pleistocene specimens from northwestern North America/Siberia (i.e., Beringia) and China; (2) Late Pleistocene specimens from northwestern North America/Siberia (i.e., Beringia); (3) Early/Middle Pleistocene specimens from the contiguous United States; (4) Late Pleistocene specimens from the northeastern United States; (5) Late Pleistocene specimens from the Great Plains and Great Lakes (Canada and USA); (6) Late Pleistocene specimens from the Rocky Mountains (USA); (7) Late Pleistocene specimens from the southern United States and Mexico.

Results

Radiocarbon dating

Table 3 presents new and previously published radiocarbon data for some of the mammoth teeth included in our analyses. Of the 13 specimens with age data, only a single specimen has a finite age (CMN 17845). We interpret the previous finite age for P97.11.1T as erroneous, given that reevaluation of that specimen with newer equipment and techniques produced a non-finite age (Table 3).

Our radiocarbon results indicate that most of the known record of mammoth teeth from Alberta consists of specimens that predate the last glacial maximum (LGM). Whether that represents a biological reality or not (i.e., mammoths were rare in Alberta in finite time leading to the LGM and following the LGM) remains a testable scenario, awaiting additional specimens and radiocarbon data. There are finite ages on other mammoth elements found in Alberta (see Jass and Barrón-Ortiz, 2017), but many of those records represent ages that likely should be reassessed with newer pretreatment and analytical techniques, particularly given the result for P97.11.1T. Collectively, our radiocarbon results mean that our discussion of mammoth teeth and taxonomy in Alberta is primarily focused on pre-LGM time.

Table 3. Radiocarbon data for last molars (M6/m6) of *Mammuthus* from Alberta.

Spec. number	Lab number	^{14}C yr BP	δ^{13}C	C:N	Citation
CMN 17845	TO-8514	10,930 ± 100[a]	n/a	n/a	Hills and Harington (2003)
RAM P91.10.4	UCIAMS 271825	>42,700	−20.5	3.2	This report
RAM P97.11.1T*	BGS 2145	43,300 ± 3000[b]	−21.4	n/a	Metcalfe et al. (2016)
RAM P02.8.70	Beta-368273	>43,500	−20.6	n/a	Jass and Barrón-Ortiz (2017)
RAM P94.4.3	Beta-431961	>43,500	−19.9	n/a	Jass and Barrón-Ortiz (2017)
RAM P84.5.1	UOC-15830	>44,000	−20.2	n/a	This report
RAM P97.8.1	UOC-15831	>44,000	−20.7	n/a	This report
RAM P21.391.1	UOC-15832	>44,000	−20.3	n/a	This report
RAM P99.3.164	UCIAMS 271829	>45,000	−20.6	3.1	This report
RAM P97.10.144	UCIAMS 271827	>45,400	−19.8	3.2	This report
RAM P97.10.143	UCIAMS 271826	>47,200	−20.0	3.2	This report
RAM P97.11.1T*	UCIAMS 271828	>47,200	−20.6	3.2	This report
RAM P18.319.4	n/a (lacked collagen)	n/a	n/a	n/a	This report

Notes: Unless otherwise noted (i.e., CMN 17845) all specimens are housed at the Royal Alberta Museum. C:N represents the atomic ratio. n/a, not available. P97.11.1T is a postcranial fragment that represents part of an individual animal (P97.11.1), and the date provided is inferred to be equivalent to the age of the dentary preserving the m6 (P97.11.1b) included in this study.

[a] 13,073–12,740 cal yr BP (95.4% probability; calculated with OxCal v.4.4.4 using the IntCal20 calibration curve; Bronk Ramsey, 2021; Reimer et al., 2020).

[b] 52,761–42,914 cal yr BP (88.7% probability; calculated with OxCal v.4.4.4 using the IntCal20 calibration curve; Bronk Ramsey, 2021; Reimer et al., 2020).

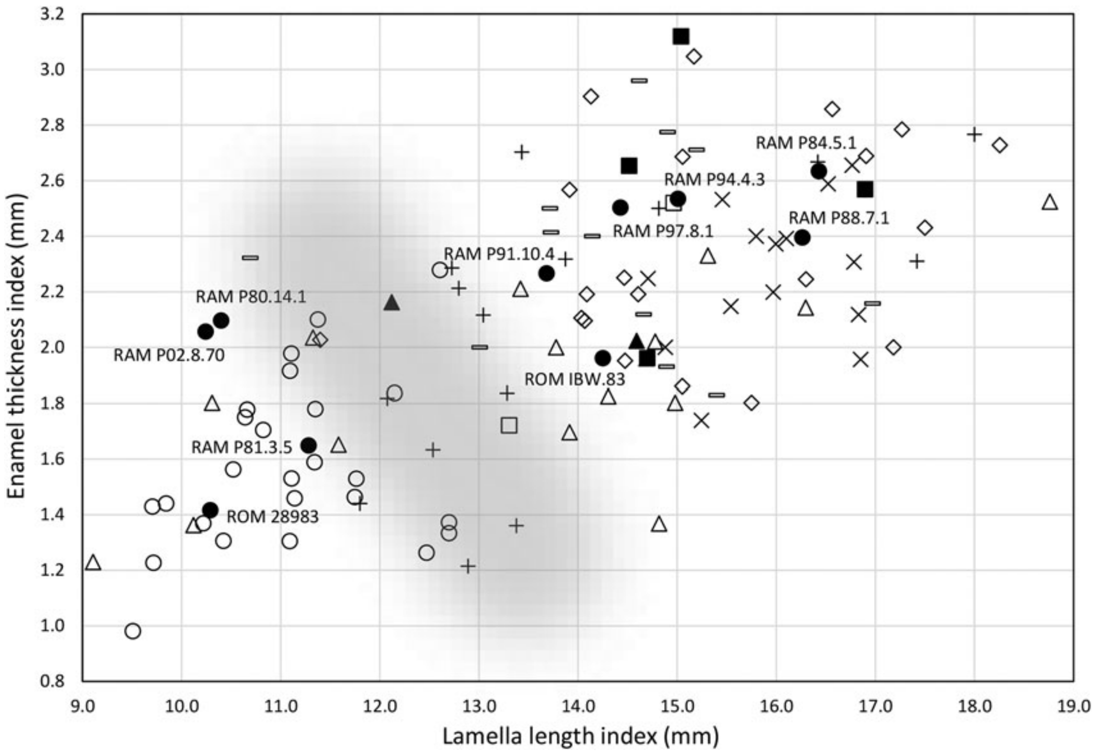

Figure 5. Plots of enamel thickness index (EI) vs. lamella length index (LLI) for M6s of *Mammuthus* from Alberta and other sites in Eurasia and North America (following Lister and Sher, 2015). Symbols: black circles (●) = specimens from Alberta; open circles (○) = *M. primigenius* from northwestern North America/Siberia (i.e., Beringia); (x) = *M. trogontherii* from China and northwestern North America/Siberia (i.e., Beringia); open diamonds (◇) = *M. columbi* from the Early and Middle Pleistocene of the contiguous United States; open triangles = (Δ) Late Pleistocene *Mammuthus* from the Great Plains and the Great Lakes (Canada and USA); plus signs (+) = Late Pleistocene *Mammuthus* from the Rocky Mountains (USA); rectangles (▭) = Late Pleistocene *Mammuthus* from the southern United States and Mexico; black squares (■) = Osborn's (1922) neotype of *M. columbi* and other specimens from the neotype locality; open squares (□) = holotype (Leidy, 1858) and neotype (Osborn, 1922) of *M. imperator*; black triangles (▲) = specimens from one of Osborn's (1942) *M. jeffersonii* "ideotype" localities. Shaded area = *M. columbi*–*M. primigenius* area of overlap. Data for Alberta, this study; other data from Lister and Sher (2015).

Taxonomic evaluation and geographic distribution

Tables 1a, b and 2a, b summarize the measurements and calculated indices for the Alberta specimens in our study. Figures 5–9 are scatter diagrams of lamellae length and enamel thickness indices for the Alberta sample and comparative data sets from Lister and Sher (2015) and Widga et al. (2017).

In this study, we identified specimens that plot with other mammoth molars displaying "typical" *M. columbi* morphology as *M. columbi*, and we identified specimens that plot with molars displaying "typical" *M. primigenius* morphology as *M. primigenius*. We referred to specimens that plot in the *M. columbi*–*M. primigenius* area of overlap as individuals with intermediate *M. columbi*–*M. primigenius* morphology, without making any specific taxonomic assignments or interpretations about their affinity.

Some Late Pleistocene North American mammoth specimens outside of Beringia with tooth morphologies that are intermediate to "typical" *M. columbi* and *M. primigenius* morphologies were previously identified as a distinct taxon, *M. jeffersonii* (see Lister and Sher, 2015; Lister, 2017). Some researchers hypothesized that *M. jeffersonii* evolved from *M. columbi* and developed more advanced dental traits approaching those observed in *M. primigenius* (Osborn, 1922; Kurtén and Anderson, 1980; Lister, 2017). Those morphological changes are now hypothesized as likely the result of introgression between *M. columbi* and *M. primigenius* (Enk et al., 2016), a process that led to *M. columbi* populations with different degrees of "advancement" relative to the "typical" *M. columbi* morphology (Lister and Sher, 2015; Lister, 2017). Lister (2017) suggested referring to the "advanced" individuals as "Jeffersonian" *M. columbi*, without assigning formal taxonomic separation. Intermediate morphologies from Alberta that plot in the *M. columbi*–*M. primigenius* area of overlap could represent individuals of *M. primigenius*, *M. columbi*, hybrids of the two, or possibly "Jeffersonian" *M. columbi*. Without a strong analytical basis for any taxonomic interpretation, we prefer to simply note the existence of specimens with morphologies that fall within a range of overlap between *M. columbi* and *M. primigenius*. Moreover, using "Jeffersonian" *M. columbi* for specimens with intermediate morphologies implies that introgression only morphologically affected populations of *M. columbi* without similar effects in populations of *M. primigenius*, a process that seems unlikely in Alberta, given the known biogeographic fluidity of the region throughout the Pleistocene (e.g., Heintzman et al., 2016; Karpinski et al., 2020).

The 10 upper molars analyzed from Alberta cluster into two morphological groups (Figs. 5–7) thought to represent two distinct taxa. We recovered this pattern whether we employed the methodology and comparative data sets of Lister and Sher (2015) or Widga et al. (2017), although we note that the Alberta sample size decreases by two specimens (ROM IBW.83 and ROM 28983) when using the methodology of Widga et al. (2017). Six of the 10 Alberta specimens (RAM P84.5.1, P88.7.1, P91.10.4, P94.4.3, P97.8.1, and ROM IBW.83) plot with molars

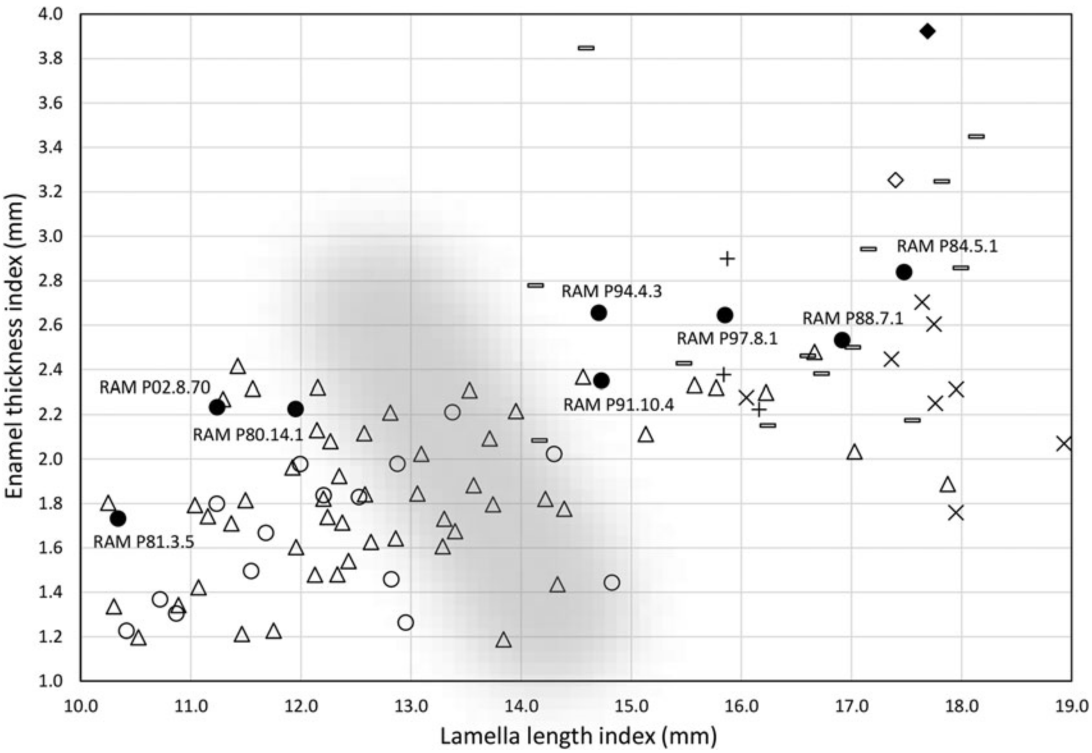

Figure 6. Plots of enamel thickness index (EI′) vs. lamella length index (LLI′) for M6s of *Mammuthus* from Alberta and other sites in Eurasia and North America (following Widga et al., 2017). Symbols: black circles (●) = specimens from Alberta; open circles (○) = *M. primigenius* from Eurasia and northwestern North America (Alaska); (x) = *M. trogontherii* from China and northwestern North America/Siberia (i.e., Beringia); open diamond (◇) = *M. columbi* from the Early and Middle Pleistocene of the contiguous United States; black diamond (◆) = Late Pleistocene *Mammuthus* from the northeastern United States; open triangles (Δ) = Late Pleistocene *Mammuthus* from the Great Plains and the Great Lakes (Canada and USA); plus signs (+) = Late Pleistocene *Mammuthus* from the Rocky Mountains (USA); rectangles (▭) = Late Pleistocene *Mammuthus* from the southern United States. Shaded area = estimated *M. columbi*–*M. primigenius* area of overlap. Data for Alberta, this study; other data from Widga et al. (2017) and Lister and Sher (2015).

displaying “typical” *M. columbi* morphology (Figs. 5–7), including the neotype specimen proposed by Osborn (1922) and specimens from the neotype locality (Fig. 5). The remaining four molars (RAM P80.14.1, P81.3.5, P02.8.70, and ROM 28983) plot with specimens displaying “typical” *M. primigenius* morphology (Figs. 5–7). When compared with only northern North America (Fig. 8), a similar pattern exists, but morphologies consistent with *M. columbi* occur in Early Pleistocene records in Beringia whereas morphologies consistent with *M. primigenius* occur in Late Pleistocene records in Beringia. Since some North American *Mammuthus* are hypothesized to represent chronospecies (e.g., *M. trogontherii* vs. *M. columbi*; Lister and Sher, 2015), some specimens that we assigned to *M. columbi* could represent *M. trogontherii*, assuming that Early Pleistocene records represent that taxon.

In contrast to the pattern observed in the upper molars, the six lower m6 molars analyzed from Alberta do not cluster into two distinct groups (Fig. 9). These specimens form a morphological gradient that ranges from molars displaying “typical” *M. primigenius* morphology to molars displaying “typical” *M. columbi* morphology (Fig. 9). Molars with “typical” *M. primigenius* morphology include RAM P97.10.143 and P97.10.144. Two other molars, RAM P97.11.1b and P99.3.164, plot within the *M. columbi*–*M. primigenius* area of overlap. We note that RAM P97.11.1b plots within the *M. columbi*–*M. primigenius* area of overlap whether we use the estimated LLBI or the LLBI calculated only from the medial side of the tooth (see “Materials and Methods”). Molars with “typical” *M. columbi* morphology include RAM P21.391.1 and P18.319.4, and CMN 17845.

The mammoth teeth we studied are distributed over a wide geographic area in Alberta (Fig. 1). Molars with “typical” *M. columbi* morphology range from the Peace River region in northwestern Alberta to the Medicine Hat area in the southeastern region of the province. Molars with “typical” *M. primigenius* morphology range from the Edmonton area in central Alberta to the Medicine Hat area in southeastern Alberta. Molars with intermediate or overlapping *M. columbi*–*M. primigenius* morphology were recovered from the Edmonton area.

Discussion

Morphological variation and taxonomic identity of Alberta mammoth molars

Our analyses of upper and lower sixth molars (M6/m6) recovered from Pleistocene deposits in Alberta demonstrate the presence of morphologies consistent with *M. primigenius* and *M. columbi*, along with the occurrence of two lower molars with intermediate morphologies. Some of the taxonomic identifications suggested by our morphometric analyses are consistent with the identifications presented in previous studies, but others are substantially different (Table 4).

For the upper molars we evaluated, our results support the previous or tentative identifications of *M. primigenius* (Jass and Barrón-Ortiz, 2017; Lister, 2017) for RAM P81.3.5, RAM

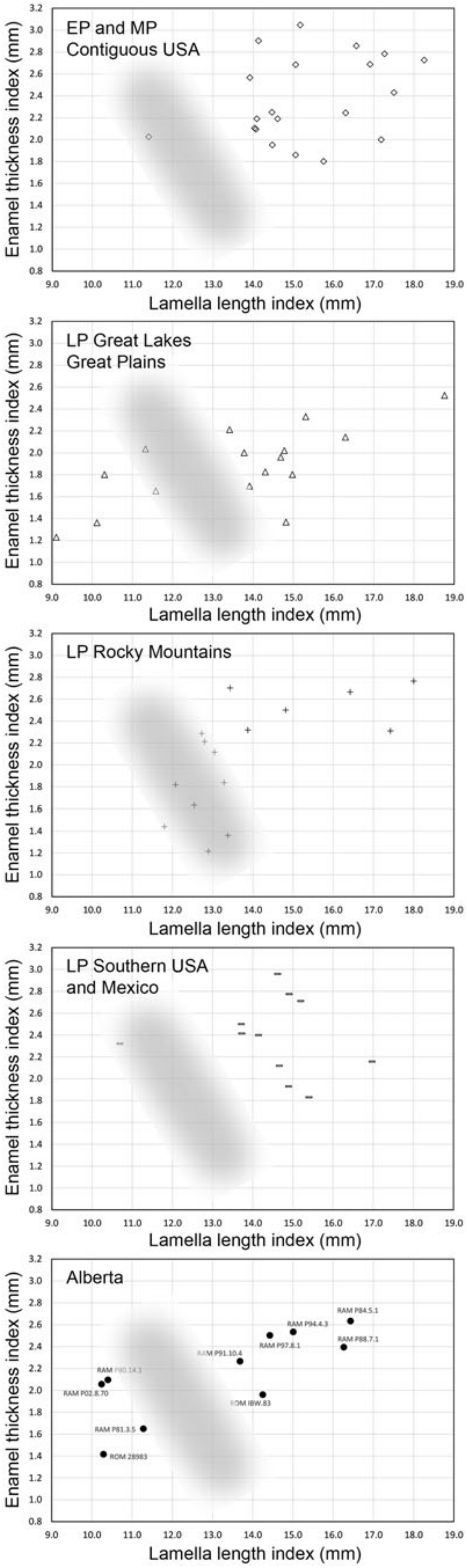

Figure 7. Plots of enamel thickness index (EI) vs. lamella length index (LLI) for M6s of *Mammuthus* from the Early (EP), Middle (MP), and Late Pleistocene (LP) of the contiguous United States and Mexico, based on data reported by Lister and Sher (2015). Data for Alberta, this study. Shaded area = *M. columbi*–*M. primigenius* area of overlap.

P02.8.70, and ROM 28983, although we note that the latter specimen was also previously identified as *M. columbi* (Widga et al., 2017). Previous or tentative identifications of *M. columbi* (Jass and Barrón-Ortiz, 2017; Widga et al., 2017) supported by our analyses include RAM P94.4.3, RAM P88.7.1, and ROM IBW.83. We revise previous or tentative identifications (see Jass and Barrón-Ortiz, 2017) of RAM P91.10.4, RAM P97.8.1, and RAM P84.5.1 to *Mammuthus columbi*.

For the lower molars we evaluated, our results support the previous identification of *M. columbi* for CMN 17845. CMN 17845 was originally described as *Mammuthus imperator* (Churcher, 1972), but was reassigned by Hills and Harington (2003) to *M. columbi* following the species concept for this taxon proposed by Kurtén and Anderson (1980). In more recent studies, CMN 17845 was referred to *M. columbi* (Widga et al., 2017), and this taxonomic assignment is supported by our study, as this specimen plots with molars displaying “typical” *M. columbi* morphology.

The remaining lower molars in our study have revised identifications based on our analysis, and we present identifications for two previously undescribed specimens. The new records (RAM P18.319.4 and RAM P21.391.1) are assigned to *M. columbi*. RAM P97.10.143 and RAM P97.10.144 are reassigned from *Mammuthus* cf. *M. columbi* to *M. primigenius*. Intermediate morphologies of *M. columbi* and *M. primigenius* are preserved in RAM P99.3.164 and RAM P97.11.1b.

The discrepancies between our results and the tentative identifications of Jass and Barrón-Ortiz (2017) are likely due to the quantitative methodologies employed here and our comparisons with baseline data sets of Lister and Sher (2015) and Widga et al. (2017) versus the more qualitative observations that formed the basis for the original taxonomic hypotheses. Perhaps the most surprising result is the recovery of nine specimens that represent *M. columbi*, but recovery of only six specimens assigned to *M. primigenius*. That result contradicts our hypothesis that *M. primigenius* would be the most prevalent form of mammoth recovered in Alberta. At the very least, our results reemphasize the importance of quantitative evaluation of mammoth teeth, rather than reliance on other factors (e.g., geographic location). As predicted, mammoth teeth recovered from Upper Pleistocene deposits in Alberta show a large range of quantitative variation, ranging from “typical” *M. primigenius* to “typical” *M. columbi* morphologies, although with fewer intermediate morphologies than we might have speculated.

Biogeographic and spatial-temporal trends in the distribution of mammoth taxa in Alberta

Although some of our taxonomic results were unexpected, the range of morphological variation observed in our sample may support the hypothesis that *M. columbi* and *M. primigenius* occupied western Canadian landscapes in the Pleistocene and is consistent with studies that indicated that animal populations of southern and northern affinities inhabited this geographic region in the past (e.g., Shapiro et al., 2004; Wilson et al., 2008; Burns, 2010; Heintzman et al., 2016). In our sample, *M. columbi* is the most abundant form (9/17 = 53%), followed by *M. primigenius* (6/17 = 35%), and specimens with intermediate morphologies (2/17 = 12%).

The fossil record of *M. columbi* suggests that this species was particularly abundant from the North American midcontinent south to Mexico and into Central America (e.g., Siebe et al., 1999; McDonald and Dávila A, 2017; Smith and Graham,

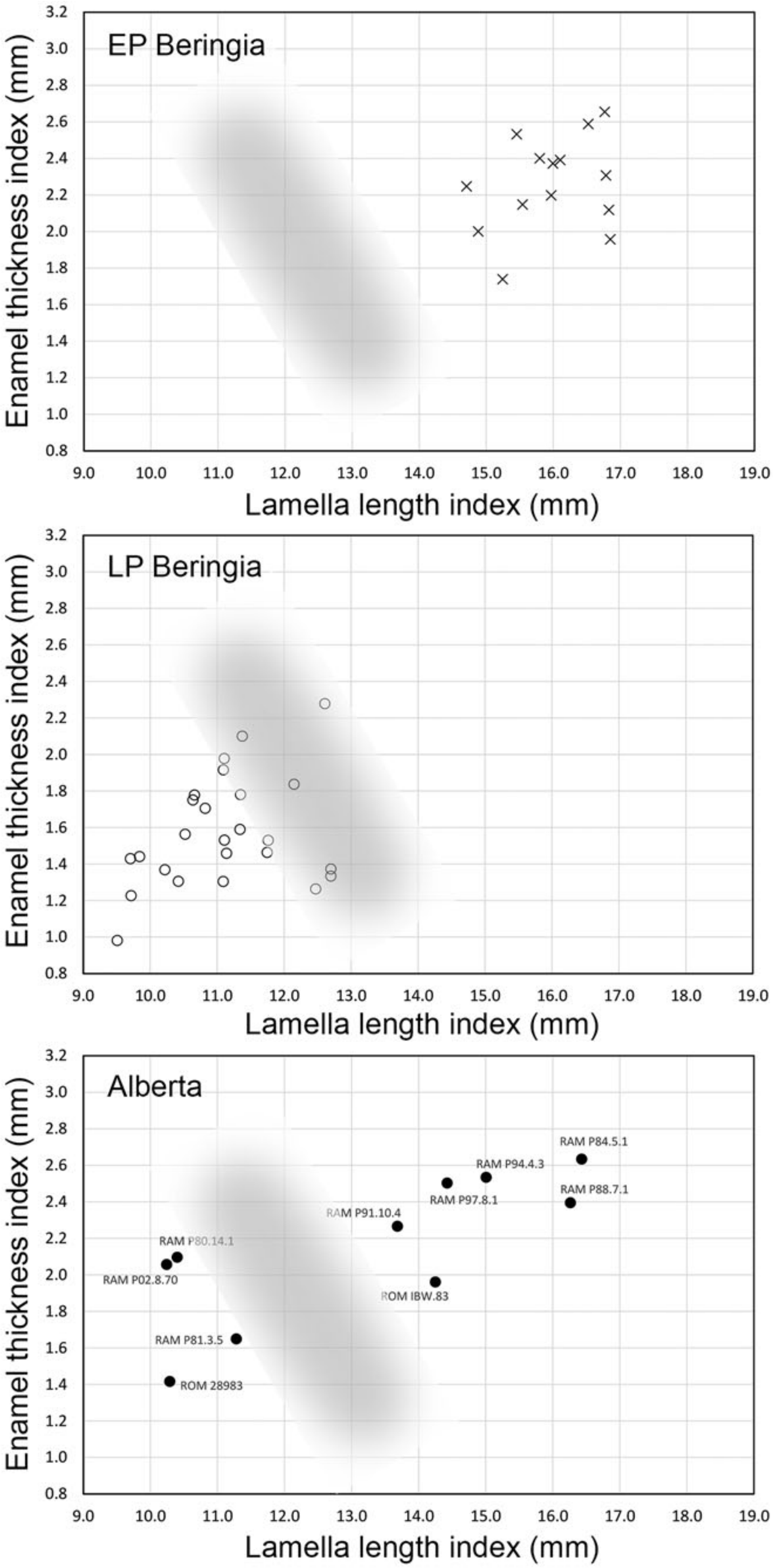

Figure 8. Plots of enamel thickness index (EI) vs. lamella length index (LLI) for M6s of *Mammuthus* from the Early (EP) and Late Pleistocene (LP) of northern North America and Siberia (i.e., Beringia), based on data reported by Lister and Sher (2015). Data for Alberta, this study. Shaded area = *M. columbi*–*M. primigenius* area of overlap.

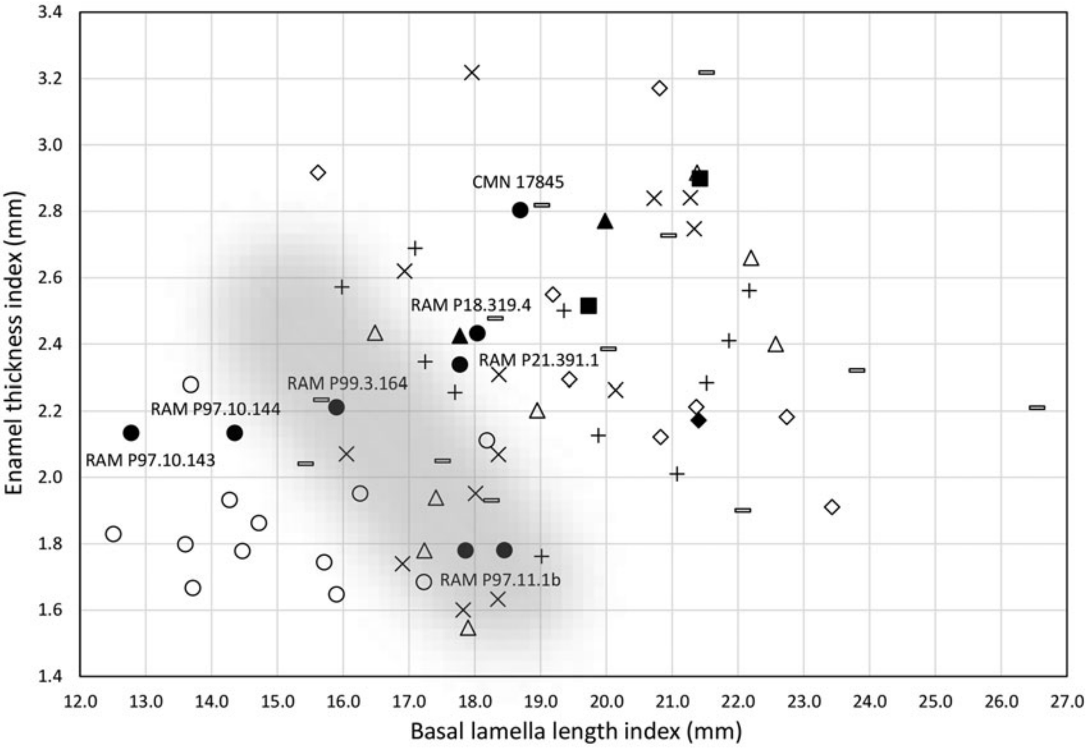

Figure 9. Plots of enamel thickness index (EI) vs. basal lamella length index (LLBI) for m6s of *Mammuthus* from Alberta and other sites in Eurasia and North America (following Lister and Sher, 2015). Symbols: black circles (●) = specimens from Alberta; open circles (○) = *M. primigenius* from northwestern North America/Siberia (i.e., Beringia); (x) = *M. trogontherii* from China and northwestern North America/Siberia (i.e., Beringia); open diamonds (◇) = *M. columbi* from the Early and Middle Pleistocene of the contiguous United States; open triangles (Δ) = Late Pleistocene *Mammuthus* from the Great Plains and the Great Lakes (USA); plus signs (+) = Late Pleistocene *Mammuthus* from the Rocky Mountains (USA); rectangles (▭) = Late Pleistocene *Mammuthus* from the southern United States and Mexico; black diamond (◆) = holotype of *M. columbi* (Falconer, 1857); black squares (■) = Osborn's (1922) neotype of *M. columbi* and other specimens from the neotype locality; black triangles (▲) = one of Osborn's (1942) *M. jeffersonii* "ideotypes" and specimens from the same "ideotype" locality. Shaded area = *M. columbi*–*M. primigenius* area of overlap. Data for Alberta, this study; other data from Lister and Sher (2015). Note that there are two data points for specimen RAM P97.11.1b; the data point to the left is based on the estimated LLBI for the tooth, the data point to the right is based on the calculated LLBI for the medial side of the tooth (refer to "Materials and Methods" for more details).

2017), but our results may show a somewhat more consistent presence at northern latitudes than we would have predicted (Fig. 1). Those geographic data may indicate that *M. columbi* ranged as far north as the Peace River Country of northwestern Alberta (Fig. 1). That distribution could indicate a more widespread presence of that taxon in portions of Canada in the Pleistocene, or may suggest a pattern of northward migration during specific timeframes, consistent with the northward movement of other populations of "southern" megafauna during interglacial timeframes (e.g., *Mammut americanum*; Karpinski et al., 2020). Although those may both represent plausible interpretations, we would be remiss to not offer an alternative explanation for our observations.

Only one specimen (CMN 17845) that we assigned to *M. columbi* has a finite radiocarbon date (10,930 ± 100 yr BP; 13,073–12,740 cal yr BP at 2σ probability; Table 3), and that specimen was recovered from southeastern Alberta (Fig. 1). All other radiocarbon data for the specimens we describe as *M. columbi* are non-finite ages (Table 3). While those data are consistent with biogeographic hypotheses presented above, they are also potentially consistent with an interpretation that the teeth represent older records of *M. trogontherii*. Descriptions of camelid remains from gravel deposits in Alberta included a record of "Giant Camel," possibly indicative of an Irvingtonian or older fauna, and therefore significantly older than many other remains recovered from sand and gravel deposits in Alberta (Jass and Allan, 2016). The occurrence of *M. trogontherii* in the Alberta record would potentially be consistent with that observation, and would suggest an even greater amount of mixing of specimens of disparate age in regional gravel deposits than is already recognized. Such a scenario would be consistent with previous interpretations that portions of Alberta represented extensions of the mammoth steppe during some portions of the Pleistocene (Schwartz-Narbonne et al., 2019). However, because the majority of Quaternary fauna recovered in Alberta represents isolated finds with no detailed contextual information, we have no other definitive basis for this interpretation at present.

Collectively, our records of *M. columbi* may indicate (a) a broader, sympatric geographic distribution for *M. columbi* and *M. primigenius* in western Canada, (b) a northward dispersal of *M. columbi* during interglacial time that may or may not have been sympatric with *M. primigenius*, or (c) previously unrecognized, geologically older records of *M. trogontherii*, an Early to Middle Pleistocene form with tooth morphology indistinguishable from *M. columbi*. All three are plausible scenarios that cannot be resolved by molar morphology alone, although given our understanding of other records (e.g., *Mammut*, Karpinski et al., 2020; camelids, Jass and Allan, 2016) either scenario (b) or (c) seems the most likely explanation. Determining which scenario is more likely could be vastly improved by the discovery of

Table 4. Comparison of previous taxonomic hypotheses with current taxonomic hypothesis for M6/m6 molars of *Mammuthus* from Alberta. Unless otherwise noted, previous hypotheses are from Jass and Barrón-Ortiz (2017)

Specimen number	Previous identification	This paper
	M6	
ROM 28983	*Mammuthus columbi* (Widga et al., 2017) *Mammuthus primigenius* (Lister, 2017)	*Mammuthus primigenius*
RAM P80.14.1	*Mammuthus* cf. *M. primigenius*	*Mammuthus primigenius*
RAM P02.8.70	*Mammuthus* cf. *M. primigenius*	*Mammuthus primigenius*
RAM P81.3.5	*Mammuthus* cf. *M. primigenius*	*Mammuthus primigenius*
ROM IBW.83	*Mammuthus columbi*	*Mammuthus columbi*
RAM P91.10.4	*Mammuthus* sp.	*Mammuthus columbi*
RAM P97.8.1	*Mammuthus* cf. *M. primigenius*	*Mammuthus columbi*
RAM P94.4.3	*Mammuthus* cf. *M. columbi*	*Mammuthus columbi*
RAM P88.7.1	*Mammuthus* cf. *M. columbi*	*Mammuthus columbi*
RAM P84.5.1	*Mammuthus* sp.	*Mammuthus columbi*
	m6	
RAM P97.10.143	*Mammuthus* cf. *M. columbi*	*Mammuthus primigenius*
RAM P97.10.144	*Mammuthus* cf. *M. columbi*	*Mammuthus primigenius*
RAM P99.3.164	*Mammuthus* cf. *M. primigenius*	*M. columbi/primigenius* (intermediate morphology)
RAM P97.11.1b	*Mammuthus* sp.	*M. columbi/primigenius* (intermediate morphology)
RAM P21.391.1	Not previously evaluated	*Mammuthus columbi*
RAM P18.319.4	Not previously evaluated	*Mammuthus columbi*
CMN 17845	*Mammuthus imperator* (Churcher, 1972) *Mammuthus columbi* (Hills and Harington, 2003; Widga et al., 2017)	*Mammuthus columbi*

additional remains in geologic context, but that may be a rare hope. The nature of the record in Alberta is such that Quaternary fossils deeply buried in gravels do not typically reveal themselves without the work of industry, and that usually means the remains are not recovered until the primary context is impacted. Another approach to further resolution would be to evaluate the genetic character of mammoth remains described here, as each scenario could potentially be evaluated on a genetic basis, and such an analysis would allow for further integration of our observations with emerging evolutionary observations based on aDNA (e.g., Enk et al., 2016; van der Valk et al., 2021).

In contrast to the predominant distribution of *M. columbi* in Alberta, the fossil record of *M. primigenius* in North America suggests that this species was primarily distributed along northern latitudes ranging from Alaska and Yukon south to the Great Lakes region (Saunders et al., 2010; Smith and Graham, 2017; Wang et al., 2021). In our sample, molars with *M. primigenius* morphology occur as far south as the Medicine Hat area in southeastern Alberta, a pattern that is not surprising given that specimens of *M. primigenius* were recovered further south into the northern contiguous United States. Although scarce in the western United States, records of *M. primigenius* are known as far south as The Mammoth Site of Hot Springs, in southwestern South Dakota (Agenbroad et al., 1994).

The two specimens with intermediate *M. columbi*–*M. primigenius* morphology were recovered from the central region of Alberta in the Edmonton area (Fig. 1). Whether these morphologies reflect sympatry and introgression of these two taxa or simply represent the margins of morphological space occupied by one species or the other is an open question that could be addressed by other types of analyses (e.g., aDNA).

At a broad timescale, individuals with morphologies in the core ranges of the morphological space of *M. columbi* and *M. primigenius*, and individuals with morphologies plotting in the intermediate zone between those ranges were present in central Alberta prior to the onset of the LGM. However, we do not have the resolution to determine more specific patterns of chronological distribution within pre-LGM time. Only one directly dated specimen from Alberta, a molar with *M. columbi* morphology recovered from a gravel pit in Bindloss, southeastern Alberta (CMN 17845), produced a radiocarbon date that postdates the LGM (Table 3). The age of this specimen suggests that *M. columbi* spread into the area that is now Alberta as the ice sheets receded during post-LGM times. Other post-LGM mammoth records lack elements that permit species assignment, but have associated or direct radiocarbon data indicative of dispersal into Alberta following deglaciation (e.g., Burnco Pit; Burns, 2010). Given our biogeographic interpretation for CMN 17845, we hypothesize that these are also likely representative of south-to-north movement and likely represent *M. columbi.*

Tooth morphology and evolutionary models in mammoths

Temporal and spatial morphological trends in dental characters have traditionally been used to establish species boundaries and devise models of mammoth evolution (Osborn, 1942; Maglio, 1973; Madden, 1981; Lister and Sher, 2015; Lister, 2022), and we utilized those taxonomic approaches in this paper. However, recent molecular studies provide evidence to suggest that the evolutionary history of mammoths is more complex than originally hypothesized based on dental characters (Enk et al., 2016; Chang et al., 2017; Palkopoulou et al., 2018; van der Valk et al., 2021). Ultimately, integrating morphological patterns of dental variation with variation at the molecular level and accurate dating of individual specimens will be necessary to advance our understanding of mammoth evolution, systematics, and phylogeography. In this regard, mammoth teeth recovered from Alberta, or from similar areas that may serve as biogeographic corridors, may play a significant role in advancing our understanding of morphological and molecular variation in Late Pleistocene North American mammoths, given the intermediate geographic location between Beringia to the north and the North American midcontinent to the south.

The occurrence of discrepancies between evolutionary models based on dental morphology and those based on molecular data are not overly surprising. The study of molar morphology in mammoths and other elephantids has undoubtedly revealed major events in the evolutionary history of these animals (Maglio, 1973; Madden, 1981; Lister and Sher, 2015; Saarinen and Lister, 2023). However, the molar dentition is one of many character complexes that are subject to evolutionary change, each of which can evolve at different times and rates. Furthermore, the evolution of molar morphology in mammoths and other elephantids appears to be largely influenced by developmental timing, the interplay between structural and functional constraints, and selective pressures associated with feeding ecology and/or environmental parameters such as aridity (Maglio, 1973; Herridge, 2010; Saarinen and Lister, 2023). Therefore, it is unrealistic to expect that molar dentition by itself can inform us about the complete evolutionary history of mammoths. Nevertheless, some instances of population divergence may be recognized by dental characters and perhaps some morphologies represent instances of hybridization if interbreeding between species resulted in intermediate tooth morphologies (e.g., Lister and Sher, 2015; Lister, 2017). Some instances of population isolation and divergence in the absence of developmental or selection pressures on tooth morphology may remain cryptic. A potential example of this cryptic divergence in an unnamed lineage with *M. trogontherii* dental morphology was recently identified based on genetic evidence (van der Valk et al., 2021). Likewise, instances of hybridization between lineages with similar tooth morphologies may remain cryptic. A potential example of this cryptic hybridization is the postulated hybrid origin of *M. columbi* (van der Valk et al., 2021). As a result, it may be unsurprising, or even expected, that molecular phylogenies may depart from phylogenies derived from tooth morphology.

Teeth have played a significant role in developing models of mammoth evolution (e.g., Maglio, 1973; Lister and Sher, 2015; Saarinen and Lister, 2023), but by focusing on a single character complex, we inevitably miss grasping the whole history. We should not discard using teeth for understanding mammoth evolution, but they should continue to be analyzed in a broader morphological and molecular context. Likewise, evolutionary models based on molecular data cannot be fully understood in the absence of paleontological data about mammoths, other organisms they interacted with, and the habitats in which they lived. Rather than a final word on mammoth taxonomy and distribution in Alberta, the data we present here represent a starting point for understanding the taxonomic character and evolutionary history of mammoths across a regional, dynamic Pleistocene landscape. Ultimately, understanding the mosaic of mammoth morphology, spatial and temporal distribution, and molecular history across distinct geographic settings will provide a more complete, nuanced understanding of evolution of *Mammuthus* as a whole.

Conclusions

The evolutionary history of mammoths (or any taxon) is a collective of regional patterns, and our work provides a starting point for understanding the evolutionary history of mammoths across a regional landscape in northern North America that is characterized by a history of major ecological disturbances (e.g., LGM), climatic change, and consequential biogeographic change, including the arrival of humans. At least three mammoth tooth morphologies are preserved in the Alberta record (*M. columbi*, *M. primigenius*, and morphologies falling within the intermediate zone of those taxa). The presence of teeth with a morphology indicative of *M. columbi* may document a broader geographic range for that taxon than previously recognized, but could also represent a much deeper time component to the history of *Mammuthus* in Alberta (i.e., *M. trogontherii*).

Morphological and ancient DNA studies suggest that hybridization and introgression played an important role in the evolution of several proboscidean taxa, including *M. columbi* and *M. primigenius* (Enk et al., 2016; Chang et al., 2017; Palkopoulou et al., 2018; van der Valk et al., 2021). Our morphometric study allowed us to identify specimens with intermediate morphologies in the sample of Alberta mammoth teeth, and that observation deserves further attention to determine if those teeth simply lie at the margins of morphological space that delineate different taxa or represent a morphological expression of interbreeding of distinct taxa. The blessing and the curse of working in the Pleistocene (and on mammoths, in particular) is a record in close enough proximity to the modern that we can document the existence of complex biological and morphological patterns, but sparse enough that our understanding of underlying mechanisms driving those patterns remains elusive.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/qua.2024.47

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