Re-evaluation of mastodon material from Oregon and Washington, USA, Alberta, Canada, and Hidalgo and Jalisco, Mexico (#94276)

First revision

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Re-evaluation of mastodon material from Oregon and Washington, USA, Alberta, Canada, and Hidalgo and Jalisco, Mexico

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The presence of at least two contemporaneous Pleistocene mastodon taxa in North America (*Mammut americanum* and *M. pacificus*) invites re-examination of specimens at the geographic margins of each species, in order to determine range boundaries, overlaps, and fluctuations. Third molars from Oregon in the United States, as well as from Hidalgo and Jalisco in Mexico, were found to be morphologically consistent with *M. pacificus*. Washington in the United States includes one mandible referrable to *M. americanum*, and a number of additional specimens that could not be confidently assigned to either taxon. Alberta in Canada was found to have some specimens that were consistent with *M. pacificus*, but others that were identified as *M. americanum*. The Alberta specimen referred to *M. pacificus* is the same tooth found to have a Pliocene divergence time from *M. americanum* based on mitochondrial genome data from a previous study, suggesting a deep divergence time between the two taxa. The apparent presence of both mastodon taxa in close geographic proximity has interesting paleobiogeographic implications. It is not yet clear if both taxa were present simultaneously in a given location; if not, it suggests fluctuating ranges that may reflect shifting climates and/or biomes over time. Alternatively, if both taxa were simultaneously present in the same place, is may suggest a high degree of niche partitioning in mammutids. Additional accurately dated specimens will be required to resolve this question.

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Abstract (English)

The presence of at least two contemporaneous Pleistocene mastodon taxa in North America (*Mammut americanum* and *M. pacificus*) invites re-examination of specimens at the geographic margins of each species in order to determine range boundaries, overlaps, and fluctuations. Third molars from Oregon in the United States, as well as from Hidalgo and Jalisco in Mexico, were found to be morphologically consistent with *M. pacificus*. Washington in the United States includes one mandible referrable to *M. americanum*, and a number of additional specimens that could not be confidently assigned to either taxon. Alberta in Canada was found to have some specimens that were consistent with *M. pacificus*, but others that were identified as *M. americanum*. The Alberta specimen referred to *M. pacificus* is the same tooth found to have a Pliocene divergence time from *M. americanum* based on mitochondrial genome data from a previous study, suggesting a deep divergence time between the two taxa.

The apparent presence of both mastodon taxa in close geographic proximity has interesting paleobiogeographic implications. It is not yet clear if both taxa were present simultaneously in a given location; if not, it suggests fluctuating ranges that may reflect shifting climates and/or biomes over time. Alternatively, if both taxa were simultaneously present in the same place, is may suggest a high degree of niche partitioning in mammutids. Additional accurately dated specimens will be required to resolve this question.

Abstract (Spanish)

La presencia de al menos dos especies de mastodontes en el Pleistoceno de Norteamérica (*Mammut americanum* y *M. pacificus*), conduce a revaluar ejemplares reportados en los límites

geográficos de cada especie. Esto con la finalidad de conocer su área geográfica, cambios y sobrelapamiento en distribución. En este estudio, se reconoció que terceros molares procedentes de Oregón, Estados Unidos, así como de Hidalgo y Jalisco, México, tienen una morfología consistente con la de *M. pacificus*. Por su parte, en Washington, Estados Unidos y Alberta, Canadá, se encontraron algunos ejemplares pertenecientes a *M. pacificus* y otros a *M. americanum*. En particular, el ejemplar de *M. pacificus* de Alberta, es el mismo que indica un tiempo de divergencia de *M. americanum* en el Plioceno, esto con base en datos de genoma mitocondrial derivado de un estudio previo, lo cual sugiere una separación temprana entre estos taxones.

La aparente presencia de ambos taxónes de mastodonte en cercana proximidad geográfica tiene interesantes implicaciones paleobiogeográficas. Todavía no está claro si ambos taxónes estaban presentes simultáneamente en una misma localidad; si no, sugiere rangos fluctuantes que pueden reflejar climas y/o biomas cambiantes a lo largo del tiempo. Alternativamente, si ambos taxónes estuvieran presentes simultáneamente en el mismo lugar, podría sugerir un alto grado de partición de nicho en mamútidos. Se requerirán especímenes adicionales fechados con precisión para resolver esta pregunta.

Abstract (French)

La présence d'au moins deux taxons contemporains de mastodontes durant le Pléistocène en Amérique du Nord (*Mammut americanum* et *M. pacificus*) invite un réexamen des spécimens en marge géographique de chaque espèce, afin de déterminer les limites d'aires de répartition, les chevauchements possibles et fluctuations des aires. Les troisièmes molaires des spécimens de

l'Orégon aux États-Unis, ainsi que de l'Hidalgo et de Jalisco au Mexique, s'avèrent morphologiquement cohérentes avec *M. pacificus*. Certaines de l'état de Washington aux États-Unis et de l'Alberta au Canada sont compatibles avec *M. pacificus*, alors que d'autres ont été identifiés comme *M. americanum*. Le spécimen de l'Alberta référé comme *M. pacificus* avait précédemment fait l'objet d'une étude de son génome mitochondrial. Les résultats de cette analyse avaient démontré un temps de divergence dans le Pliocène avec *M. americanum*, s'avérant donc profond entre les deux taxons.

La présence apparente des deux taxons de mastodontes en proximité géographique a des implications paléobiogéographiques intéressantes. Il n'est pas encore clair si les deux taxons étaient présents simultanément en un endroit donné; si cela n'était pas le cas, cela suggère des fluctuations des aires de répartition qui pourraient refléter des changements du climat et / ou des biomes au fil du temps. Alternativement, si les deux taxons étaient simultanément présents au même endroit, cela pourrait suggérer un haut degré de partitionnement des niches chez les mammutidés. Des spécimens supplémentaires datés avec précision seront nécessaires pour résoudre cette question.

Introduction

Mastodons (*Mammut*) are a nearly ubiquitous part of the Late Pleistocene fauna of North America and have been scientifically studied for more than 200 years. With such a lengthy period of study, it is perhaps surprising that recent research has revealed surprising new information about mastodons, including unexpected regional concentrations of specimens (e.g., Springer et al. 2009, 2010; Fisher et al. 2014), information about life histories and extinctions

(Fisher 2008, 2009; Miller et al. 2022; Smith and Fisher 2011; Widga et al. 2017, 2021), genetic information documenting complex biogeographic patterns (Karpinski et al. 2020), and previously unrecognized taxa (Dooley et al. 2019).

Dooley et al. (2019) established *M. pacificus* based primarily on statistically narrower M3/m3 for a given length, as well as several additional characters including (relative to *M. americanum*) smaller diameter male tusks for a given Laws Group age and accompanying differences in the maxillae, femora with a greater mid shaft diameter for a given length, six sacral vertebrae (4-6, typically 5 in *M. americanum*), and the absence of mandibular tusks (present in 27% of *M. americanum*).

When describing *M. pacificus*, Dooley et al. (2019) took a conservative approach in referring specimens to *M. pacificus*. They only referred specimens for which there was compelling morphological and biogeographic data to *M. pacificus*, while all other specimens were considered *M. americanum* (i. e., essentially, the null hypothesis was that a specimen was *M. americanum*). As a result, they considered material from the Pacific Northwest and from Mexico to be *M. americanum,* as at the time there was little biogeographic or morphological support for referral of these specimens to *M. pacificus*. Additional studies on mammutids since 2019, including McDonald et al. (2020) and Karpinski et al. (2020) invite reassessment of material from these regions.

The discovery of the Pacific mastodon (*Mammut pacificus*) on the west coast of North America (Dooley et al. 2019) and the high level of endemism indicated in genetic data (Karpinski et al. 2020) both suggest that much remains to be learned about the diversity and relationships of

different regional populations of mastodons. Indeed, the discovery of a Pacific mastodon specimen in Montana (McDonald et al. 2020), hundreds of kilometers east of any other records of this taxon, confirmed the potential for valuable data to be derived from locations not traditionally considered as “mastodon country”.

Here we report several new recognized occurrences of *Mammut pacificus* in Canada, the United States, and Mexico, based on specimens previously referred to *M. americanum*. Most of these represent considerable range extensions for *M. pacificus*, and indicate a more complex biogeographic history of Pleistocene mastodons.

Materials & Methods

Direct measurements were taken of *Mammut* molars and femora of specimens from Alberta in Canada, Oregon and Washington in the United States, and Hidalgo and Jalisco in Mexico. These were compared with specimens, casts, and printed replicas of *Mammut* elements housed at the Western Science Center, as well as to published data on other *Mammut* specimens, based on taxon assignments from Dooley et al. (2019). Measurements and calculations for length/width (L:W) ratios of mastodon third molars follow Dooley et al. (2019); measurements of femora follow Hodgson et al (2008). Methods for assessing the width of incomplete molars described with the relevant specimen.

We assign a specimen to *M. pacificus* if it meets one of the following conditions: a) the M3 or m3 falls outside of 2σ for *M. americanum* as described in Dooley et al. 2019, or b) if the M3 or m3 falls outside of 1σ for *M. americanum*, and the specimens shares an additional character

associated with *M. pacificus* as described in the diagnosis presented in Dooley et al. 2019, with no characters unique to *M. americanum*.

Institutional Abbreviations

F-, Tualatin Public Library, Tualatin, Oregon, USA; **DMNH**, Denver Museum of Natural History, Denver, Colorado, USA; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **RAM**, Royal Alberta Museum, Edmonton, Alberta, Canada; **LSUMG**, Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA; **NMC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **SBMNH**, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; **SDSNH**, San Diego Natural History Museum, San Diego, California, USA; **UAHMP**, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo, México; **UCMP**, University of California, Berkeley Museum of Paleontology, Berkeley, California, USA; **USNM**, United States National Museum of Natural History, Washington DC, USA; **UWBM**, University of Washington Burke Museum Seattle, Washington, USA; **WSC**, Western Science Center, Hemet, California, USA.

Results

Oregon

Dooley et al. (2019) considered Pleistocene mammutid material from Oregon in their study as *Mammut americanum*. All of the teeth they examined were either non-diagnostic for distinguishing between *M. americanum* and *M. pacificus* (e.g., M2), or came from tooth positions with very small sample sizes (e.g., premolars). Even so, Oregon specimens of tooth positions with small sample sizes, such as P3, still had L:W ratios that were more similar to *M.*

pacificus than to *M. americanum*. Dooley et al. (2019) noted that these remains were biogeographically and anatomically anomalous if assigned to *M. americanum* and hypothesized that they may in fact represent *M. pacificus*.

One specimen not examined by Dooley et al. (2019) was the Tualatin mastodon (F-30282), recovered in 1962 and currently on display in the Tualatin Public Library. Nearly the entire left side of the animal is preserved, including the left tusk and a portion of the maxilla with the preserved M2 and M3 (Figure 1A). Based on photos of the excavation and rudimentary notes, the remains were situated approximately 3.5-5 feet (1.067-1.52 m) below the surface in a marsh. The Tualatin mastodon dates to the Late Pleistocene (Gilmour et al. 2015), post-dating the Missoula floods and human colonization of the area (Davis et al. 2019; O'Connor et al. 2020). The M3 has a L:W ratio of 1.91, which is just inside the range of M3s of *M. americanum* in our dataset (1.59-1.95), but well within the range of *M. pacificus* (1.69-2.33) (Table 1, Figure 2). Additionally, the left femur (Figure 1B) is complete and has a maximum length of 807 mm and mid-shaft width of 130 mm, placing it close to small *M. pacificus* specimens from California, (Dooley et al. 2019: Figure 25; Figure 3), and well apart from *M. americanum*. These measurements indicate that the Tualatin mastodon is *M. pacificus*, suggesting that other Oregon material previously reported as *M. americanum* may be *M. pacificus* as well.

Another noteworthy Oregon specimen is USNM 4911, an isolated left M2 described as *Mammut oregonense* by Hay (1926). Dooley et al. (2019) showed that M2 does not differ in any consistent way between *M. pacificus* and *M. americanum*, even in L:W ratio. As *M. oregonense* is only represented by an M2 and no other specimens have ever been referred to this taxon, we concur

with assessment of Dooley et al. (2019) that *M. oregonense* should be considered a *nomen dubium*, and its use restricted to the holotype.

Washington

Dooley et al. (2019) assigned three specimens from Washington to *M. americanum*, two mandibles that included m3s and an isolated M3, all from different localities. The isolated right M3 (UWBM 83312) from Jefferson County is a tetralophodont tooth missing large areas of enamel (Figure 4F). There is little to no wear on lophs 4 and 5, but damage on the first three lophs make it impossible to assess the wear in these areas. The L:W ratio is 1.82, closer to the average of *M. americanum* (1.76) that to *M. pacificus* (1.98), but within the known range of values for both taxa (Figure 2).

UWBM 88099 is a mandible from Lewis County that includes the left m2 and m3, and the right m3 (Figure 4C-E). The anterior tip of the mandible is damaged, as are both ascending mandibular rami, which are missing the condyles. While the anterior tip of the mandible is imperfectly preserved, there is no indication of alveoli for mandibular tusks. The L:W ratio of the left m3 is 1.94. This value is just outside of 2σ for *M. pacificus* (the lowest known value for M. pacificus is 1.95, average 2.26), and close to the mean value for *M. americanum* (1.89) (Figure 4).

UWBM 14491 is a complete mandible from Clallam County that includes both left and right m1, m2, and m3 (Figure 4G-I). The m1s show heavy wear, the m2s are in moderate wear, and the m3s are not yet fully erupted and show only slight wear on the first lophids. This is most

equivalent to Laws (1966) Group XVII or XVIII, indicating and age of 28-30 ±2 African elephant equivalent years. There are no alveoli for mandibular tusks. The right m3 has a L:W ratio of 2.11. This is well within the known range for *M. pacificus* and is greater than all but one *M. americanum* in our dat≡se (N=134), but still with the 2σ range of *M. americanum* (Figure 5).

The Manis mastodon was not included in Dooley et al. (2019). This specimen was discovered during excavation of a holding pond near Sequim, Clallam County, Washington in 1977, and became well known because of a reported bone projectile point embedded on one of the ribs (Gustafson et al. 1979; Waters et al. 2011), although debate continues over the interpretation of this specimen (Haynes and Huckell 2016; Waters et al. 2023). Carbon dates from bone collagen yielded an age of approximately 13,800 ybp (Waters et al. 2011). The Manis mastodon has never been fully described or figured, but Gustafson et al. (1979) mention tusk segments up to 2 m in length, suggesting that the individual may have been a male. Field sketches reproduced in Gustafson et al. (1979) indicate the presence of numerous ribs, and at least portions of a forelimb including the scapula, humerus, and ulna. They also figure a heavily worn m2, and mention numerous skull fragments.

A number of elements from the Manis mastodon are on exhibit at the Sequim Museum and Arts in Sequim, including a complete right dentary with an *in situ* m3 (Figure 4A, B). The mandibular symphysis does not have alveoli for mandibular tusks. The m3 is pentaloph, with wear on all five lophids and heavy wear on the first two. This level of wear is consistent with Laws Group XXII or XXIII, yielding an age of 39-43 ± 2 AEY. The L:W ratio of this tooth is 2.09, within the

normal range for *M. pacificus* and much narrower than typical *M. americanum* m3s (only two *M. americanum* specimens out of 134 in our dataset are narrower), but still within the 2σ range of *M. americanum* (Figure 5).

The Washington State specimens present an interesting dilemma for taxon identification. All the known specimens lack mandibular tusks, but this absence of tusks is not diagnostic in its own right. One specimen (UWBM 88099) has an m3 that falls just outside the 2σ value of *M. pacificus* and close to the mean of *M. americanum*; thus we refer this specimen to *M. americanum*. All other Washington specimens have M3/m3 have L/W ratios that within the 2σ range of both taxa, although generally closer to the averages for *M. pacifcus* than *M. americanum,* but lack any definitive characters. Therefore we refer to the Washington specimens other than UWBM 88099 to *Mammut sp.* until such time as unequivocal diagnostic material is reported.

Hidalgo

Multiple elements of a single mastodon are known from Rancholabrean deposits at Ventoquipa, Hidalgo, Mexico (UAHMP-311; Bravo-Cuevas et al. 2015) (Figure 6). Dooley et al. (2019) included this specimen as *M. americanum* in their database, even though the L:W ratio of the M3 of UAHMP-311 is 1.93, close to the mean for *M. pacificus* (1.98) and close to the maximum value known for *M. americanum* (1.95) (Table 1, Figure 2). Measurements of the m3 of this specimen are now available; it has a L:W ratio of 2.29. This is higher than any specimen of *M. americanum* in our database (maximum=2.23, n=134), and is greater than the mean for *M. pacificus* (2.25) (Table 2, Figure 5). As both M3 and m3 of UAHMP-311 fall within the known

range of *M. pacificus*, and m3 falls outside the 2σ range of *M. americanum*, we refer this specimen to *M. pacificus*.

Jalisco

A left M3 (LACM 1854) (Figure 7) was recovered in 1955 from Lago de Chapala, near San Luis Soyatlan, Jalisco, Mexico. A rich fauna from this site includes remains from both *Mammuthus* and *Cuvieronius* (Lucas 2008), but LACM 1854 is the only mammutid element identified thus far. The age of the Lago de Chapala specimens has been problematic, potentially ranging from Rancholabrean to Blancan, but the material from San Luis Soyatlan appears to be Rancholabrean (Lucas, 2008; Rufolo, 1998).

LACM 1854 is a tetralophodont left M3. Large portions of the tooth, including the entire root area, are encrusted with what appears to be a carbonate or other evaporitic mineral. While there is some damage to the pretrite side of the first loph, the other lophs are undamaged. The lophs are simple, lacking the additional conelets that commonly fill the troughs between lophs in gomphotheriids. There is light to moderate wear on the pretrite side of the first three lophs, with the fourth loph showing only very slight wear. There is a distinct cingulum on the anterior margin, but this does not appear to extend to other portions of the tooth.

The length:width ratio of this tooth is 2.07, well within the known range of *M. pacificus* (1.69 - 2.33; mean = 1.98) (Table 1, Figure 2). No *M. americanum* M3 in our database has such a high L:W value (maximum = 1.95; mean = 1.77), and this value falls outside the 2σ range of *M. americanum*, justifying the referral of LACM 1854 to *M. pacificus*.

279

280 **Alberta**

281 A limited number of mammutid remains are known from Alberta, and were reviewed by Jass and
282 Barrón-Ortiz (2017). Nearly all of those records represent isolated specimens recovered from
283 gravel pits in the Edmonton area. The most complete specimen is a partial mandible, RAM
284 P94.16.1 (Figure 8) from the Apex Galloway Pit, located near Edmonton. The m3 in this
285 specimen has a L:W ratio of 1.90, well outside the 2σ range of *M. pacificus* and within the
286 known range of *M. americanum*. Moreover, RAM P94.16.1 has well-developed alveoli for lower
287 tusks, which are unknown in *M. pacificus* but occur in about 30% of *M. americanum* mandibles
288 (Green 2006), regardless of age or sex.

289

290 A second specimen, RAM P97.7.1 (Figure 8), also comes from an Edmonton-area gravel pit (Pit
291 46). Although damaged, this specimen is identified as a partial left M3 based on the right angle
292 formed by the loph axis and the long axis of the tooth (note: this specimen was reported as an m3
293 in Jass and Barrón-Ortiz (2017)). The tooth includes five lophs, but the first two lophs are
294 damaged, making direct measurement of the maximum tooth width impossible, as in M3 the
295 widest part of the tooth is always at either the first or second loph.

296

297 In order to estimate the likely maximum width of RAM P97.7.1, we calculated individual loph
298 widths as a percentage of maximum loph width for 34 *Mammut* M3s, including 17 specimens
299 each of *M. pacificus* and *M. americanum* (Table 3). This enabled us to calculate a range of likely
300 values of the maximum width of a tooth for a given width of the third loph.

301

RAM P97.7.1 is 183.69 mm long, while the third loph has a width of 81.27 mm. Using the values of *Mammut* specimens from Table 3 as a guide yields a range of likely widths for the widest loph, from 82.6 – 94.1mm. These values result in a LW ratio between 1.95-2.26 (with an average of 2.12). Reconstructions of RAM P97.7.1 using the estimated maximum and minimum loph widths are shown in Figure 8. As almost this entire range of values falls outside the 2σ values of *M. americanum* (1.56-1.96), we refer this specimen to *M. pacificus*.

Discussion

The presence of *M. pacificus* in Oregon and Washington is consistent with earlier reports of this taxon from northern California, Idaho, and Montana (Dooley et al. 2019; McDonald et al. 2020) (Figure 9). These records highlight a broad distribution of *M. pacificus* across the Pacific Northwest and northern Rocky Mountain region of the western United States. At least some of those records (e.g., Montana) pre-date the late Pleistocene and may provide an opportunity to explore further paleobiological questions (e.g., do early records in Montana reflect greater capacity to occupy an array of environmental niches or are they a reflection of earlier Pleistocene environmental perturbations?).

The presence of *M. pacificus* in Jalisco and Hidalgo is a significant and surprising range extension for this taxon. The Mexican record represents the southernmost occurrences of Rancholabrean *M. pacificus*, inhabiting areas that now are part of west-central and central Mexico. Given that Texas and New Mexico specimens are assignable with some confidence to *M. americanum* (Dooley et al. 2019), it seems that the range boundary near the southern margins

of the distribution for these two species lay somewhere in northern Mexico during the Late Pleistocene.

Karpinski et al. (2023) reported the presence of mitochondrial genome material consistent with *M. americanum* from American Falls, Idaho, a site that has produced specimens referred to *M. pacificus* based on morphology (Dooley et al. 2019). Here we add Alberta to Idaho as states/provinces that have produced specimens of both *M. americanum* and *M. pacificus*, although it is unclear if these taxa were present contemporaneously in each location. Nearly all mastodon specimens from Alberta, and much of the record of megafauna of Alberta, were recovered as part of industrial gravel extraction (Jass and Barrón-Ortiz 2017). Precise contextual data are not available for most specimens, inhibiting our ability to temporally relate individual specimens from the region that lack C-14 data or exceed the capabilities of radiocarbon dating. Direct dates on the Alberta specimens discussed here are either infinite (P97.7.1; >41,100 ^{14}C yr BP; Metcalfe et al. 2016) or close to infinite and in need of re-evaluation (P94.16.1; 40,700±3000 ^{14}C yr BP; Jass and Barrón-Ortiz 2017). Although our ability to relate the specimens in time is somewhat challenged, that does not diminish the significance of the observation of both taxa in the same geographic region.

The eastern Montana *M. pacificus* specimen reported by McDonald et al. (2020) lies far to the east of the Washington and Alberta occurrences of *M. americanum*, suggesting that the ranges of these taxa may have overlapped significantly in the northern Great Plains or that the range boundaries may have fluctuated over time. Although limited temporal control leaves that question presently unresolved, we note that the record of both *M. americanum* and *M. pacificus*

in Alberta and Washington points to further complexity in movement of taxa through the interior of northern North America during the Pleistocene. South-to-north dispersals through Alberta may have been influenced by population sources from both sides of the Rocky Mountains.

These data are of particular interest when considered in the context of mitochondrial genome data *for Mammut* described by Karpinski et al. (2020). They found a high level of endemism in *Mammut* populations in all regions they studied except in Alberta, where there were specimens with phylogenetic affinities to Missouri, Alaska, and Mexico. The single specimen with genetic affinities to Mexican specimens was RAM P.97.7.1, and is the same tooth that we have morphologically identified as *M. pacificus*. This suggests that the "Clade M" of Karpinski et al. (2020), which included RAM P97.7.1 and the Mexican specimens, may represent *M. pacificus*, while their clades Y, G, L, N, and A, taken together, represent *M. americanum*. According to Karpinski et al. (2020), Clade M diverged from the other clades at 3.03 Ma, indicating that *M. pacificus* and *M. americanum* likely diverged from each other sometime in the Pliocene. Examination of Early Pleistocene and Pliocene mammutids along with better age constraints on known specimens should help illuminate the nature of the divergence of these taxa as well as the biogeographic changes that have taken place in North America during the Neogene.

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Figure 1

Mammut pacificus F-30282 (Tualatin mastodon).

A. left M3, occlusal view, 5cm scale bar. B. left femur in articulation with pelvis, 10cm scale bar.

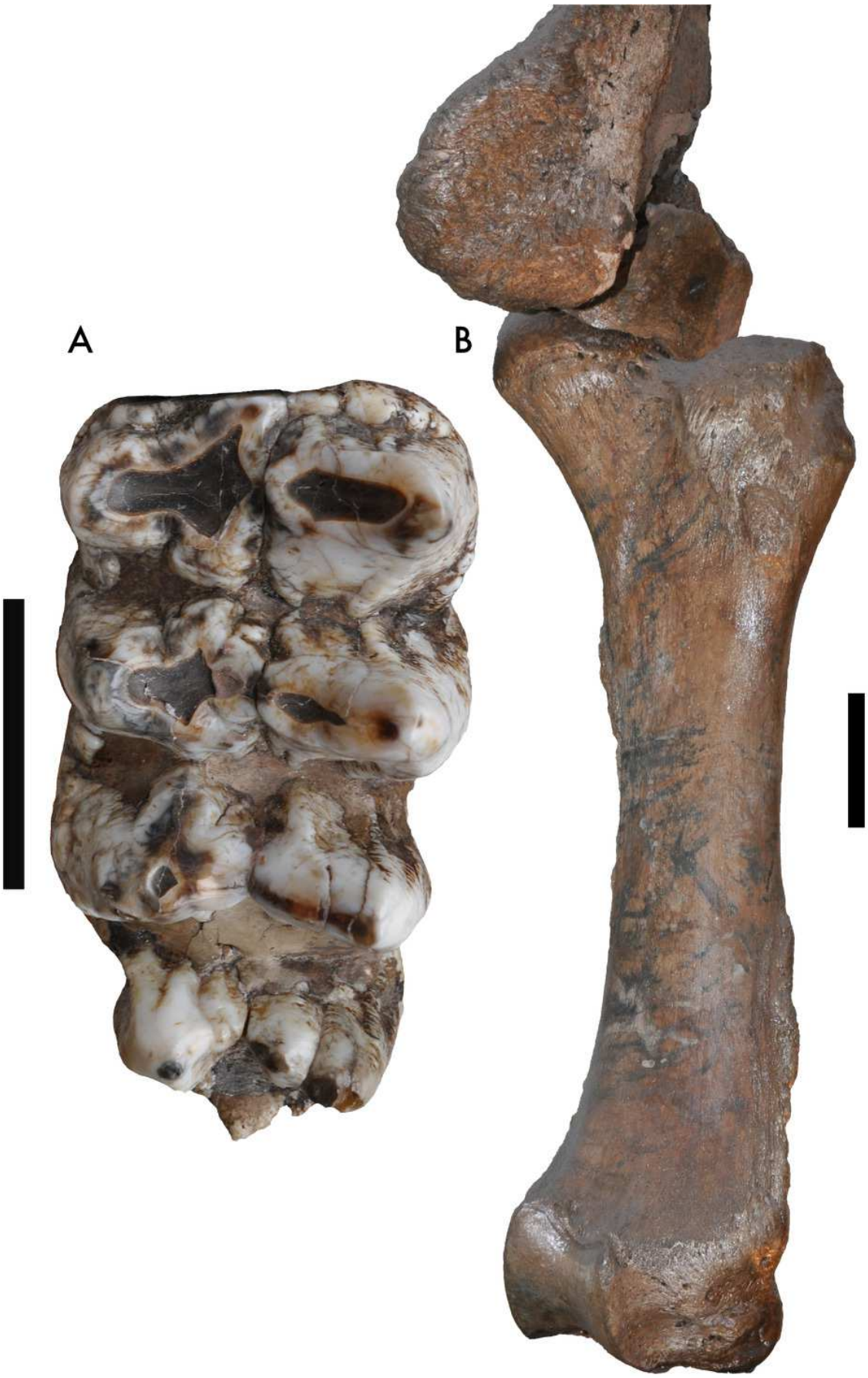
A
B

Figure 2

Length/width ratios of *Mammut* M3s.

Symbols in red are *M. pacificus*. Pink boxes represent the 1σ range for each taxa. Blue boxes represent the 2σ range and black x's mark the means. The vertical red bar represents the range of possible values for RAM P97.7. Specimen data is based on Dooley et al. 2019 with additional specimens from this manuscript; specimens used are included in Supplemental Table 1.

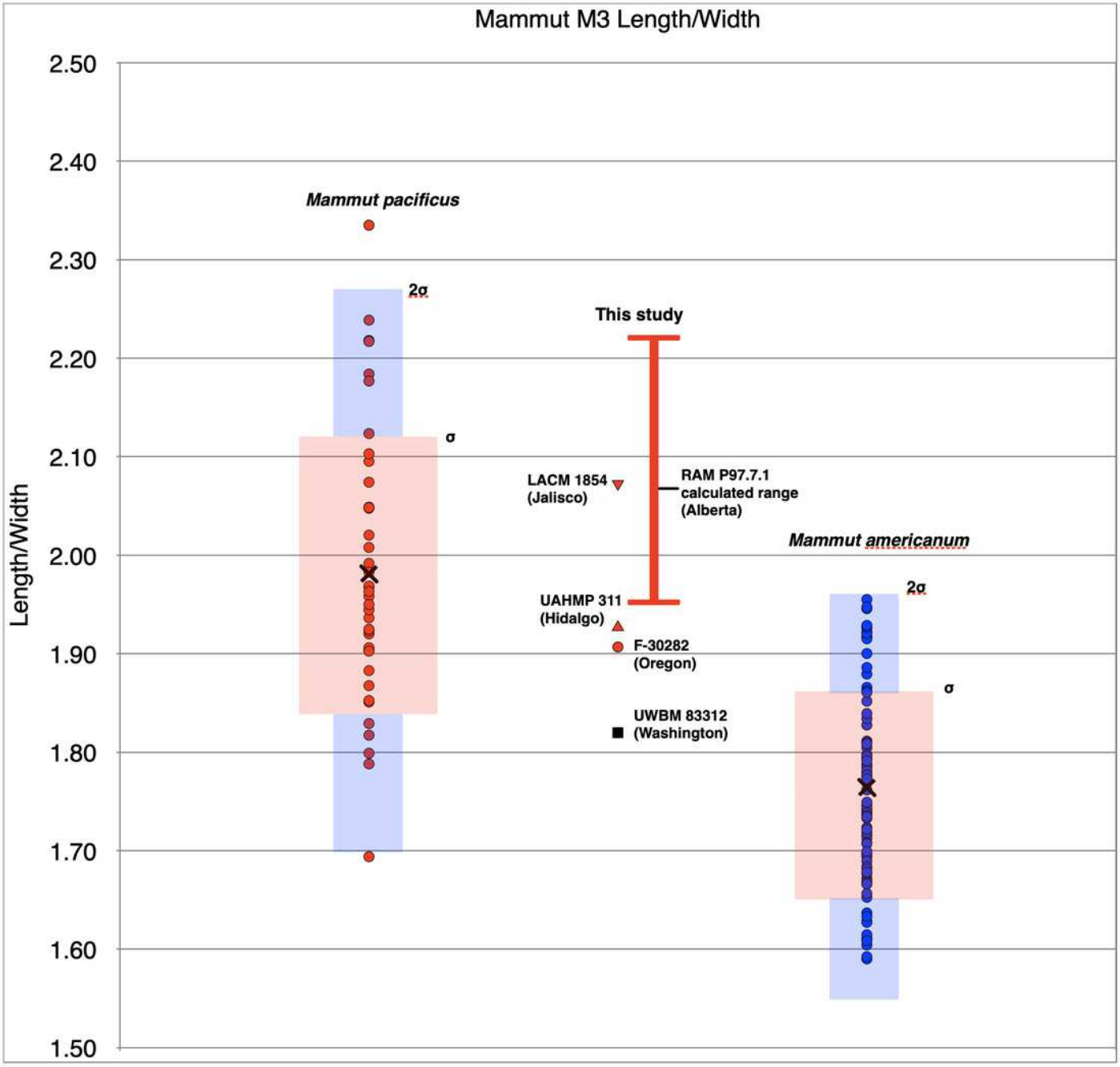
Mammut M3 Length/Width
Length/Width
2.50
2.40
2.30
2.20
2.10
2.00
1.90
1.80
1.70
1.60
1.50
Mammut pacificus
2σ
σ
This study
LACM 1854
(Jalisco)
RAM P97.7.1
calculated range
(Alberta)
UAHMP 311
(Hidalgo)
F-30282
(Oregon)
UWBM 83312
(Washington)
Mammut americanum
2σ
σ

Figure 3

Graph plotting *Mammut* femur length vs midshaft width.

Specimen data is based on Dooley et al. 2019 with addition of the Tualatin mastodon (F-30282) from this manuscript. Direct measurements are in mm.

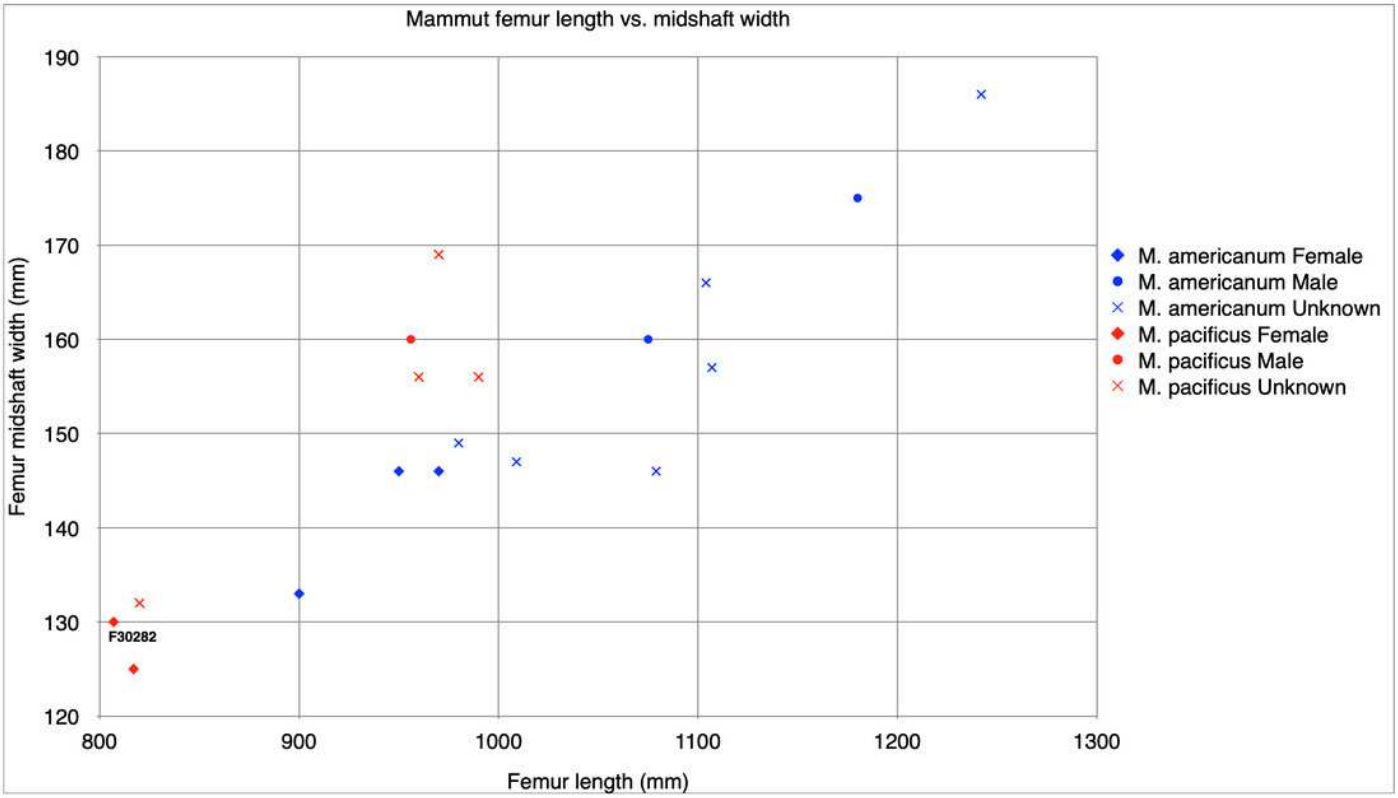

Figure 4

Mammut specimens from Washington, USA.

A, B: *Mammut* sp. (Manis mastodon) right m3, occlusal view (A), right dentary, medial view (B). C-E: *Mammut americanum* mandible UWBM 88099, dorsal (C), left lateral (D), and right lateral (E). F, *Mammut sp.* right M3 UWBM 83312, occlusal view. G-H: *Mammut sp.* mandible UBMW 14491, dorsal (G), left lateral (H), and right lateral (I). All scales = 5 cm.

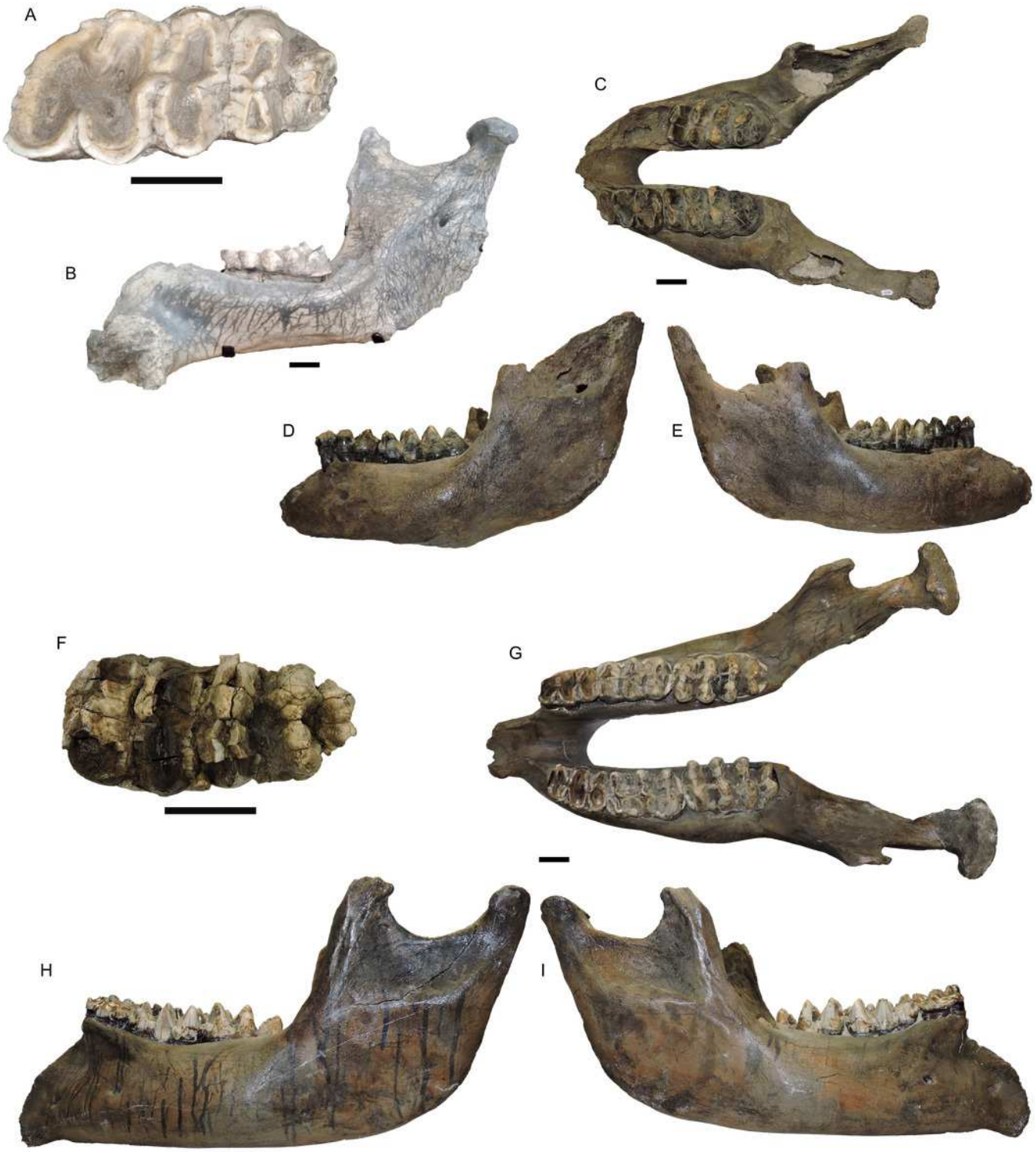
A
B
C
D
E
F
G
H
I

Figure 5

Length/width ratios of *Mammut* m3s, segregated by state/province.

Symbols in blue are *M. americanum*; in black, *Mammut* sp. Symbols in red are *M. pacificus*. Pink boxes represent the 1σ range for each taxa. Blue boxes represent the 2σ range and black x's mark the means. Specimen data is based on Dooley et al. 2019 with additional specimens from this manuscript; specimens used are included in Supplemental Table 2.

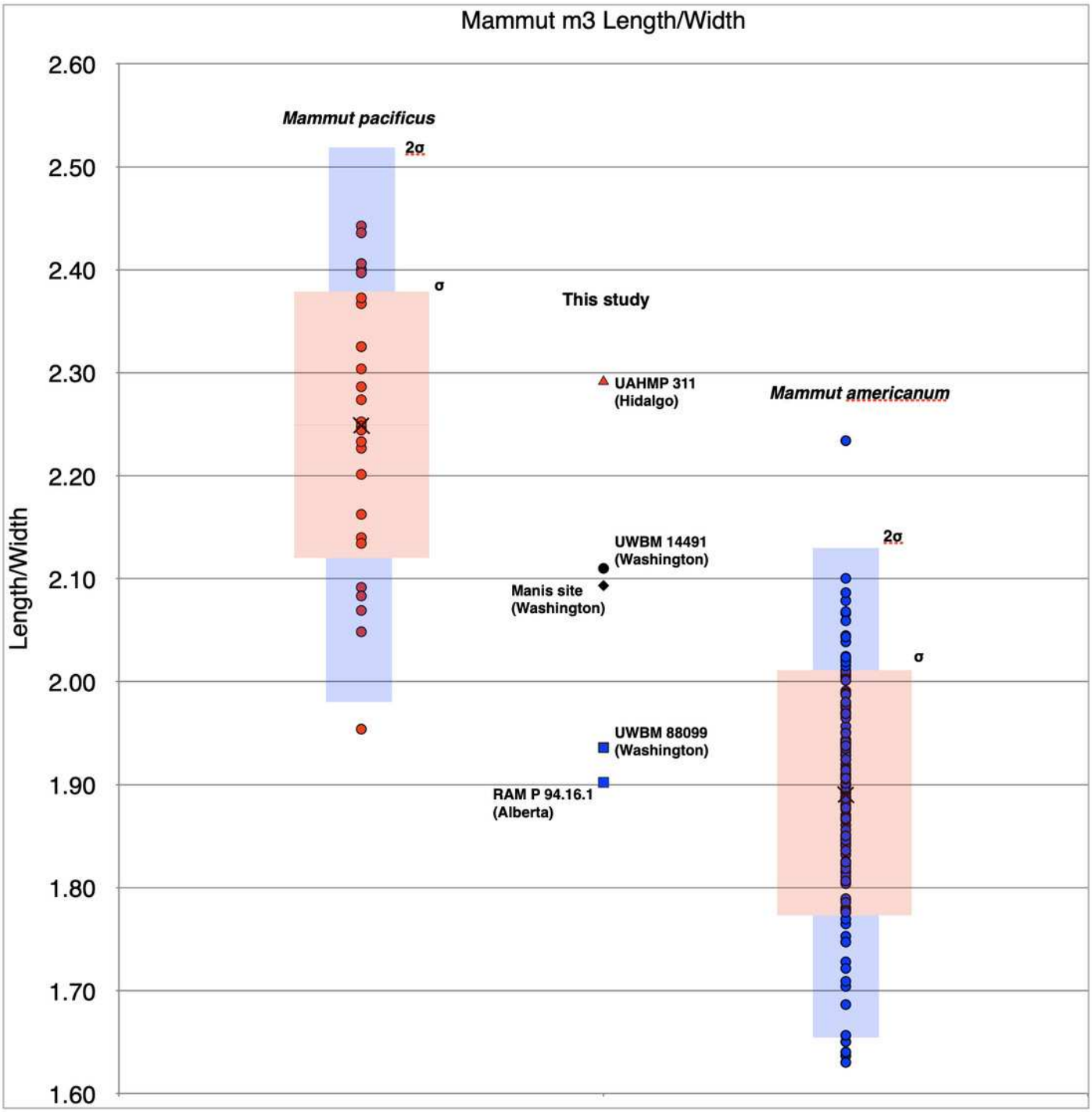
Mammut m3 Length/Width
Length/Width
2.60
2.50
2.40
2.30
2.20
2.10
2.00
1.90
1.80
1.70
1.60
Mammut pacificus
2σ
σ
This study
UAHMP 311
(Hidalgo)
Mammut americanum
UWBM 14491
(Washington)
Manis site
(Washington)
2σ
σ
UWBM 88099
(Washington)
RAM P 94.16.1
(Alberta)

Figure 6

Mammut pacificus UAHMP-311 right M3.

(A) and right m3 (B), occlusal view.

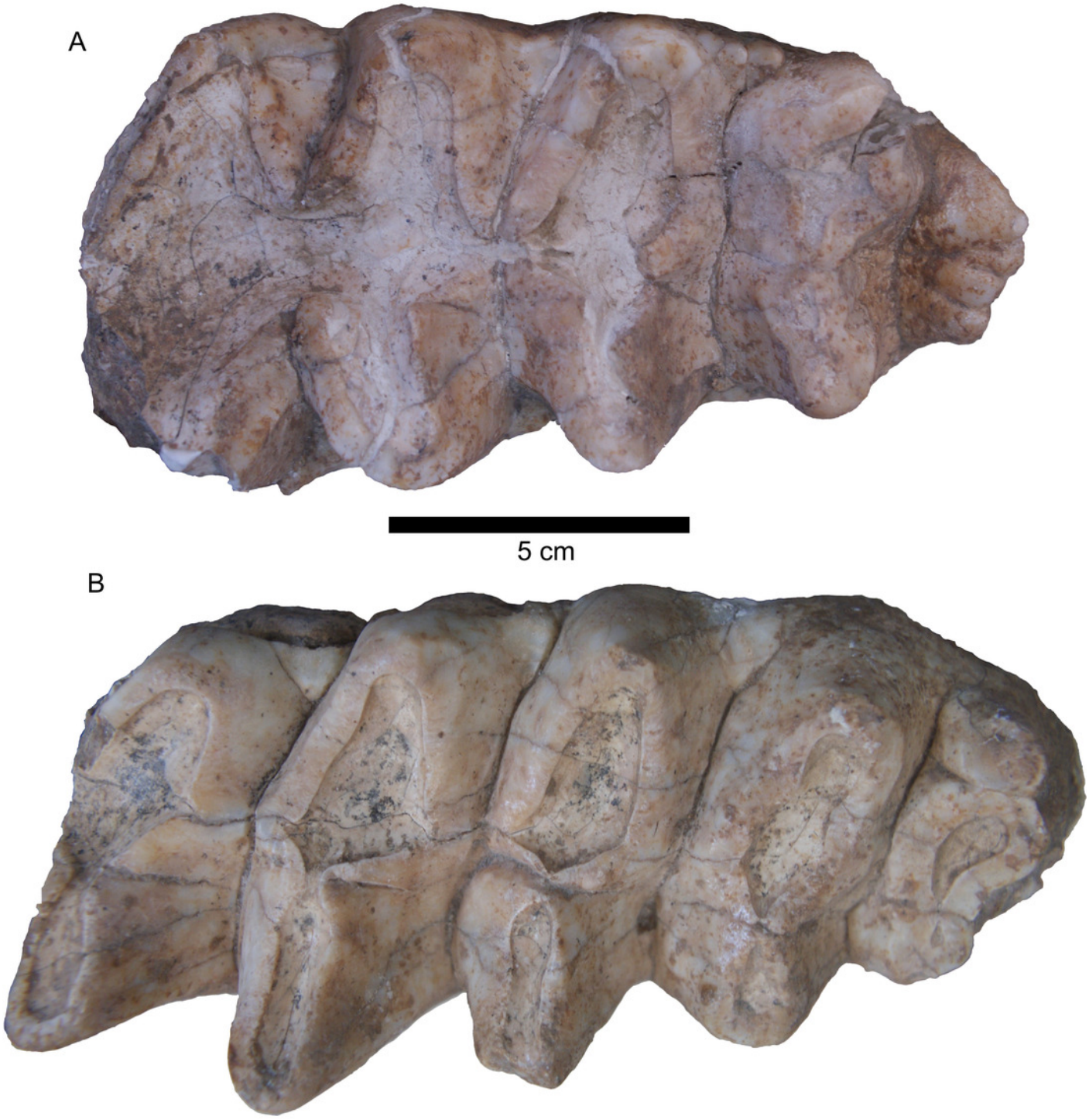
A
5 cm
B

Figure 7

Mammut pacificus LACM 1854 left M3.

Occlusal (A), labial (B) and lingual (C) views.

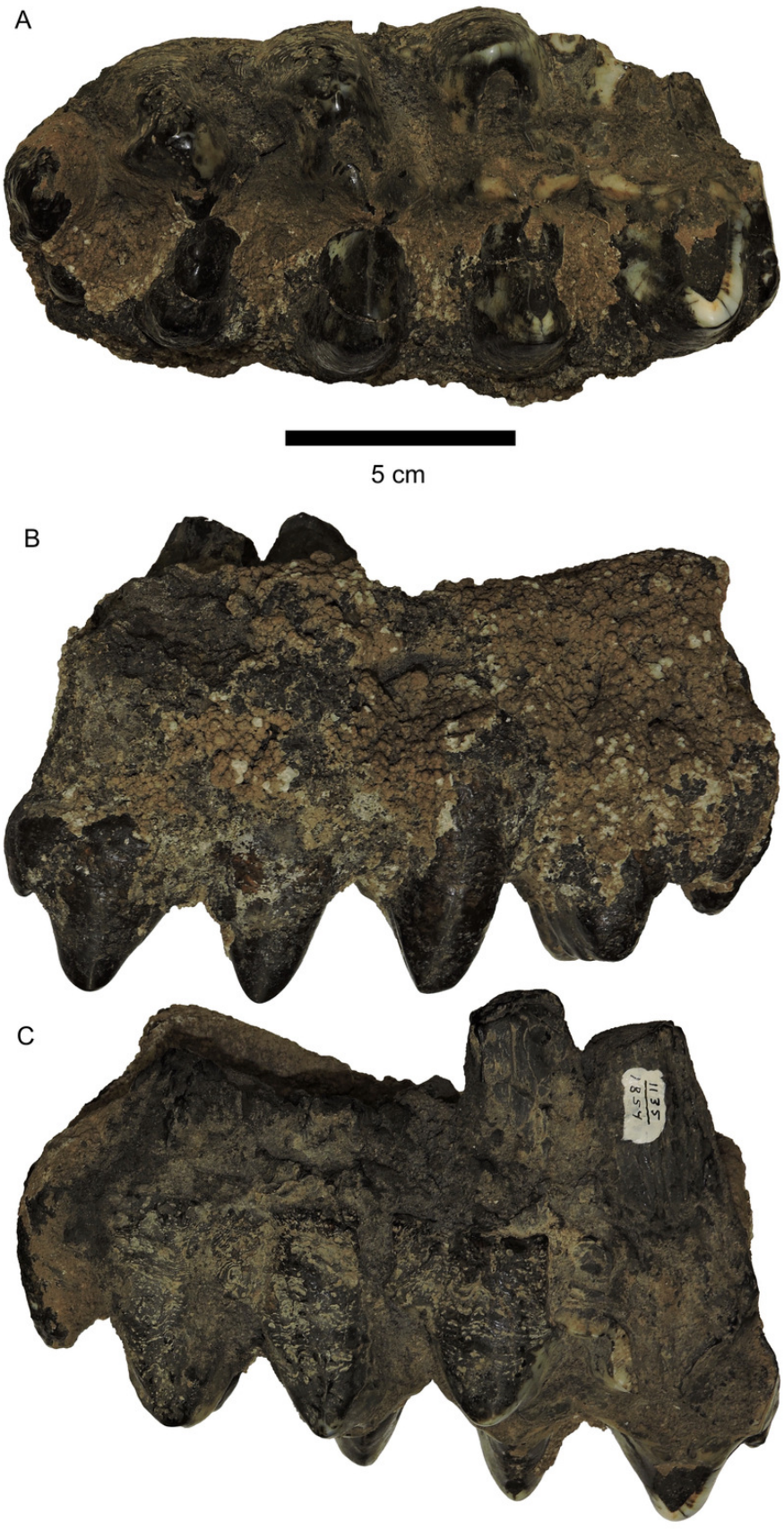
A
5 cm
B
C

Figure 8

Mammut specimens from Alberta.

A-C, *Mammut americanum* mandible RAM P94.16.1 in dorsal (A), anterior (B), and right lateral (C) views. Note the large chin tusk alveolar in (B). D- E, *Mammut pacificus* left M3 RAM P.97.7.1 M3 in labial (D) and occlusal (E) views, with a (F) reconstruction of min/max loph widths (blue=min, red=max).

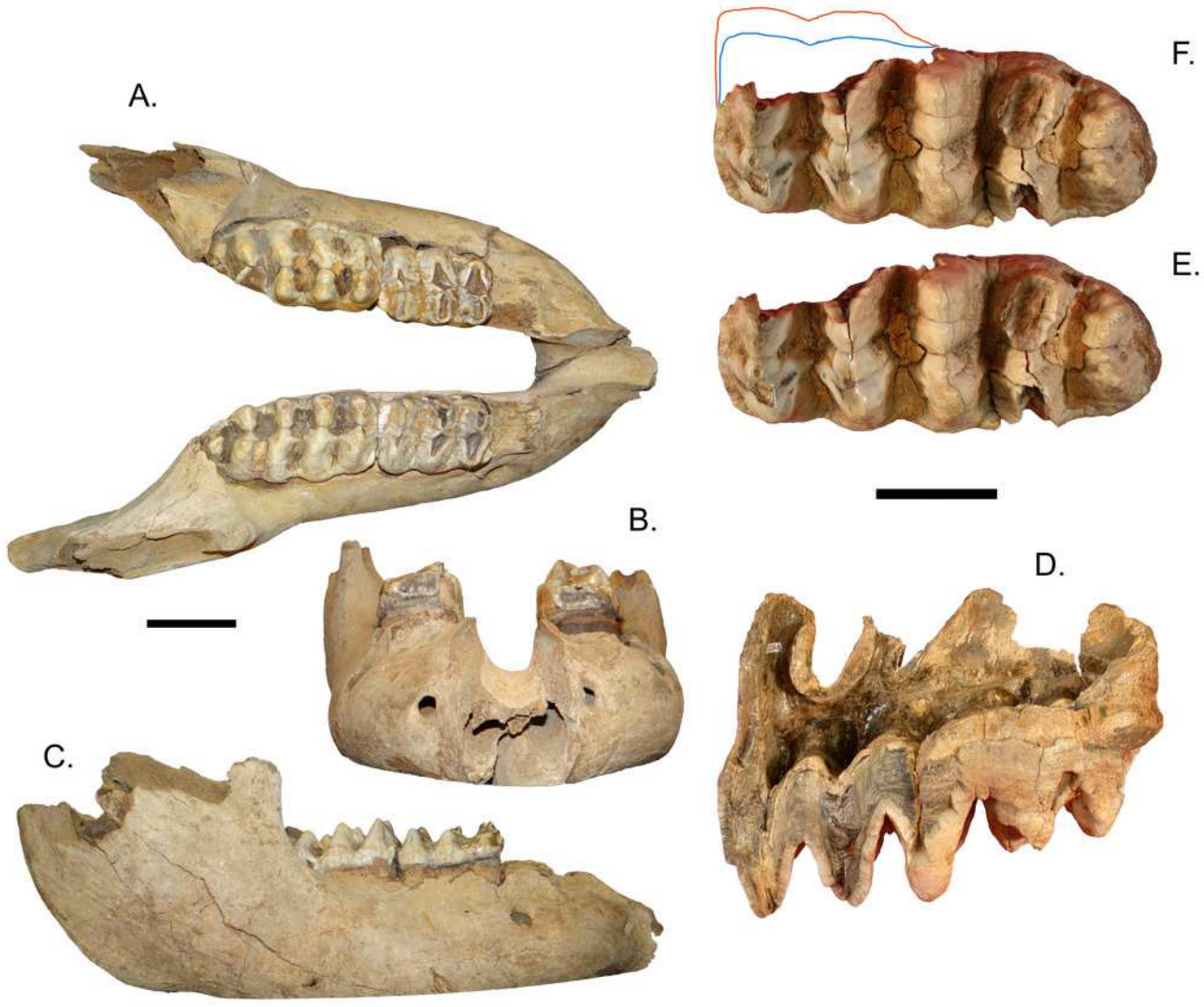

Figure 9

Late Pleistocene distribution map of *Mammut pacificus* and *Mammut americanum.*

Based on specimens examined in this paper, Karpinski et al. 2020, McDonald et al. 2021, and Dooley et al. 2019. Note that these distributions are approximate and most likely fluctuated with time.

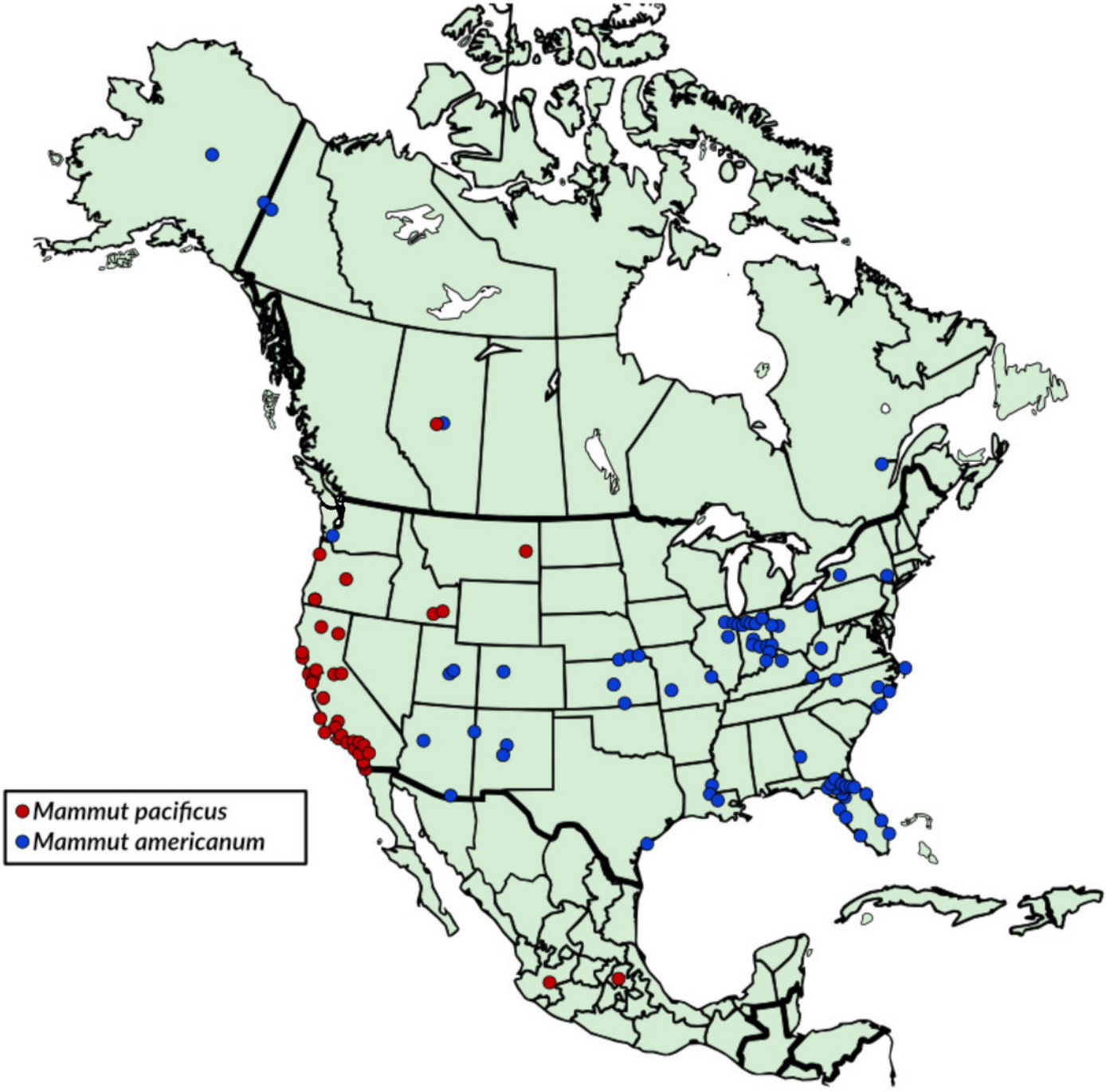
Mammut pacificus
Mammut americanum

Table 1(on next page)

Table 1: Aggregate M3 Data

Aggregate M3 length and width measurements, segregated by state/province. Based on published date from Dooley et al. 2019, with additional specimens from this manuscript. Specimens from the first five states listed are assigned to *M. pacificus*; all other listed specimens are assigned to *M. americanum*. Measurements are in mm.

Aggregate M3 data

State/Province	n	Mean maximum length	Median maximum length	SD	Max	Min	Mean maximum width	Median maximum width	SD	Max	Min	Mean L/W	Median L/W	SD	Max	Min
California	39	168.76	168.00	14.79	202.77	142.50	85.39	85.20	6.00	104.26	73.08	1.98	1.96	0.14	2.33	1.69
Montana	1	174.70	174.70		174.70	174.70	78.80	78.80		104.26	78.80	2.22	2.22		2.22	2.22
Oregon	1	149.89	149.89		149.89	149.89	78.61	78.61		104.26	78.61	1.91	1.91		1.91	1.91
Hidalgo	1	158.00	158.00		158.00	158.00	82.00	82.00		104.26	82.00	1.93	1.93		1.93	1.93
Jalisco	1	168.97	168.97		168.97	168.97	81.60	81.60		104.26	81.60	2.07	2.07		2.07	2.07
Alaska	2	157.00	157.00	10.32	164.30	149.7	95.58	95.58	2.02	104.26	94.2	1.64	1.64	0.07	1.69	1.59
Arizona	1	188.2	188.20		188.20	188.2	98.2	98.20		104.26	98.2	1.92	1.92		1.92	1.92
Colorado	4	163.50	163.50	0.58	164.00	163.00	99.30	99.25	1.70	104.26	97.50	1.65	1.65	0.03	1.67	1.61
Florida	15	177.35	177.30	15.20	197.40	143.20	99.07	100.60	7.51	104.26	82.20	1.79	1.79	0.11	1.95	1.59
Georgia	1	184.00	184.00		184.00	184.00	104.00	104.00		104.26	104.00	1.77	1.77		1.77	1.77
Illinois	3	181.81	175.94	11.00	194.50	175.00	104.15	102.00	6.42	104.26	99.07	1.75	1.75	0.03	1.78	1.72
Indiana	8	175.32	180.50	20.10	203.00	150.04	99.86	99.75	7.16	104.26	87.85	1.75	1.71	0.14	1.95	1.60
Kentucky	2	164.73	164.73	5.58	168.67	160.78	91.89	91.89	7.16	104.26	86.83	1.80	1.80	0.08	1.85	1.74
Louisiana	4	176.02	174.00	17.7	196.6	159.4	106.18	104.36	9.7	104.2	98.00	1.66	1.66	0.0	1.6	1.6

				8	0	6			3	6				2	8	3	
Missouri	23	181.99	181.70	18.07	213.51	144.30	101.02	101.70	7.92	104.26	86.60	1.80	1.80	0.08	1.93	1.63	
Nebraska	4	180.50	184.13	29.73	207.01	146.73	100.08	100.93	### #	104.26	87.46	1.80	1.87	0.15	1.88	1.57	
New York	1	172.20	172.20		172.20	172.20	100.20	100.20		104.26	100.20	1.72	1.72		1.72	1.72	
North Carolina	6	166.82	165.16	13.96	185.00	152.80	94.58	93.80	6.30	104.26	86.00	1.76	1.74	0.08	1.93	1.70	
Ohio	4	180.03	181.75	25.67	205.40	151.20	102.30	104.85	8.97	104.26	89.50	1.76	1.74	0.14	1.93	1.61	
Texas	3	171.68	167.00	11.74	185.04	163.00	99.30	97.00	9.66	104.26	91.00	1.73	1.72	0.05	1.79	1.68	
Tennessee	1	174.48	174.48		174.48	174.48	98.42	98.42		104.26	98.42	1.77	1.77		1.77	1.77	
Utah	2	151.50	151.50	0.71	152.00	151.00	85.50	85.50	2.12	104.26	84.00	1.77	1.77	0.05	1.81	1.74	
Washington	1	161.63	161.63		161.63	161.63	88.82	88.82		104.26	88.82	1.82	1.82		1.82	1.82	
Yukon	5	153.04	154.98	5.27	159.56	146.48	88.44	88.56	0.80	104.26	87.29	1.73	1.73	0.05	1.81	1.68	
M. americanum	89	176.03	174.59	17.71	213.51	143.20	98.84	99.04	8.01	118.00	82.20	1.76	1.77	0.10	1.95	1.57	2.000
M. pacificus	43	168.20	167.75	14.66	202.77	142.50	84.99	84.28	5.97	104.26	73.08	1.98	1.95	0.14	2.33	1.69	1.000

1

Table 2(on next page)

Table 2: Aggregate m3 Data

Aggregate m3 length and width measurements, segregated by state/province. Based on published date from Dooley et al. 2019, with additional specimens from this manuscript. Specimens from the first three states listed are assigned to *M. pacificus*; all other listed specimens are assigned to *M. americanum*. Measurements are in mm.

1

Aggregate m3 data

State/Province/Country	n	Mean maximum length	Median maximum length	SD	Max	Min	Mean maximum width	Median maximum width	SD	Max	Min	Mean L/W	Median L/W	SD	Max	Min
California	23	185.84	187.00	13.54	208.82	159.74	82.86	82.90	6.28	94.03	68.00	2.25	2.25	0.14	2.44	1.95
Idaho	3	185.93	192.90	19.70	201.20	163.70	82.70	192.90	6.81	90.10	76.70	2.25	2.23	0.12	2.37	2.13
Hidalgo	1	180	180.00		180.00	180	78.55	78.55		78.6	78.6	2.29	2.29		2.29	2.29
Alaska	3	167.56	169.79	20.64	187.00	145.9	90.76	92.07	10.95	101.0	79.2	1.85	1.84	0.01	1.85	1.84
Arizona	1	171.1	171.10		171.10	171.1	82.8	82.80		82.8	82.8	2.07	2.07		2.07	2.07
Colorado	9	182.44	174.80	11.39	202.40	171.00	95.97	95.70	6.09	106.80	87.80	1.91	1.93	0.17	2.23	1.64
Florida	23	181.59	183.00	14.35	216.50	155.00	96.12	95.90	5.45	111.60	89.10	1.89	1.93	0.13	2.04	1.63
Illinois	10	192.87	187.65	19.54	240.78	167.00	102.52	101.50	9.51	121.91	85.00	1.88	1.85	0.06	1.98	1.82
Indiana	9	185.02	188.50	14.00	202.30	164.00	100.13	99.00	5.02	108.00	91.70	1.85	1.81	0.12	2.04	1.66
Kansas	2	195.00	195.00	11.31	203.00	187.00	100.74	100.74	6.41	105.27	96.20	1.94	1.94	0.01	1.94	1.93
Kentucky	9	185.35	182.50	14.85	202.70	165.00	98.62	97.10	7.72	116.50	90.74	1.88	1.85	0.10	2.01	1.73
Louisiana-Mississippi	14	189.12	188.30	25.72	226.50	113.07	103.58	102.46	7.86	119.05	93.00	1.83	1.88	0.22	2.06	1.17
Missouri	24	189.65	188.65	14.36	213.00	162.00	98.46	98.85	5.93	109.80	86.00	1.93	1.91	0.06	2.07	1.82
Nebraska	4	181.18	181.05	3.63	184.70	177.90	100.10	100.20	1.27	101.50	98.50	1.81	1.81	0.05	1.87	1.75
New Mexico	3	166.33	168.00	12.58	178.00	153.00	89.00	93.00	8.26	94.50	79.50	1.87	1.91	0.08	1.92	1.78
New York	1	196.70	196.70		196.70	196.70	97.60	97.60		97.60	97.60	2.02	2.02		2.02	2.02

North Carolina	4	180.45	188.90	18.10	190.60	153.40	91.63	92.15	3.00	94.40	87.80	1.97	2.01	0.15	2.10	1.75	
Ohio	4	191.30	191.20	25.25	222.20	160.60	99.40	101.85	8.72	106.90	87.00	1.92	1.89	0.12	2.08	1.82	
Quebec	1	136.00	136.00		136.00	136.00	79.00	79.00		79.00	79.00	1.72	1.72		1.72	1.72	
Tennessee	1	160.90	160.90		160.90	160.90	90.60	90.60		90.60	90.60	1.78	1.78		1.78	1.78	
Texas	5	188.80	195.00	13.37	200.00	168.00	99.40	100.00	5.08	106.00	93.00	1.90	1.91	0.06	1.95	1.81	
Utah	2	169.50	169.50	0.71	170.00	169.00	82.50	82.50	2.12	84.00	81.00	2.06	2.06	0.04	2.09	2.02	
Virginia	1	165.60	165.60		165.60	165.60	89.50	89.50		89.50	89.50	1.85	1.85		1.85	1.85	
West Virginia	1	177.00	177.00		177.00	177.00	97.00	97.00		97.00	97.00	1.82	1.82		1.82	1.82	
Yukon	2	160.40	160.40	3.75	163.05	157.75	81.88	81.88	0.66	82.34	81.41	1.96	1.96	0.03	1.98	1.94	
M. americanum	133	183.62	184.15	15.70	226.50	136.00	96.83	96.95	7.20	121.91	79.00	1.89	1.91	0.12	2.23	1.17	2.000
M. pacificus	27	185.63	187.00	13.65	208.82	159.74	82.68	82.41	6.14	94.03	68.00	2.25	2.25	0.13	2.44	1.95	1.000

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Table 3(on next page)

Table 3: Mammut M3 Loph Width

Mammut M3 loph widths. The last five columns describe the width of the given loph divided by the width of the widest loph in each specimen. Yellow fields indicate the widest loph on each tooth. Direct measurements are in mm.

1 Mammut M3 Loph Width

Specimen	Taxon	County	State/Province	1st loph width	2nd loph width	3rd loph width	4th loph width	5th loph width	1st loph width/widest loph width	2nd loph width/widest loph width	3rd loph width/widest loph width	4th loph width/widest loph width	5th loph width/widest loph width
Perris mastodon	*M. pacificus*	Riverside	CA	87	82.3	82.4	60.8	44	1.000	0.946	0.947	0.699	0.506
SBMNH specimen B	*M. pacificus*	Santa Barbara	CA	83.9	85.97	81.72	71.18	49.9	0.976	1.000	0.951	0.828	0.580
SBMNH specimen A	*M. pacificus*	Santa Barbara	CA	94.88	104.26	102.39	87.02		0.910	1.000	0.982	0.835	
SDSNH 116399	*M. pacificus*	San Diego	CA	84.46	80.79	77.31	65.35		1.000	0.957	0.915	0.774	
UCMP 1060	*M. pacificus*	Tuolumne	CA	78.13	75.79	72.87	55.12		1.000	0.970	0.933	0.705	
LACM-HC 87076	*M. pacificus*	Los Angeles	CA	73.08	72.54	67.97	53.3		1.000	0.993	0.930	0.729	
UCMP 1567	*M. pacificus*	Tuolumne	CA	78.54	80.04	74.95	57.64		0.981	1.000	0.936	0.720	
UCMP 212936	*M. pacificu*	Alameda	CA	94.64	95.5	91.05	81.69	60.93	0.991	1.000	0.953	0.855	0.638

	s												
UCMP 36684	*M. pacificus*	Alameda	CA	77.91	76.18	73.47	66.12	47.31	1.000	0.978	0.943	0.849	0.607
UCMP 41642	*M. pacificus*	Sonoma	CA	90	89.36	87.64	71.06		1.000	0.993	0.974	0.790	
UCMP 45265	*M. pacificus*	Contra Costa	CA	86.33	89.27	87.81	74.53	49.74	0.967	1.000	0.984	0.835	0.557
UCMP 70139	*M. pacificus*	Sonoma	CA	86.14	84.35	79.22	66.35		1.000	0.979	0.920	0.770	
WSC 10829	*M. pacificus*	Riverside	CA	85.2	81.8	80.3	65.9		1.000	0.960	0.942	0.773	
WSC 19730	*M. pacificus*	Riverside	CA	89.5	89.3	84.2	60.5		1.000	0.998	0.941	0.676	
WSC 22587.1	*M. pacificus*	Riverside	CA	86.8	84.4	80.9	72.4		1.000	0.972	0.932	0.834	
WSC 9964.7	*M. pacificus*	Riverside	CA	75.4	74	65.1	46.8		1.000	0.981	0.863	0.621	
WSC 18743	*M. pacificus*	Riverside	CA	79.97	84.1	73.31	55.69		0.951	1.000	0.872	0.662	
NMC 8060	*M. americanum*		AK	93.86	94.15	90.39	59.34		0.997	1.000	0.960	0.630	
DMNH 60675	*M. america*	Pitkin	CO	98.3	96.1	87.8	58.4		1.000	0.978	0.893	0.594	

	num											
DMNH 69327	*M. americanum*	Pitkin	CO	99.4	100.2	95.1	75.6		0.992	1.000	0.949	0.754
DMNH 69331	*M. americanum*	Pitkin	CO	96.3	98.2	90.4	65.7		0.981	1.000	0.921	0.669
DMNH 69943	*M. americanum*	Pitkin	CO	101.2	97.9	95.5	77.3		1.000	0.967	0.944	0.764
LACM 130386	*M. americanum*	Bureau	IL	108.07	111.37	102.91	93.1		0.970	1.000	0.924	0.836
LACM 154685	*M. americanum*	Allen	IN	83.35	87.85	87.78	62.81		0.949	1.000	0.999	0.715
ANSP 13309	*M. americanum*	Boone	KY	96.95	92.68	90.2	68.37		1.000	0.956	0.930	0.705
ANSP 13310	*M. americanum*	Boone	KY	86.83	83.1	82.32	65.99		1.000	0.957	0.948	0.760
LSUMG V-17071	*M. americanum*	West Feliciana	LA	118	117.7	115	94.8		1.000	0.997	0.975	0.803
USNM 437571	*M. americanum*	Dare	NC	96	93	89	78	56	1.000	0.969	0.927	0.813	0.583
UNSM1642	*M. americanum*	Dodge	NE	100.9	108.58	102.1	95.45	44.7	0.929	1.000	0.940	0.879
UNSM2042-69	*M. america*	Nuckolls	NE	93.28	87.2	82.42	57.72		1.000	0.935	0.884	0.619

	num												
UNSM1491	*M. americanum*	Cass	NE	109.24	110.98	107.5	95.02	56.41	0.984	1.000	0.969	0.856	
UNSM1369	*M. americanum*	Thurston	NE	86.15	87.46	81.88	70.56	36.15	0.985	1.000	0.936	0.807	
25BJS76	*M. americanum*	Hickory	MO	107.01	105.25	103.6	81.36		1.000	0.984	0.968	0.760	
NMC8707	*M. americanum*		Yukon	86.91	87.29	83.05	56.73		0.996	1.000	0.951	0.650	
								Maximum	1	1	0.999	0.879	0.638
								Minimum	0.910	0.935	0.863	0.594	0.506
								Average	0.987	0.984	0.939	0.752	0.579

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