Off Ramp of the Pleistocene: A Review of the Taxonomy, Osteology, and Biogeographic Distribution of Late Pleistocene Mammoths of Idaho

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by

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Authorization to Submit Thesis

This thesis of Jonathan Erdman, submitted for the degree of Master of Science with a major in Geology and titled "Off Ramp of the Pleistocene: A Review of the Taxonomy, Osteology, and Biogeographic Distribution of Late Pleistocene Mammoths of Idaho," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Mammoths were endemic on the North American continent during the late Pleistocene to early Holocene and are considered a keystone species in paleoecology. Here, I examined the skeletal remains of a mammoth excavated from southeastern Idaho to provide insight into its depositional age, taxonomy, and ontogeny. This multidisciplinary analysis revealed possibly the first *M. jeffersonii* hybrid reported in Idaho that lived 11,700 +/- 40 years ago. The remains belonged to a male mammoth that was a juvenile between 18 and 28 years old. Its remains were preserved in an ancient hot spring deposit during a time within 500-1000 years of the final megafaunal extinction on the continental landmasses. This mammoth is one of the last mammoths in mainland North America before the species' ultimate extinction.

Acknowledgements

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Chapter 2 includes work that was contributed by Natalya Usachenko at the University of Idaho. This work, along with other undergraduate researchers that contributed to studies on Cola are Kate Brooks and Shilah Waters.. Their work has been excluded here but is included in a paper that is currently in review in the journal, Quaternary International.

Dedication

To Kayley Carey and Dr. Renee Love, without them none of this would be possible.

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Chapter 1: History of Mammoth Evolution and Thesis Premise

INTRODUCTION

Belonging to the order proboscideans, including the only extant family *Elephantidae*, mammoths were endemic to North America until the last glacial retreat in the late Pleistocene epoch around 11,700 years ago (MacPhee, 2018). During this epoch two different mammoth species certainly called Idaho home, the Woolly (*M. primigenius)* and Columbian (*M. columbi)* mammoths. Another possible species or subspecies is the Jeffersonian Mammoth (*M. jeffersonii or M. c. jeffersonii),* although there is some debate as to the phylogenetic relationship between *M. columbi* and *M. c. jeffersonii* (Lister, 2017).

Mammoth phylogeny and evolution across North America are still not completely understood. Diverging from a common ancestor to elephants during the late Miocene 5-6 Ma, mammoths spread across Eurasia 3 Ma and eventually crossed over the Bering Land Bridge into North America during the early-middle Pleistocene, with the most primitive specimens excavated that occur from New Mexico dating to 1.3-1.4 Ma (Lister and Sher, 2015; Enk, et al., 2016; Lucas, et al., 2017). By the end of the Pleistocene, mammoths had radiated across the North American continent, reaching as far south as Central America and Costa Rica (Maglio, 1973). Two dominant species of mammoths, *M. columbi* and *M. primigenius*, occupied different ecosystems and possibly interbred (Enk et al., 2016), but their evolutionary relation to each other is up for debate.

Two theories are presented herein to explain mammoth migration from the old world to the new. Lister and Sher (2015) examined 182 upper (M^3) and 177 lower (M_3)

molars according to methods adapted from Maglio (1973) to determine the systematic taxonomy of the studied specimens. Accounting for anterior loss due to wear (Sher and Vladimirovich, 1987) and comparing against the specimens' normalized morphology Hypsodonty Index (HI; Length/Width x100), Lister and Sher (2015) proposed that both the Woolly and Columbian Mammoths evolved from the more primitive Steppe Mammoth (*M. trogontherii*), with *M. columbi* evolving from this common ancestor when it migrated from Eurasia during the Irvingtonian North American Land Mammal Age (1.8 – 08 Ma). *M. trogontherii* eventually evolved into *M. columbi,* adapting to the open grassland environment available on the North American continent (Lister and Sher, 2015). *M. primigenius* evolved separately from *M. trogontherii* in Siberia and would migrate to North America during the early Rancholabrean NALMA (0.8 - 0.24 Ma), occupying the "Mammoth Steppe" environment common in Canada at the time.

The larger aim of this thesis is to describe and analyze a well preserved, relatively complete (approximately 75%) mammoth fossil excavated near the Soda Springs in southeast Idaho. This mammoth is important because it may represent the evolutionary change in North American mammoths before their final extinction. Both *M. columbi* and *M. c. jeffersonii* were endemic to the United States before the final megafaunal extinction but their relationship continues to be debated in the literature (Enk et al., 2016; Lister, 2017). Here, this mammoth from southeastern Idaho will be analyzed according to the systematics framework set forth by Maglio, (1973); Richards, (1991); and Lister, (2017) and the taxonomic identification will be determined. The mammoth will also be reviewed in context of the previous literature and understanding of mammoth evolution on the mainland North American continent.

OVERVIEW OF PREVIOUS WORK PERFORMED

Taxonomy

The study of proboscideans is inextricably linked to the history of America. Fossils of mammoths and mastodons have been excavated from the country since the 1700's, but were prone to misinterpretation. From a race of giant humanoids to a quadrupedal carnivore, the classification of the American Mastodon (*Mammut americanum*) underwent several revisions. It was not until the French naturalist, Georges Cuvier, noted the similarity between modern elephants and the mysterious American predator that its true identity became apparent (Peale, 1803). Cuvier pioneered using comparative anatomy in describing the American specimens, and not only laid down the groundwork for proboscidean research, but the concept of extinction and the study of paleontology itself.

Using similar anatomical features that Cuvier erected to describe *M. americanum*, Henry Fairfield Osborn spent the early 20th century describing mammoths and mastodons from around the world. Osborn's findings included the description of over 100 distinct species in two volumes of monograms of mammoths and mastodons. After that seminal manuscript was presented, little work on mammoth taxonomy was conducted until Vincent Maglio's work in 1973.

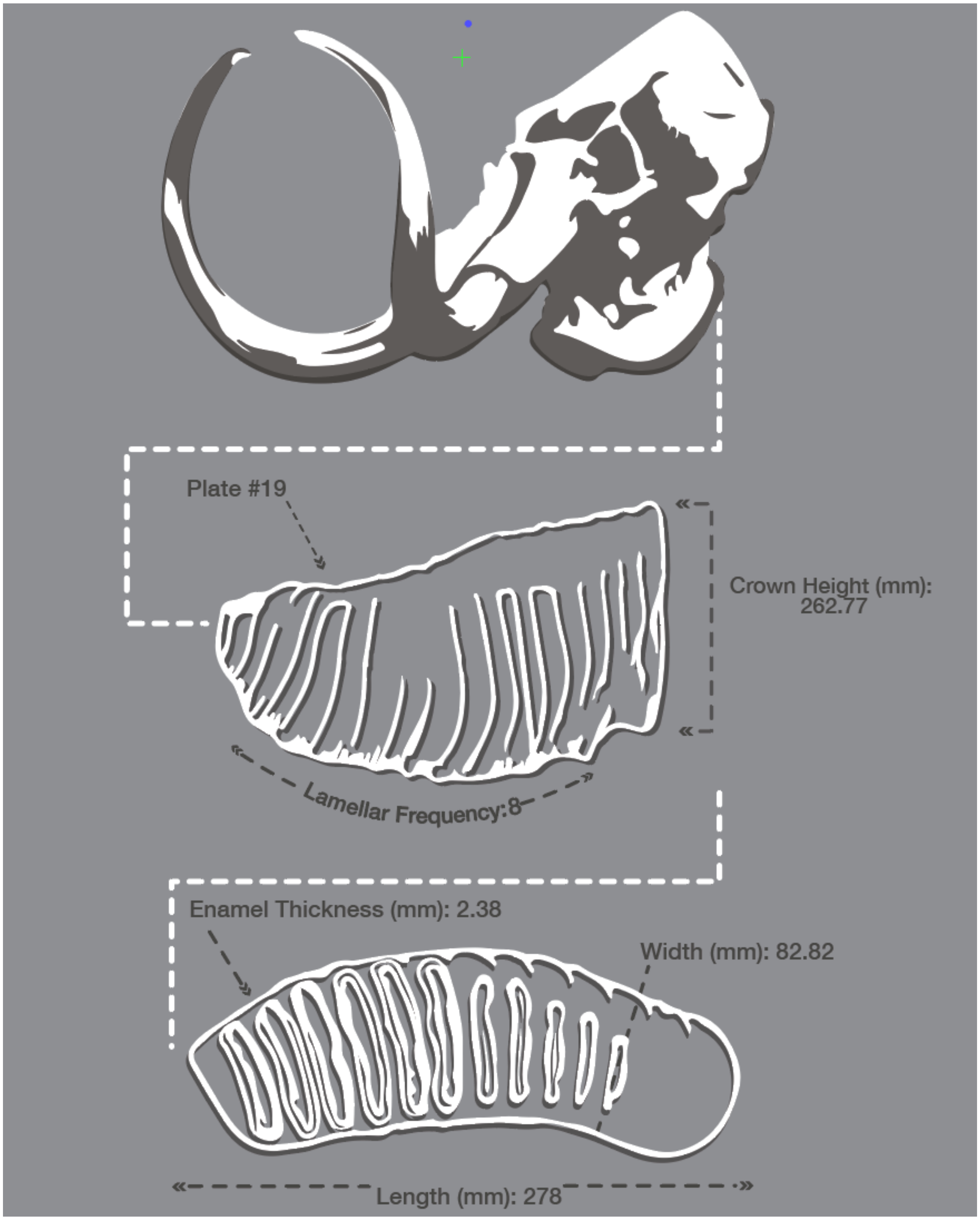
Maglio (1973) established a taxonomic framework for evaluating proboscidean species, and a possible phylogenetic line of succession. His ‘Origin and Evolution of the Elephantidae’ paper aimed to correlate the stratigraphy of the outcrops related to holotype specimens and other collected material. Maglio (1973) did not observe and describe North American species but reviewed published literature and personal communications regarding the type specimens. He used this information to de-clutter the systematics Osborn proposed, and construct a possible evolutionary lineage of mammoths onto the North American continent.

Maglio (1973) was instrumental in establishing the criteria by which researchers look at molar characteristics and determine species. This sets up an in-depth framework for establishing species and determining if variations in cranium characteristics among species is viable. Maglio (1973) used several techniques to describe mammoth dentition (Figure 1.1):

Plate Number (P):

Within mammoth molars, enamel plates have soft, dentine centers encircled by hard enamel exteriors. Each plate is perpendicular to the molar length and extends down to the root, where it connects to the plates adjacent to it. These are the only plates counted as “true” plates because they extend to the roots, but there are smaller plates that do not extend to the root nor connect with the plates in front or behind it. These smaller plates are not included in total plate count and if included, would overestimate the total plate count used in taxonomic descriptions of each species (Maglio, 1973).

FIGURE 1.1: TAXONOMIC CHARACTERISTICS RELATED TO MAMMOTH DENTITION (MAGLIO, 1973)



Length (L):

Length is the total distance from the front to the back of the molar. Given the pattern of wear on a mammoth's teeth, measurement of length can be taken from several points and can give different values. Length values of the molars are measured in lateral view, perpendicular to the enamel ridges. These measurements are obtained and averaged from three different areas: 1) along a perceived mid-line across the center of the tooth; 2) the outer (labial) surface; 3) the inner (lingual) surface. This averaged measurement corrects for factors such as the angle the tooth erupted in the mouth and how worn they are.

Width (W):

The width of a mammoth's molar is measured perpendicular to its length, along the length of the enamel plate. Width varies along the length of molar, so values are taken from the perceived widest portion of the molar (Maglio, 1973; Lister, 2017).

Height (H):

Height for a molar is the vertical measurement of the enamel plate to its highest point. Obtaining precise measurements requires adjustable calipers, since the apex is along the mid-line of the enamel ridge, which bows out from the mid-line. This measurement needs to be taken along the curved surface to measures are not underestimated (Maglio, 1973; Lister, 2017). The molar height is taken from the perceived longest enamel plate, perpendicular to the worn occlusal plane. The plate number (anterior to posterior) is usually provided with the measurement.

Lamellar Frequency (LF):

The lamellar frequency is the number of enamel plates within a distance of 10 cm (100 mm). The LF is measured on both lateral sides of the molar and at the root and crown resulting in four measurements. Taking the average of the four LF’s, an accurate estimate for the center of the molar is obtained. The LF should be measured at the portion of the molar with the perceived highest frequency of plates, and the starting plate this measurement is taken from should be denoted (Maglio, 1973).

Lamella Length and Basal Lamella Length (LL and LLB):

While the lamellar frequency is highly diagnostic as it examines the packing of enamel plates within an imaginary tooth of 100mm length, it does not allow standardization of enamel packing like the rest of the taxonomic properties. Lister (2015) introduced the lamella and basal lamella length to facilitate normalizing measurements and cross-species comparison. The LL and LLB are the inverse of the lamellar frequency, characterized by the expression:

$$LL/LLB = 10cm \times 1/p$$

Where 1 is the given distance of measurement and p is the number of plates within this distance. Measuring the LL and LLB yields the average length of enamel and dentine cement between a plate and its neighbors. This measurement also can be normalized to a molar width of 100mm, and can be compared to other taxonomic indices to make comparisons.

Enamel Thickness (ET):

Mammoth molars erupt from the jaw at an angle and are shorn down over time. Over the course of the mammoth's life, enamel thickness decreases with the increase of total plates within the molar. This occurs to preserve the internal strength of the molar by keeping the thickness of the cement and soft dentine of the molar while reducing the enamel thickness (Maglio, 1973). The ET is measured from the worn occlusal surface, but only from one side of the enamel loop to avoid introducing error from the angular wear of the molar.

Hypsodonty Index (HI), Lamella Length Index (LLI), Basal Lamella Length Index (LLBI), Enamel Thickness Index (ETI):

Maglio (1973) proposed the measurement of the hypsodonty index, which accounts for the constant growth of mammoth's teeth. This index normalizes the height and width of the specimen's molar to that with an overall crown height of 100mm. This allows comparison of the overall dimensions of a molar, even between different species and life stages.

Lister and Sher (2015) added a new suite of indices to Maglio's HI to account for the other molar morphometrics. These indices compare the enamel thickness (ET) and both lamella lengths (basal; LLBI, medial; LLI) of the previously mentioned taxonomic characteristics to the molar's width, and normalize this ratio to a molar of 100mm crown height. Which these additions, molars can be compared on all aspects of its morphology, regardless of its age or respective features (Table 1.1).

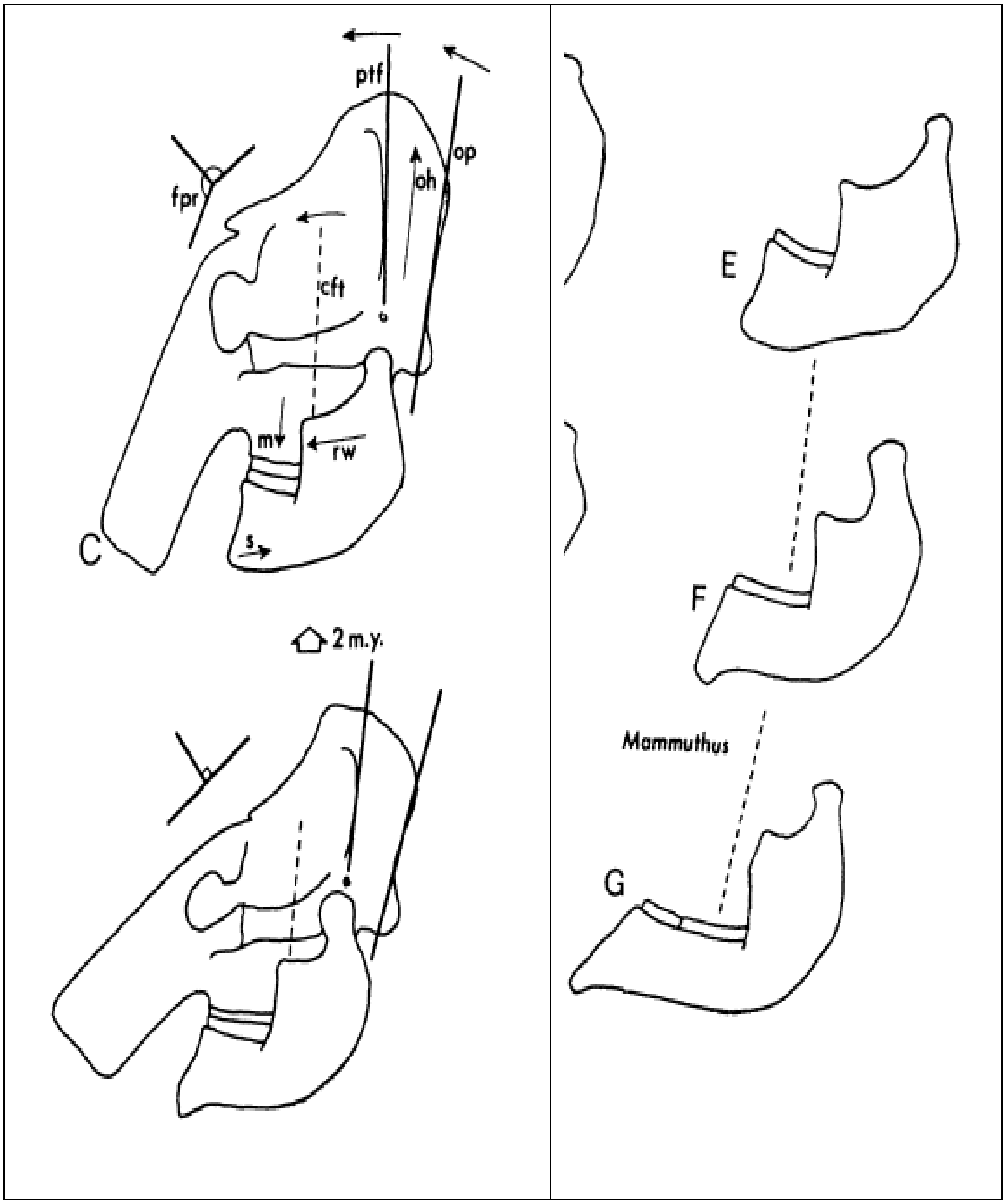
Table 1.1: List of index equations for the taxonomic characteristics of mammoth molars based on Maglio (1973) and Lister and Sher (2015). H = Crown height of molar; W = Maximum width of molar.

Index	Equation
Hypsodonty Index (HI)	HI = H/W x 100
Lamella Length Index (LLI)	LLI = LL/W x 100
Basal Lamella Length Index (LLBI)	LLBI = LL/W x 100
Enamel Thickness Index (ETI)	ETI = ET/W x 100

Taxonomic Characteristics of Mammoth Crania:

While molars have been the main focus of paleontologists in describing proboscideans because of their frequency in the fossil record, these changes in dentition correlate to changes in the morphology of a mammoth's cranium. Early paleontologists (Gregory, 1903, and Osborn, 1942) noticed increasing brachycephaly (a broad, short skull) among more advanced lineages of mammoths and their relatives, and proposed that this was due to the increased length and weight of the tusks and proboscis (trunk). Osborn (1942) summarized these observations into 7 morphological trends: 1) Hard pallet is tilted upwards posteriorly at an oblique angle; 2) Palatines are shortened in length, with a widely expanded posterior; 3) Nares progressively pushed back in the skull; 4) Pterygoid is expanded to encircle the molar-aveolar pouch; 5) The foramen ovale moves backwards to merge with the foramen lacerum; 6) Medial thickening of the presphenoid, basisphenoid, and basiocipital, so that the basal cranium is 90° to the occipital plane; 7) Tympanic bullae become flattened, pressed in towards the skull (Figure 1.2).

FIGURE 1.2: GENERAL TRENDS IN THE FUNCTIONAL MORPHOLOGY OF PROBOSCIDEANS (MAGLIO, 1973). LOWER PICTURES REPRESENTS CHARACTERISTICS OF MORE BASAL MEMBERS OF THE *MAMMUTHUS* GENUS.



While the functional relationship (increased brachycephaly with increase in hypsodonty and shearing efficiency) between the molars and the cranium has been well documented, quantifying cranial characteristics and correlating them to changes in molar morphology had proved to be difficult (Lister, 2017). The largest impediment against these comparisons include the preservation bias of mammoth's skulls. A mammoth skull is relatively porous and tends not to survive the fossilization process, and when they do, they are fragile and tend to fragment upon excavation. Mammoth molars, by contrast, are relatively abundant. Mammoths erupt and shed 6 molar sets throughout their life, and given a lack of interest in predators eating molars, tend to be preserved on a larger scale than cranium material.

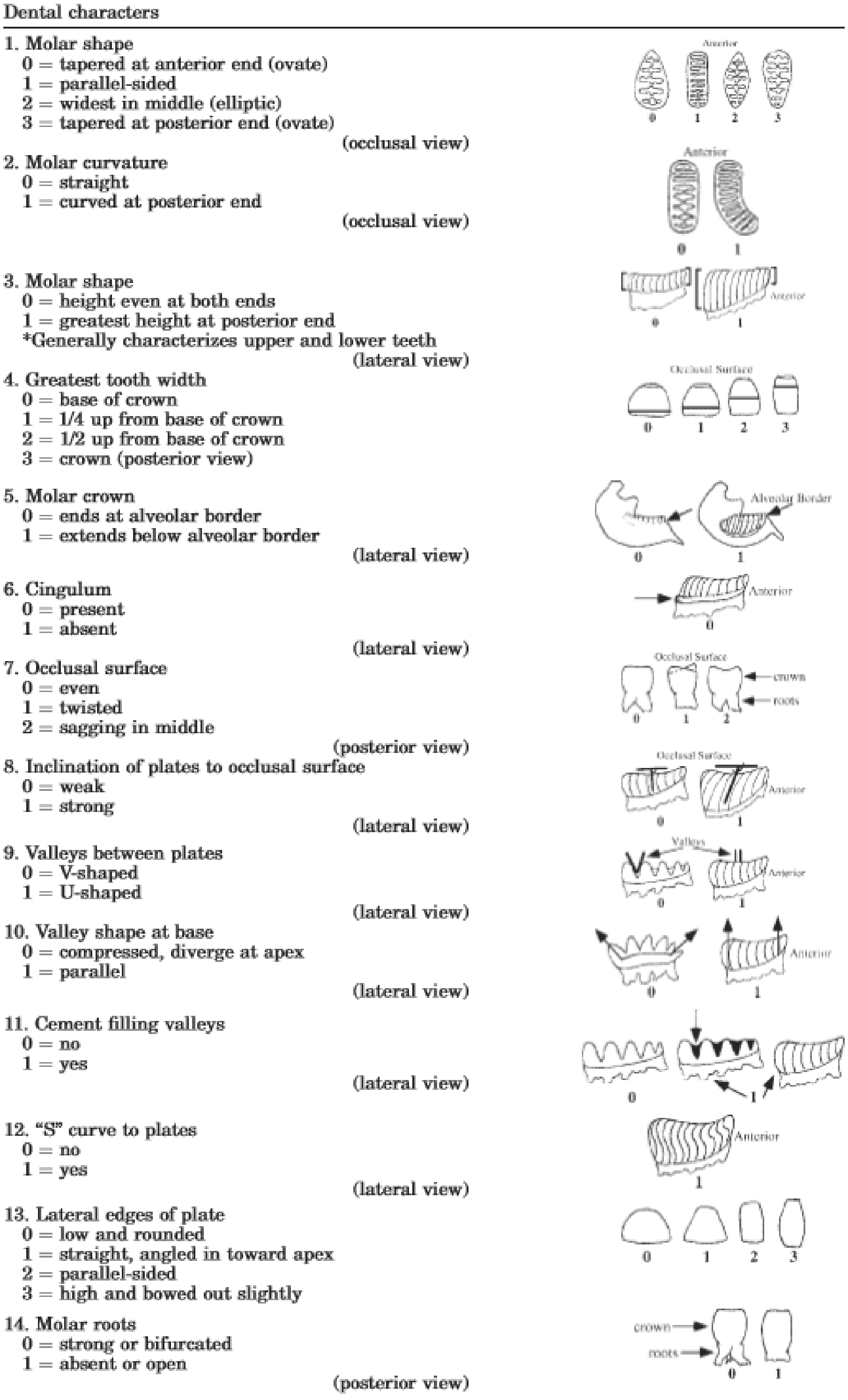
Despite the preservation bias against crania material, mammoth skull morphology has been used to clarify taxonomic ambiguity. Maglio (1973) has used the characteristics previously mentioned in Osborn (1942) to make inferences about Old World mammoths from Africa, such as the distinct evolutionary stages of *M. meridionalis.* These characteristics were still used in conjunction to molar characteristics however, and since Maglio's work has been relatively underutilized. Todd (2010) created a suite of 77 qualitative taxonomic characteristics for the dentition, mandible, and crania, and used them to construct cladograms for early elephantid evolution out of Africa, but no evolutionary taxonomic trends were reported (Table 1.2).

Todd's study highlighted the issue of homoplasy in proboscidean evolution. Homoplasy refers to a shared character between two or more taxa that did not arise from a common ancestor. The development of similar traits among evolutionarily diverse proboscideans makes determining relationships based on selective pressures difficult. These characteristics and relationships have also never been applied to North American species, which are closely related evolutionarily. The lack of cranial material and homoplasy are not the only obstacles mammoth taxonomists have to overcome, the age of a mammoth at its time of death can also affect the morphology of the crania and molars.

Ontogeny

The two primary taxonomic characteristics (plate number and lamellar frequency) in determining mammoth speciation are affected by the animal's age and could produce erroneous classification if not taken into account. Molars are worn down throughout a mammoth's life, causing it to erupt and shed 6 sets of 2 top and 2 bottom molars at distinct ontogenetic stages. These molars are erupted at an angle in the mouth, and are worn down as the mammoth grinds its teeth to feed. Successive molar sets also tend to have a greater lamellar frequency with thinner enamel loops as the animal packs more enamel plates into its teeth for greater shearing efficiency (Lister and Sher, 2015). Mammoth skulls exhibit greater rugosity as they age, specifically around the nares, and to a lesser extent than the molars affect classification (Lucus et al., 2017). These factors must be taken into account in order to make an accurate assessment of mammoth material, and fortunately for paleontologist, mammoths have a modern analogue to base our observations on.

Table 1. 2: Molar, Crania, and Mandibular Characteristics (Todd, 2010).



Dental characters

1. Molar shape
0 = tapered at anterior end (ovate)
1 = parallel-sided
2 = widest in middle (elliptic)
3 = tapered at posterior end (ovate)
(occlusal view)

2. Molar curvature
0 = straight
1 = curved at posterior end
(occlusal view)

3. Molar shape
0 = height even at both ends
1 = greatest height at posterior end
*Generally characterizes upper and lower teeth
(lateral view)

4. Greatest tooth width
0 = base of crown
1 = 1/4 up from base of crown
2 = 1/2 up from base of crown
3 = crown (posterior view)

5. Molar crown
0 = ends at alveolar border
1 = extends below alveolar border
(lateral view)

6. Cingulum
0 = present
1 = absent
(lateral view)

7. Occlusal surface
0 = even
1 = twisted
2 = sagging in middle
(posterior view)

8. Inclination of plates to occlusal surface
0 = weak
1 = strong
(lateral view)

9. Valleys between plates
0 = V-shaped
1 = U-shaped
(lateral view)

10. Valley shape at base
0 = compressed, diverge at apex
1 = parallel
(lateral view)

11. Cement filling valleys
0 = no
1 = yes
(lateral view)

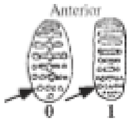
12. "S" curve to plates
0 = no
1 = yes
(lateral view)

13. Lateral edges of plate
0 = low and rounded
1 = straight, angled in toward apex
2 = parallel-sided
3 = high and bowed out slightly

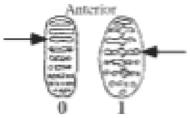
14. Molar roots
0 = strong or bifurcated
1 = absent or open
(posterior view)

Dental characters

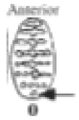
15. Apical digitations
0 = few (4 or less)
1 = many (greater than 4)
(occlusal view)



16. Appearance of complete enamel loops
0 = slow (within 6 worn plates)
1 = quick (within 3 worn plates)
(occlusal view)



17. Single column at posterior end
0 = present
1 = small plate
*May be variable
(occlusal view)



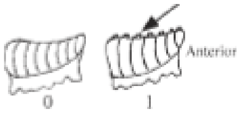
18. Anterior/Posterior columns
0 = strong anterior column
1 = strong posterior column
2 = strong anterior and posterior columns
3 = no anterior/posterior columns

19. Median cleft
0 = strong
1 = weak
2 = absent

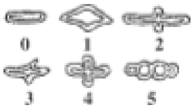
20. Tusk shape
0 = straight
1 = curved or spiralled in front
2 = straight spiral (twisted)

21. Tusk cross-section
0 = rectangular or flattened
1 = oval or "bean" shaped
2 = round

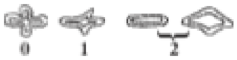
22. Enamel height above cement
0 = Low
1 = High
*May be related to wear and amount of abrasion



23. Enamel figure shape
0 = parallel-sided
1 = true lozenge
2 = parallel-sided with median loop
3 = "pseudo-lozenge"
4 = "keyhole" shaped
5 = rounded loops

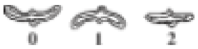


24. Median area
0 = loop
1 = fold
2 = absent or open

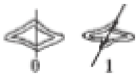


25. Lateral sides of enamel figure
0 = pinched
1 = rounded
2 = intermediate
3 = rectangular

26. Direction-lateral sides of enamel
0 = turn anterior
1 = turn posterior
2 = even
*May be variable

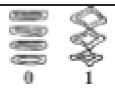


27. Symmetry of enamel figure
0 = symmetrical, in line with long axis of molar
1 = asymmetrical, offset from long axis of molar



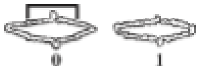
Dental characters

28. Medial edges of enamel figures
0 = separated
1 = in contact



29. Enamel folding
0 = absent
1 = regular
2 = irregular
3 = undulating
4 = crinkled

30. Placement of folds
0 = median area only
1 = entire length of enamel figure
2 = absent



31. Amplitude of enamel folding
0 = absent
1 = high
2 = low

32. Spacing between enamel folds
0 = absent
1 = tight
2 = loose

33. Crenated versus smooth enamel
0 = Smooth
1 = Crenated
*May be taphonomic

Cranial characters

34. Parietal/Occipital crest (=nuchal ridge)
0 = pronounced ridge
1 = ridge
2 = smooth

35. Shape of nares opening
0 = “dumbell” shaped
1 = turned down at lateral edges
2 = rounded and turned up at lateral edges
*May be related to sexual dimorphism (frontal view)

36. Borders of nares opening
0 = sharp and pronounced
1 = smooth and rounded

37. Center of nuchal ridge
0 = smooth and even
1 = heart-shaped
2 = concave
(frontal view)

38. Position of orbits relative to tooth row
0 = anterior to tooth row
1 = even with beginning of toothrow
2 = posterior to beginning of tooth row

39. Slope of forehead and premaxillaries
0 = premaxillaries steeper than forehead
1 = in same plane
2 = forehead steeper than premaxillaries
(lateral view)

40. Temporal line
0 = smooth
1 = line
2 = ridge

41. Parietal depression
0 = absent
1 = muscle marking
2 = furrow

Dental characters

42. Occipitals
0 = bulbous
1 = flat

43. Slope of occipitals from condyles
0 = anterior
1 = vertical
2 = posterior
(lateral view)

44. Position of supraoccipital relative to squamosal
0 = directly superior
1 = lateral
2 = medial
(posterior view)

45. Alveolar border of premaxillaries
0 = even
1 = slopes down laterally
(inferior view)

46. Premaxillaries
0 = parallel
1 = flared
2 = straight-sided but diverging
(inferior view)
*May be related to sexual dimorphism

47. Shape of occipital condyles
0 = round or square
1 = triangular, elongated triangle
2 = "bean" shaped

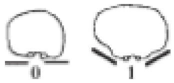
48. Condylar fossa
0 = flat and wide
1 = flat and narrow
2 = deep and wide
3 = deep and narrow

49. Condylar facet
0 = even with fossa
1 = slopes posteriorly from fossa
2 = slopes anteriorly from fossa

50. Basio-occipital
0 = plate-like, with pronounced edges
1 = smooth, completely fused

51. Basio-occipital and vomer
0 = meet
1 = separated

52. Position of exoccipital relative to condyles
0 = lateral
1 = anterior
(posterior view)



53. Forehead
0 = rounded
1 = flat
2 = concave
(lateral view)

54. Tusk sheaths
0 = rotated anteriorly
1 = even
2 = rotated posteriorly
(inferior view)

55. Ventral depression of palate
0 = no
1 = yes

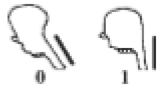
56. Position of occipital condyles relative to tooth row
0 = posterior
1 = in line with end of tooth row

Dental characters

57. Opening of external nares (lateral view)
0 = above orbit
1 = even with orbit
2 = below orbit

58. Anterior portion of zygomatic
0 = projecting anteriorly
1 = receding

59. Premaxillaries
0 = Directed out and forward
1 = Directed out and downward

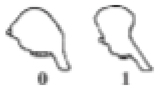


(lateral view)

60. Height of occipital condyles
0 = low
1 = elevated

61. Frontal bones
0 = elongated
1 = shortened

62. Skull shape
0 = rounded
1 = compressed parallel to facial plane



(lateral view)

63. Palate keel
0 = absent
1 = present

64. Nuchal fossa
0 = deep
1 = shallow

65. Occipital bosses
0 = in facial plane
1 = overhang forehead

(lateral view)

Mandible characters

66. Mandibular condyle shape
0 = long anterio-posteriorly
1 = oval
2 = rectangular

67. Condyle surface
0 = slopes medially
1 = even

(posterior view)

68. Ascending rami
0 = diverging
1 = curve in
2 = parallel

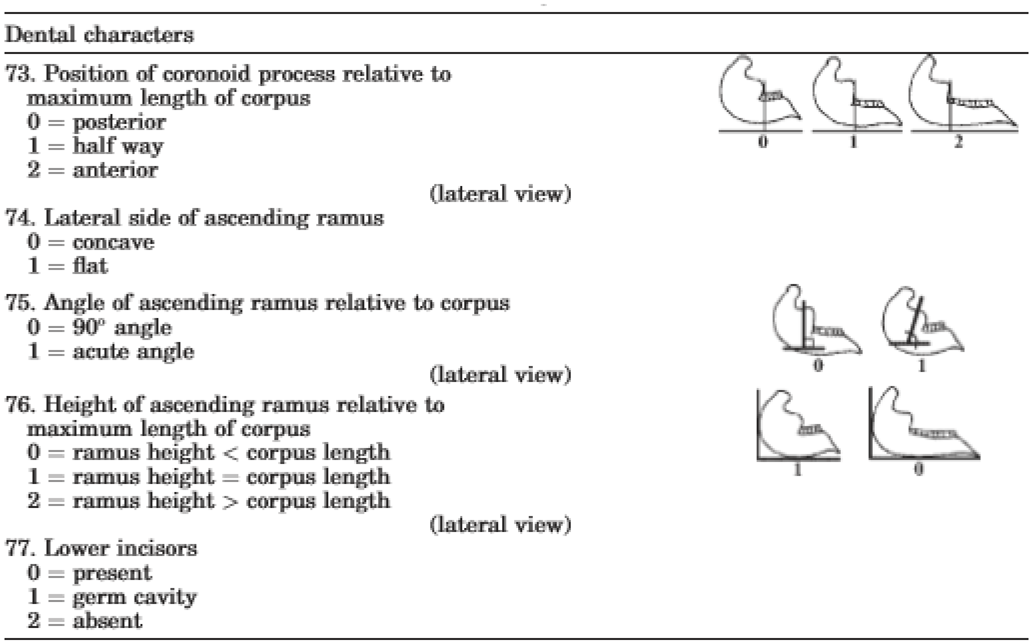
(frontal view)

69. Mandibular symphysis
0 = directed forward
1 = directed down

70. Length of mandibular symphysis
0 = long
1 = intermediate
2 = short
*Relative character

71. Shape of symphyseal trough
0 = horseshoe shaped
1 = U-shaped
2 = V-shaped

72. Mandibular corpus
0 = swollen
1 = gracile



Dental characters

73. Position of coronoid process relative to maximum length of corpus
    0 = posterior
    1 = half way
    2 = anterior
    (lateral view)

74. Lateral side of ascending ramus
    0 = concave
    1 = flat

75. Angle of ascending ramus relative to corpus
    0 = 90° angle
    1 = acute angle
    (lateral view)

76. Height of ascending ramus relative to maximum length of corpus
    0 = ramus height $<$ corpus length
    1 = ramus height $=$ corpus length
    2 = ramus height $>$ corpus length
    (lateral view)

77. Lower incisors
    0 = present
    1 = germ cavity
    2 = absent

African elephants (*L. Africana,* Cuvier 1957) were the first examined for age markers via dentition and epiphyseal fusion (Laws, 1966; Sikes, 1971). Examining 385 lower molar sets showed that *L. africana*, while variable dependent on environmental stressors, erupted and were shed at distinct ages of the elephant's life (Laws, 1966). Sikes (1971) focused on the epiphyseal fusion of the skeleton, and found that complete fusion occurs around 40 years of age, with fusion of bones occurring around certain ages. These studies laid the groundwork for understanding proboscidean ontogeny, but these methods were only applied to *L. africana* and a better comparison to mammoths is their closer relative the Asian elephant (*E. maximus)*.

Lister (1999) applied these methods to *M. primigenius* specimens. Using the methods of Laws (1966) to provide an approximate age, Lister described the fusion of the humerus, radius, ulna, scapula, femur, tibia, and fibula of relatively complete woolly mammoths. Lister's study appears to support Sikes' (1971) study, asserting that complete fusion for both

M. primigenius and *M. columbi* occurs around 44 – 49 African Elephant Equivalent Years (AEY; Lister, 1999).

Roth and Shoshani (1988) established a criterion by which to examine (*E. maximus)* molar characteristics and determine the age of the proboscideans based upon the set of molars the animal was on when it died and their wear. In their study, 599 molar samples from captive and culled Asian elephants were collected and cataloged to create a range of documented values for each of the six molar sets erupted and worn through an elephant's lifetime. This dataset was then correlated to observed molar wear characteristics for each of the six molars within living or recently deceased elephants whose age was known (Table 1.3). This study showed that an accurate diagnosis of an elephant's age is possible dependent upon the molar stage (M1-M6) erupted and its wear pattern.

Knowing the age of mammoths at their time of death also aids paleontologists in making inferences about mass death assemblages. Haynes (2016) summarized the techniques used to determine the age of recovered proboscidean material and examined what the distribution of ages in death sites can tell researchers about possible causes of death. Haynes used the techniques of skeletal maturation and plate fusion, growth increments in hard tissues, and the wear of molars from studies of modern-day analogs to create a standard for age determination of prehistoric proboscideans (Table 1.4).

Table 1.3: Worn Molars (1-6) Characteristics and Approximate age for Elephas maximus (Roth and Shoshani, 1988)

Age	Mandibular Teeth	Number of Worn Lamellae	Specimen I.D.
3 days	M1 – M2	DP1 - 2 plates; DP2 – not erupted	BMNH 15.5.1.1.
1 – 5 years	M2	6 plates	AMNH 90423
2 – 5 years	M2 – M3	DP2 – entire tooth (~8) DP3 – 3 plates	FMNH 104779
3 years	M2 – M3	DP2 – 4 plates remain DP3 – 7 & 8 plates	YPM 2613[3572]
4 – 5 years	M2 – M3	DP2 – 5 plates remain DP3 – 8 plates	FMNH 651
13 years	M4 – M5	M1 – 9 & 9.5 plates remain M2 – 2 plates	'Emma'
34 years	M5 – M6	M2 – 7.5 & 8.5 plates remain M3 – 8.5 & 9.5 plates	'Tulsa'
35 years	M5 – M6	M2 – 3.4 & 4 plates remain M3 – 6 & 8 plates	AMNH 39082
37 years	M5 – M6	M2 – 8.5 & 14 plates M3 – Distorted, approximately 4 plates	YPM 01428
46 years	M6	12 remaining, 4 & 5 plates worn	'Iki'
~50 years	M5	14 & 18 plates, 6 remain unworn	MCZ 19157
58 years	M6	Last 8 plates	FMNH 60601
62 years	M6	14 & 16 plates	YPM 1454
~67 years	M6	10 & 11, 7 remain unworn	UF (Unnumbered Toledo zoo specimen)

Table 1.4: Chart Showing age Determination for both Male and Female Elephants Using Previously Mentioned Methods. Adapted from Haynes (2016)

Laws Assigned Age (Median Years)	Laws Age Group	Stansfield Revised Age Group (Upper Limit)	Tooth in Wear	(Male) Epiphysis Fusion	(Female) Epiphysis Fusion
1 Month – 6 Years	1 – 7	1 Month – 5.5 Years	Laws 1 – 5: M1 – M2 Laws 6 – 7: M2 – M3		Laws 7: Ilium, Ischium, pubis fused at acetabellum
8 – 13 Years	8 - 10	7 – 11 Years	M3 – M4	Laws 9b: Ilium, Ischium, pubis fused at acetabellum	
15 – 30 Years	11 - 18	13 – 28.5	M4 – M5	Laws 15: Tibia Distal, Ulna Proximal, Humerus Distal Laws 18: Tibia Proximal	Laws 11 – 18: Fibula Distal, Ulna Proximal, Femur Distal/Proximal, Radius – Ulna Distal, Humerus Distal/Proximal, Tibia Proximal
32 - 38	19 - 22	30 - 42	M5 – M6	Laws 19 – 20: Femur Distal	
40 - 49	22a - 26	43 - 50	M6	Laws 22a – 26: Femur Proximal, Humerus Proximal	
52 - 60	27 - 30	51 – 70+	M6	Rib Ends, Radius Proximal/Distal, Feet, Pelvis Edges, Vertebral Colum, Sacrum	

Looking at research conducted on current elephant populations and how the distribution of ages could indicate different conditions for the die-off for ancient proboscidean species, Haynes (2016) proposed 4 different types of mortality profiles: A) Nonselective mortality; B) Selective mortality of juveniles; C) Selective mortality of mature males; D) Apparently patternless mortality. Nonselective mortality (type A) events cause rapid mass die-off, irrespective of a mammoth's age. Type B profiles were simulated from assemblages that held a greater number of juveniles, possibly due to predators targeting easier prey, or environmental stressors such as drought or food storage. Type C profiles target mature males that have left their matriarchal herd group. This death profile matches the distribution of mammoths found in the South Dakota Mammoth Hot Spring site (Agenbroad, et al., 1994). With the possible exception of one, all specimens excavated were juvenile – mature mammoths who possibly got stuck without the aid of a herd to free them (Haynes, 2016). The final death profile is random. While it is possible to use modern day analogs for determination of cause of death with mammoth age profiles, the author cautions applying such methods across assemblages spanning larger quantities of time, as the same patterns might not hold up over such great lengths of time.

Hybridization

For the purpose of this thesis, some discussion about the complex paleontological history of *M. jeffersonii* must be undertaken. In 1922, Henry Fairfield Osborn described a relatively complete mammoth skeleton and erected it as the type specimen of *M. jeffersonii*, although he had assigned it to the now defunct genera *Elephas* and *Parelephas* (Osborn, 1922; Osborn, 1942). Osborn describe this type specimen (Amer. Mus. 9950), which was excavated from the Union City moraine in Jonesboro Indiana, as displaying intermediate taxonomic characteristics between *M. columbi* and *M. primigenius,* which had previously been described as both species by Osborn (1907) and Hay (1914), respectively. Osborn (1922) went as far as to propose that *M. columbi* specimens were syntypic to *M. jeffersonii* and extended their biogeographic range from the American Midwest down to Mexico. The confusion surrounding the taxonomic assignment of specimens like the *M. jeffersonii* holotype comes from the overlap in molar morphometrics, and it is not until recently that this issue was been studied in detail.

Enk and others (2016) investigated the genetic information available among the collected material belonging to the North American mammoth species; *M. primigenius*, *M. columbi,* (including junior synonym *M. jeffersonii*), and the Pygmy Mammoth (*M. exilis*). Preserved hard and soft material representative of previously mentioned taxa were sampled and pulverized. Samples were then PCR (polymerase chain reaction) screened to replicate genomic samples. In total, 276 mammoth samples were processed and screened to create a valid database. Out of the 276 samples, after PCR screening and enhancement, 67 viable genomes were reconstructed. These reconstructed genomes for *M. columbi* and *M. primigenius* both show an affinity towards the genome of the more primitive Beringia Steppe Mammoth (*M. trogontherii*). Matches to the genetic material also are present in mixed amounts in the genomes attributed to *M. jeffersonii.*

Comparison of data between *M. columbi* and its junior synonym *M. jeffersonii* indicates hybridization due to interbreeding with *M. primigenius,* but most likely is not the only driver for the presence of mammoths intermediate to *M. columbi* and *M. primigenius.* Changes in molar and cranial characteristics are also linked to the functional morphology of the animal, which is interpreted as speciation and inferred lineages in paleontology. These changes correlate to an organism adapting to environmental stressors (Maglio, 1973). While hybridization zones certainly existed where *M. columbi* and *M. primigenius* ranges overlapped, there must be some consideration as to the difference in paleoecology across regions, and the mammoth's attempts to adapt to their local environments.

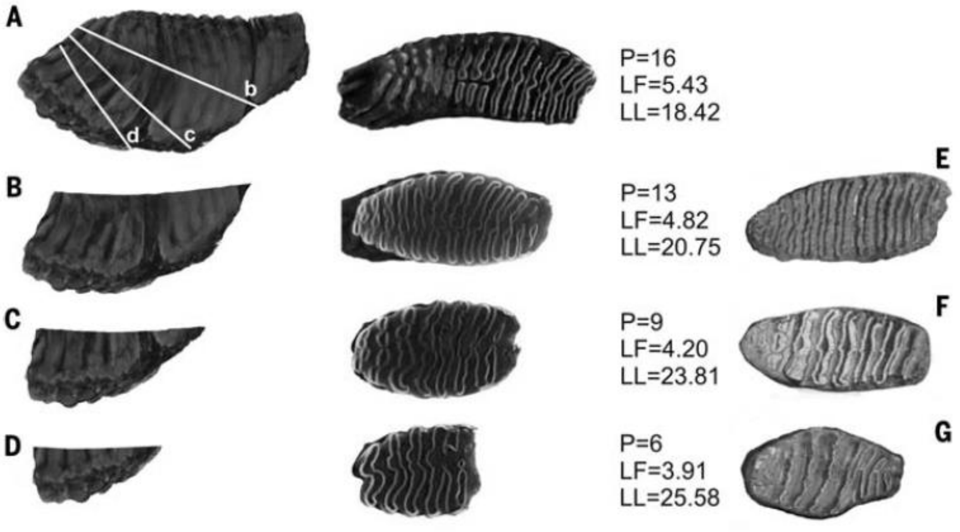
Paleoecology and Biogeographic Distribution

Enk and others (2016) also reconstructed mitogenomic data from mammoth matrilines and reaffirmed several proposed theories for mammoth phylogeny. Genetic data supports the one source model for North American mammoth evolution, where both *M. columbi* and *M. primigenius* arose from the Beringia *M. trogontherii* despite approximately 1 million years between the former and latter's arrival on the continent.

Lister and Sher (2015) hypothesized a single evolutionary source for mammoths in North America as well. The authors attempt to prove both *M. columbi* and *M. primigenius* evolved from the more primitive *M. trogontherii* from Beringia. This is divergent from the more commonly held assumption proposed by Maglio (1973) that the Southern Mammoth (*M. meridionalis*) was the first to migrate to North America and gave rise to *M. columbi.*

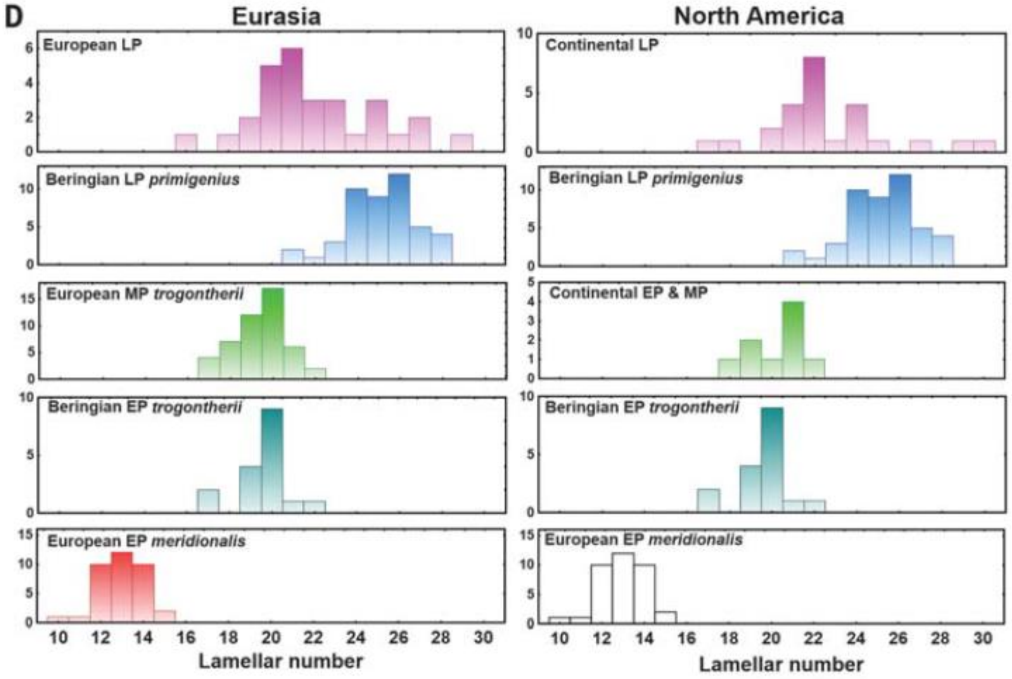
Lister and Sher (2015) compared molar characteristics for *M. trogontherii* to North American species that were considered representative of the more primitive *M. meridionalis* according to methods adapted from Maglio (1973). A *M. columbi* M_3 was also cut along the plane of eruption and wear to determine if worn molars would display what is considered more primitive characteristics (Figure 1.3).

Figure 1.3: Graphic Showing the Effects of Wear on Mammoth Molar Characteristics (Lister and Sher, 2015). This is an M_3 of M. columbi from Austin, TX. Different views show sliced and rotated positions, notice that the more primitive appearance at the base of the crown. P = lamellar number remaining, LF = lamellar frequency, LL = average lamellar length.



Examining molars attributed to *M. meridionalis*, Lister and Sher (2015) were able to estimate the plates lost through wear over time. Accounting for these estimated plates, most material attributed to *M. meridionalis* display molar characteristics more in line with *M. trogontherii*. Lower jaw material described also falls more in line with advanced characteristic including a short corpus and high ramus/symphysis. Material in Yukon and Alaska has also been dated to around 1.7 Ma, lending credence for *M. trogontherii* being in position to migrate further south into North America by approximately 1.5 Ma. *M. meridionalis* is proposed to have dispersed onto the continent at this time, however it is most likely to have been a dead-end lineage (Figure 1.4).

FIGURE 1.4: DISTRIBUTION OF CALCULATED MAMMOTH LAMELLAR NUMBER THROUGH THE EARLY, MIDDLE, AND LATE PLEISTOCENE (EP, MP, AND LP RESPECTIVELY; LISTER AND SHER, 2015).



Two years later, Lister (2017) examined the holotypes, paratypes, syntypes, and neotypes of North American Mammoths *Mammuthus columbi*, *M. imperator*, *M. jeffersonii*, *M. meridionalis*, *M. hayi*, *M. haroldcooki* and *M. primigenius* to establish a clear evolutionary lineage between the species. They examined and re-measured molars of more primitive mammoths (*M. meridionalis*, *M. hayi*, *M. haroldcooki,* and *M. imperator*) from Maglio (1973), and Lister and van Essen (2003) to account for the age of the specimen and enamel plates lost due to wear**.**

The examined molar characteristics for previously mentioned species either exhibited taxonomic characteristics that fall within the range of values for *M. columbi or* were indeterminable due to flawed reconstruction of fragmentary material, or loss of the specimen. Upon examination of molar characteristics of all holotypes, paratypes, syntypes, and neotypes, it is currently proposed that only two distinct species of mammoth were endemic to North America during the Pleistocene, *M. columbi,* and *M. primigenius*. *M. jeffersonii* is proposed to be a junior synonym to *M. columbi*, representing late Pleistocene evolutionary advancement or possible interbreeding with *M. primigenius* (Lister, 2017).

Lucus and others (2017), refuted this claim, and attempt to establish a clear phylogenetic lineage and taxonomic precedent for mammoth evolution in New Mexico, which has some of the oldest dated specimens (Table 1.5). They analyzed three mammoth specimens from Tijeras Arroyo, Mantanza Arroyo, and Adobe Ranch according to methods described in Maglio (1973). While the molars are heavily worn due to age, molar characteristics fall within the range of values for *M. meridionalis* and *M. imperator*. The lower jaw (Tijeras P-12894) was also excavated approximately 5 meters below a tuff layer that was $^{40}Ar/^{39}Ar$ dated to 1.264 +/- 0.010 Ma (Lucus et al., 2017).

Citing internal inconsistencies and inaccurate measurements in the Lister and Sher (2015) paper, such as inaccurate measurements from specimen photographs and ontogenetic changes making older mammoth jaws look more primitive not supported by previous studies from the Mammoth Hot Springs (Agenbroad, 1994). Lucus and others (2017) asserted that the phylogenetic lineage for North American mammoths proposed by Maglio (1973) is still valid. This study asserts that some of the most primitive material dated for mammoths in North America display distinct taxonomic characteristics of *M. meridionalis* and *M. imperator*.

Table 1.5: Table comparing molar characteristics of the three studied specimens to other data on populations of M. meridionalis, M. imperator, and M. columbi (Lucus et al., 2017).

New Mexico Specimens	Tooth	Plate Number	Length (cm)	Width (cm)	Height (cm)	Enamel Thickness (cm)	Lamellar Frequency
M. meridionalis							
Tijeras P – 12894	M/6	6+	282	100		3.8	4
Matanza P – 67371	M/6	11		81	150	3.8	
Adobe Ranch P – 37230	M6/ ?	8+	131+	73	147	3.3	6 – 7
Adobe Ranch UTEP – 33-32	M6/ ?					3.3	4.5
M. imperator							
Tijeras P - 12888	M6/	19+	324	93	175	3.0	5 – 6
Tortugas NMSU 140	M/6	17	300	78		3.2	6 – 7
Compiled Data							
Eurasian *M. meridionalis* (Wei, et al., 2003)	M6/ & M/6	10 – 15	215 - 335	69 – 126	75 – 135	2.2 – 4.1	3.5 – 6.5
M. imperator (Madden 1981)	M6/	15 – 19	222 – 340	81 – 125	139 – 208	1.6 – 3.4	4.0 – 8.7
M. imperator (Madden 1981)	M/6	14 – 22	251 – 434	61 – 129	113 – 183	1.9 – 3.6	3.6 – 7.8
M. columbi (Dutrow, 1980, Agenbroad, 1994)	M6/	18 – 24	227 – 360	75 – 120	139 – 230	1.2 – 3.2	5.2 – 8.8
M. columbi (Dutrow, 1980, Agenbroad, 1994)	M/6	18 – 23	259 – 382	73 – 111	114 – 177	1.2 – 3.2	3.7 – 8.5
M. columbi (Dutrow, 1980, Agenbroad, 1994)	M6/	10 + - 18+	122+ - 276+	86 – 104		1.7 – 3.0	4.4 – 9.0
M. columbi (Dutrow, 1980, Agenbroad, 1994)	M/6	15 + - 21+	189+ - 299	84 – 102		1.9 – 3.0	5.2 – 9.0
M. imperator (Leisey) (Webb and Dudley, 1995	M6	12 + - 19+	242 – 265	92 – 97		2.2 – 3.1	5.0 – 6.5
M. imperator (Leisey) (Webb and Dudley, 1995	M6	4 + - 17 +	102+ - 284+	75 - 108	95+ - 189	2.1 – 3.3	4.0 – 6.2

Fisher (2018) provided a review of the current scientific understanding of proboscideans during the Pleistocene (2.588 Ma – 11.7 Ka). His goal was to provide theories regarding paleoecology and behavior of proboscideans, evidence for climate change and its impact in the late Pleistocene. In his paper, he provided a compilation of research material regarding molar characteristics, as well as radioisotope data, osteology, and trace fossils (Figure 1.5).

Most of Fisher's (2018) results were presented in the form of a summarization of previous research conducted and the possible inferences that can be made. He concluded that specifically for North American mammoth evolution, Lister and Sher's (2015) interpretation of molar characteristics that suggests both *M. columbi* and *M. primigenius* descended from *M. trogontherii* was upheld. While the author does propose this phylogenetic relationship (Figure 1.6), they still state that the relationship between the two taxa, and possible primitive species such as *M. meridionalis* and *M. imperator*, is still unclear. Examination of carbon and nitrogen radioisotopes also display an oscillation of values inferred to display seasonality, showing reduced values during inferred winter periods when the mammoths would be subsisting primarily on fat reserves. Evidence for coprophagy and carnivorous activity is also presented with evidence for these behaviors from material extracted from the intestines of exceptionally preserved *M. primigenius* specimens.

Fisher (2018) also discussed that matriarchal herd behavior has been supported using both osteology and ichnology implying groups of mature females with juveniles, and males forming small groups while young and being solitary in their later years. This herd behavior used to be assumed from observing modern day elephants as analogs; however using trace fossil and osteological evidence lends credence. Mastodon trackways in Michigan (Figure 1.7) suggests a herd of females with juveniles using the overall size of the footprints to infer the size of the animal and most likely gender (Fisher, 2018).

FIGURE 1.5: MOLAR AND TUSK CHARACTERISTICS (FISHER, 2018) SHOWING THE HIERARCHY OF DENTAL CHARACTERISTICS IN ELEPHANTS

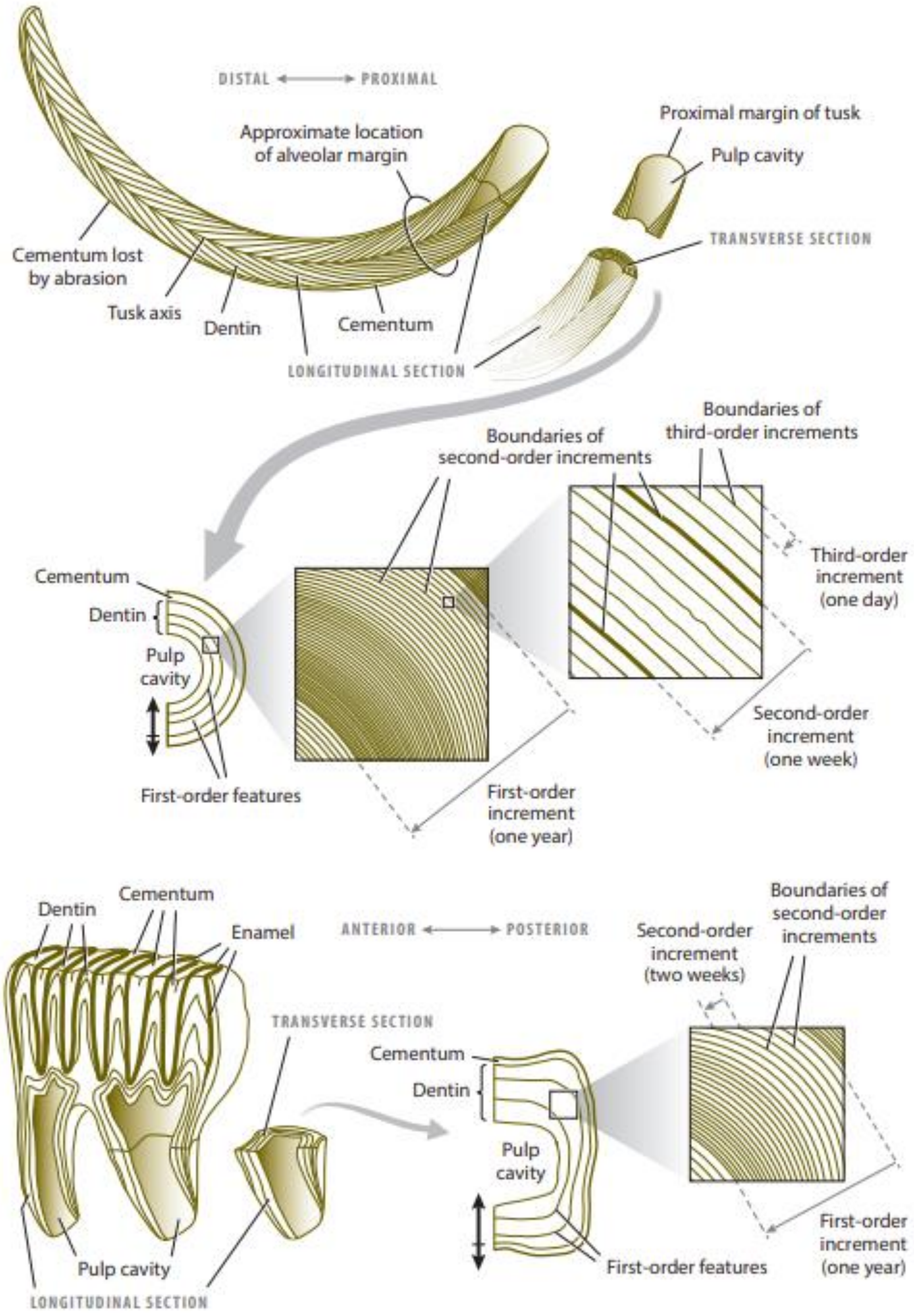


FIGURE 1.6: PROPOSED PHYLOGENETIC LINEAGE OF PROBOSCIDEANS (FISHER, 2018)

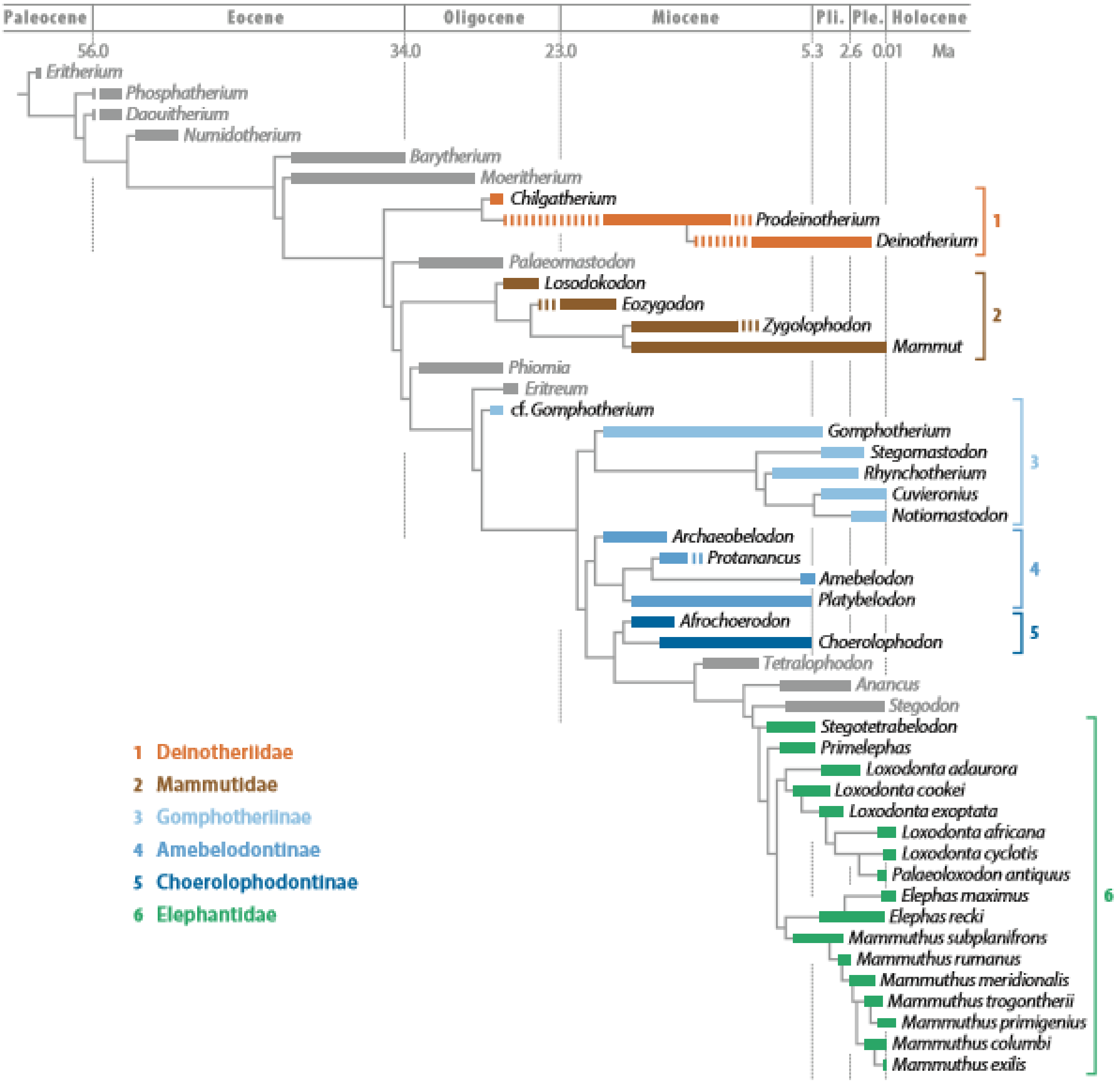
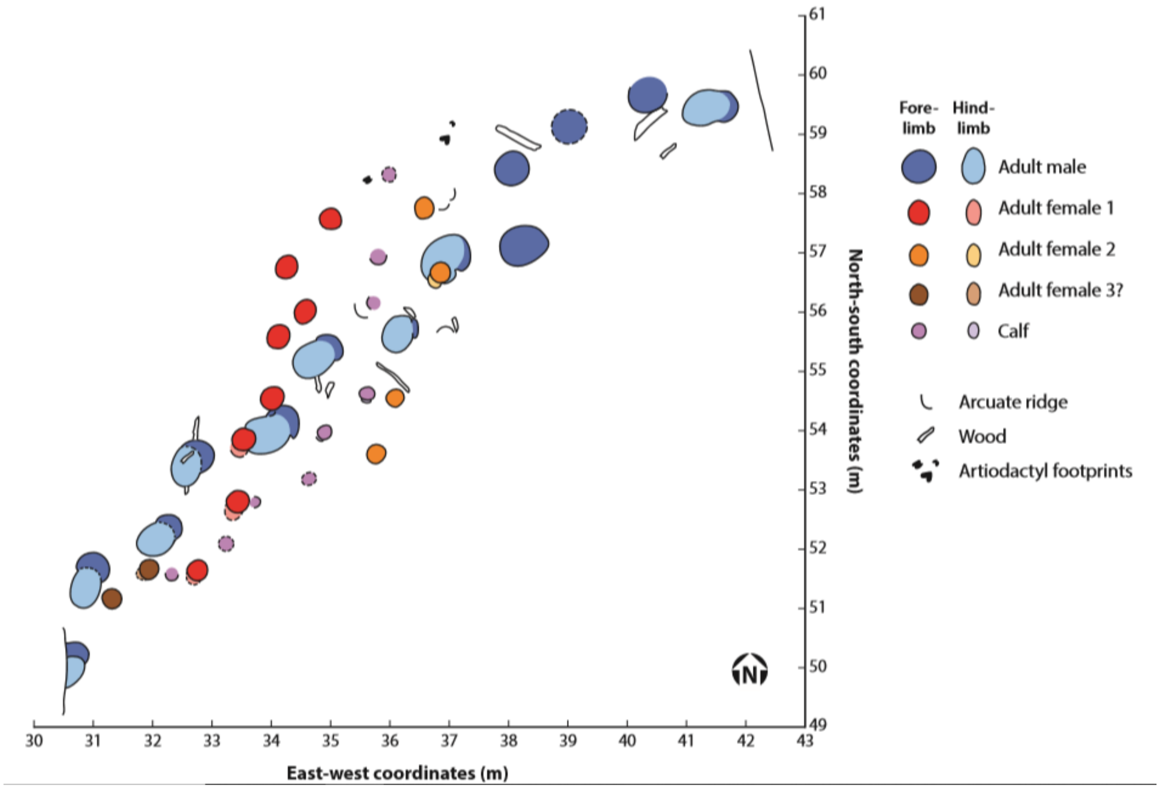


FIGURE 1.7: MASTODON TRACK WAY IN MICHIGAN SHOWING A MATRIARCHAL HERD MADE UP OF ADULT FEMALES AND A CALF, WITH A SOLITARY MALE CROSSING THE PATH. THE OVERPRINT OF THE MALE'S TRACKS IMPLIES THE MALE MOVED THROUGH THE AREA AT A LATER TIME THAN THE HERD, POSSIBLY IN SEARCH OF SUSTENANCE OR THE MASTODON HERD ITSELF (FISHER, 2018)



Saunders and others (2010) outlined late Pleistocene proboscidean evolution, mainly the succession of *M. primigenius,* and specimens were proposed to be *M. jeffersonii*. They examined mammoth and mastodon molar characteristics in conjunction with radiocarbon dating of the sites where the proboscideans were excavated. The dated specimens of both species display *M. americanum* (the American Mastodon) outlived mammoths in Illinois by over 100 years.

They concluded that *M. jeffersonii* was a more adaptive species for forest and parkland habitats created by the last glacial retreat occurring during the late Pleistocene. These mammoths were better suited for this ecological niche, as the cold adapted *M.*

primigenius was better suited to the now shrinking mammoth steppe environment. Evidence that mastodons outlived mammoths indicates that it was most likely better adapted for such an environment and outcompeted the endemic mammoth species.

Yansa and Adams (2012) examined evidence for diets of the two mammoth species, *M. jeffersionii*, and *M. primigenius*, as well as the American mastodon, *M. americanum* that lived in the Great Lakes region during the late Pleistocene, and how these species could coexist without competition. They utilized proboscidean fossils from the Great Lakes region (Minnesota, Wisconsin, Illinois, Michigan, Indiana, Ohio, United States and southern Ontario, Canada; Figure 1.8). Most specimens were intact, having been preserved in lacustrine clay sediments (most likely due to the animal breaking through thin ice layer and drowning), and their biogeographic distribution was examined to determine possible range of the species.

They determined that mastodons were more abundant (4:1 ratio) than mammoths in Michigan and Ohio, while the distribution is reversed moving westwards. Mastodons are interpreted to have a browser diet, eating shrubs and tree leaves, while mammoths had a more grazing diet, consisting of grass type plants. Woolly mammoths are observed to chase the northward retreat of the tundra habitat that existed on the margin of the Laurentide glacier, while those specimens attributed to *M. jeffersonii* occupied a parkland environment to the south (Figure 1.9). Proboscidean skeletons were excavated and dated (using carbon 14 radioisotope methods) to approximately 11.5 Ka, during the megafaunal extinction event. These skeletons also display signs of ecological stress, appearing to reach maturity around 9-12 years of age, earlier than the average 14-16.

Mastodons and mammoths were able to coexist in the same habitat due to occupation of separate ecological niches. Towards the end of the Pleistocene both species appear stressed, most likely due to the creation of more closed deciduous forests coinciding with a global warming period. Both proboscidean taxa display an attempt to adapt to the changing ecology, but ultimately faced extinction.

FIGURE 1.8: SITE LOCATION FOR SPECIMENS EXAMINED IN YANSA AND ADAMS (2012)

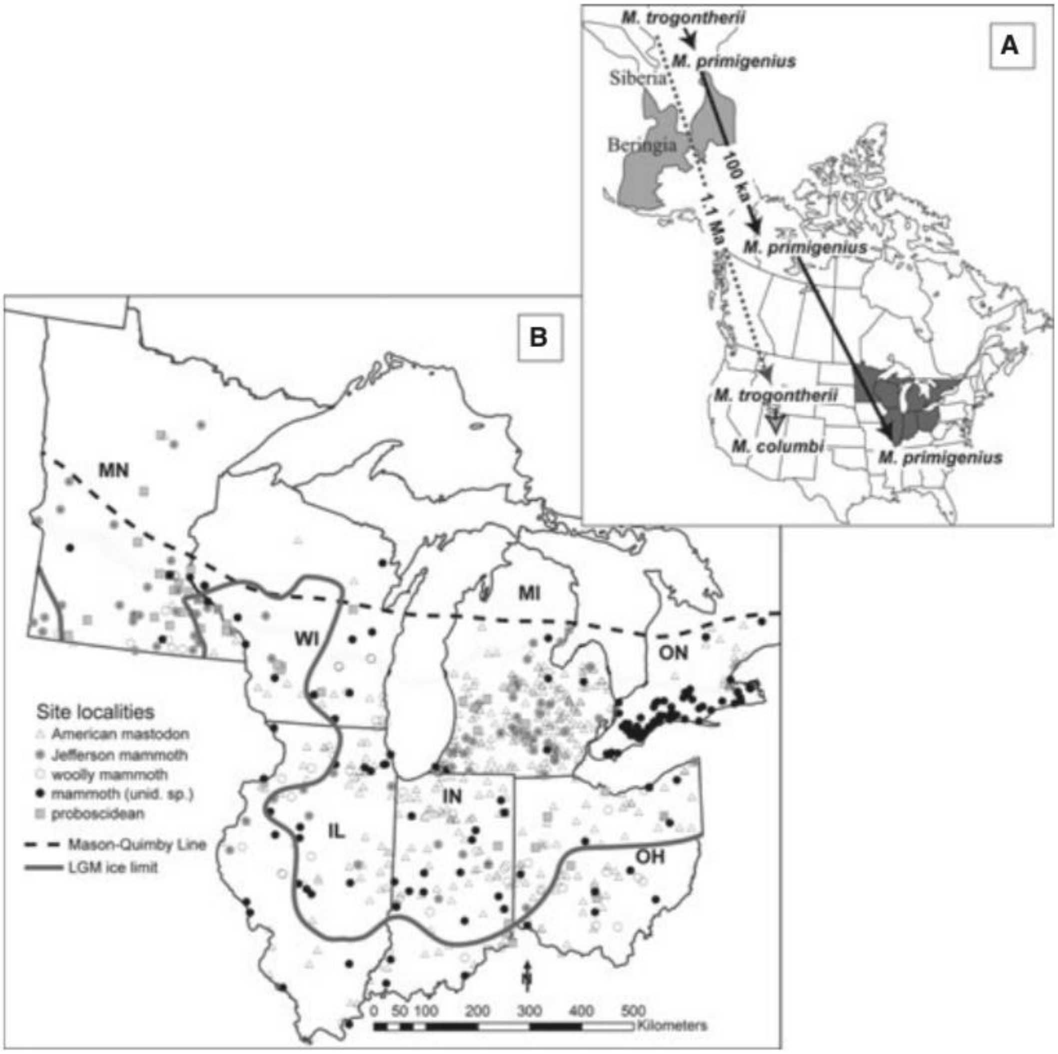
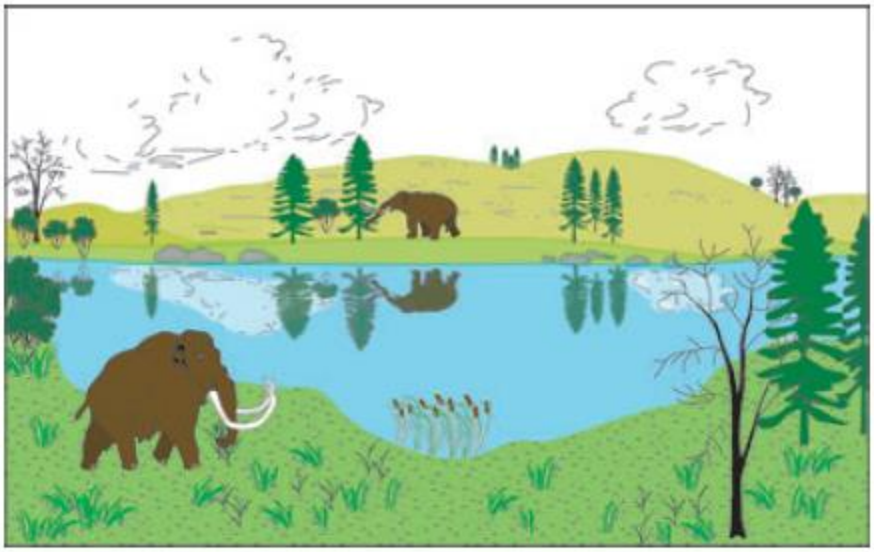


FIGURE 1.9: ARTISTIC REPRESENTATION OF PARKLAND HABITAT TO THE SOUTH OF THE LAURENTIDE ICE SHEET (YANSA AND ADAMS, 2010)



Uncertainty in species designation and paleoenvironmental influences

The previous studies mentioned in this chapter highlight the issues of North American mammoth taxonomy, even when viewed from a paleoecological context. This is primarily due to aforementioned controversy surrounding the taxonomic assignment of mammoths based on molar characteristics that can overlap and an assumption on the biogeographic range of each species. The Great Lakes region (Figure 1.8) has the most prolific finds, and best evidence for *M. jeffersonii*. Attribution of excavated specimens to this species is based on their molar characteristics as described by Osborn (1942). The distinguishing characteristics described is a sixth molar set with 25/24 enamel plates in the upper and lower molars respectively and a bodily size larger than the 2.4 – 2.7 m (8 -9 ft) at the shoulder than reported for *M. primigenius* (Stauffer, 1924; Skeels, 1962; Holman et al., 1988; Kapp, 2002).

While there was certainly interbreeding between *M. columbi* and *M. primigenius* populations, assignment to *M. jeffersonii* is prone to error. Some specimens were given this designation based on the biogeographic distribution proposed by Osborn (1922), with Jeffersonian mammoths occupying the northern United States and Midwest and Columbian and Imperial mammoths prolific in the southern states into Mexico (Stauffer, 1924). Studies based on molar morphometrics suffer from previously mentioned taxonomic and ontogenetic issues.

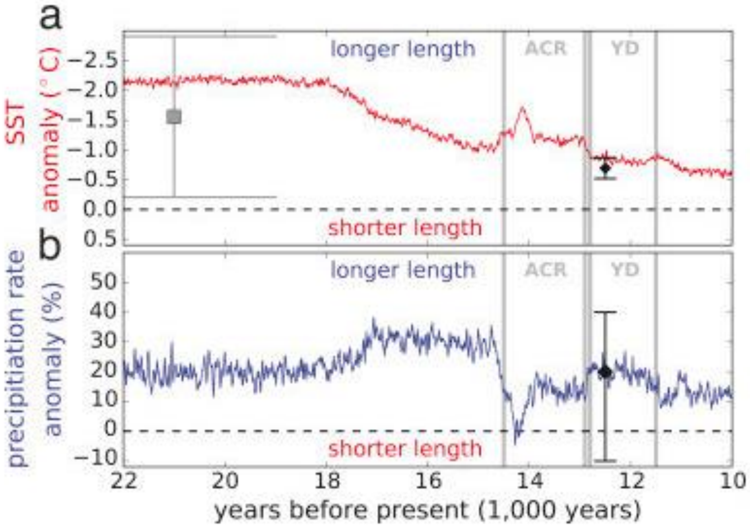
While there is still uncertainty surrounding the number and distribution of mammoth species across North America, Widga and others (2017) synthesized available genetic and taxonomic data to make regional inferences. With the exception of mammoths on the west coast and southward into Mexico that display a lower plate count with thicker enamel, this study found no real discernable morphological trends across the United States and along the US/Canadian border. Widga and others (2017) propose that mammoths across the United States represent a single species comprised of introgressing metapopulations whose molar morphometrics are indicative of adaptation to a regional population’s environment.

This interpretation is most likely a better representation of mammoth evolution. The study of taxonomy is an attempt to put discrete boundaries on a continual process, and by necessity morphological changes in an organism’s skeleton are interpreted as changes to environmental stressor and speciation. Due to the migratory habits of mammoths, regional populations of mammoths most likely introgressed with other regional population creating homogenization.

While not representative of the evolutionary process, taxonomic description aids understanding of natural processes. It is the opinion of the author that *M. jeffersonii,* while synonymous to *M. columbi* or representing hybridization between Columbian and Wooly mammoths, is useful to this study to denote mammoths that display molar characteristics intermediate to *M. columbi* and *M. primigenius*.

The changing environment had its own influence on the flora and fauna of the time. Paleotemperature was in flux, with the Bolling Allerod (14.6 Ka – 12.6 Ka) warming period causing glacial retreat. This was immediately followed by the Younger Dryas period, with a marked drop in temperature and increase in precipitation (Figure 1.10; Malone et al., 2015). This variability in climate has been proposed as a potential driver for the extinction of megafauna at this time, and certainly created changes in the ecology across a geologically short period of time.

FIGURE 1.10: RECONSTRUCTION OF PALEOTEMPERATURE AND PRECIPITATION RATES DURING THE YOUNGER DRYAS PERIOD (MALONE ET AL., 2015)



Paleoenvironmental trends appear to support this assertion. Most mammoth specimens attributed to *M. jeffersonii* and *M. primigenius,* including the *M. jeffersonii* holotype, excavated from the United States are correlated to the final pulses of Wisconsin glaciation, approximately 15 Ka – 10 Ka (Osborn, 1922; Wayne, 1967; Wilson, 1967). The retreat of this glaciation marked the end of the ice age, and a transition to climatic conditions analogous to modern conditions. In areas such as the Great Lakes region, east coast, and Midwest, humid parkland environments developed, while more arid conditions persisted from the Rocky Mountains westward (Doerner and Carrara, 2001; Saunders et al., 2010; Widga et al., 2017). This is represented in the molar morphometrics of mammoth populations, as mammoths in humid parkland environments have molars packed with a higher number of enamel plates and thinner enamel and western mammoths exhibiting more primitive characteristics due to selective grazing of coarser foliage (Widga et al., 2017).

GOALS OF THIS THESIS

As I outlined above, in the late Pleistocene to early Holocene, 126,000 – 11,700 years ago, *M. primigenius* (Woolly) and *M. columbi* (Columbian) mammoths were endemic to North America. For nearly 80 years researchers (Yansa and Adams, 2012) have debated the validity of a third species, the *M. jeffersonii*, and recent genetic findings determined that it may be a Woolly, Columbian mammoth hybrid (Enk et al., 2011). Given the lack of abundant and reliable testable genetic material in the fossil record, molar dimensions have been used to determine mammoth species (Maglio, 1973). Molar characteristics are problematic, however; molars display different characteristics dependent on the tooth's age, state of wear, and age of the mammoth and can lead to misinterpretation of a mammoth's species. Due to these factors, there is overlap in the ranges of measurements for each species. Therefore, multiple proxies are needed for comparison to confirm specific mammoth species.

Cranium characteristics can also reveal mammoth species and factors such as gender, age, and ecological variables that affected the morphology of the skull during growth. Although comparing molar dimensions has been tested in North America (Maglio, 1973), assessing the other cranium and dental characteristics have not. Todd (2010) recently proposed a character dataset with 77 new measurements to determine species of modern elephants and extrapolated those characteristics to interpret fossil remains in Eurasia.

To clarify this ambiguity of mammoth species based on fossil occurrences requires an interdisciplinary paleontological approach in the fields of taxonomy, ontogeny, and phylogeny. My research goals are to: 1) measure and compare other molar measurements of the mammoth excavated from southeastern Idaho (termed Cola) to other mammoth remains in previous literature in North America, 2) determine the time when Cola lived using radiocarbon isotope techniques and compare the date with the current understanding of mammoth hybridization, 3) estimate age of Cola when it died and factor in understanding of ontogenetic results, 4) obtain successful DNA extraction and analysis by the UCSC Paleogenomics Lab of Cola to compare resultant DNA libraries to taxonomic assignment based on the molar characteristics, and 5) put the results into a paleobiogeographical context. There is one final goal to this research and it is to make it accessible and understandable to K-12 students to excite them in the STEM fields and to show them an example of what research in the sciences include.

Methodology

I will be focusing on three taxa constrained to the latest Pleistocene to early Holocene (20 Ka – 10 Ka); the Columbian (*M. columbi*), Woolly (*M. primigenius*), and Jeffersonian Mammoth (*M. jeffersonii*). These three mammoths include the most prolific finds in the fossil record across North America and will provide a robust sample size to perform taxonomic descriptions on. I have constrained my focus to the very end of the mammoth's reign for several reasons. The first reason is that most literature surrounding a specimen's assignment to *M. jeffersonii* report specimens with radiocarbon dates from 20 Ka – 10 Ka and constraining my study to this timeframe will increase the likelihood of accurate taxonomic description and assignment. *M. primigenius* and *M. columbi* also coexisted at this time. Along with *M. jeffersonii, M. primigenius* and *M. columbi* will also be measured to aid in constructing a better framework to determine mammoth speciation in North America. I will use previous DNA tests to initially measure specific mammoth species' remains to set up my comparison proxy. I will then examine specimens according to the methods listed below.

Goal 1: Establishing mammoth species' skull characteristics (taxonomy)

Determining mammoth speciation based on molar characteristics focuses on the morphological changes that affect mammoth dentition as they adapted to different biomes and ecology. These changes correspond to differences in the overall plate count, the frequency of the plates within 100 mm (lamellar frequency), thickness of the enamel, as well as overall height and width of the molar itself (Maglio, 1973). Although these measurements have been used by previous authors to describe species, factors such as the age of the specimen at the time of its death the state of wear, and limited genetic material to test can lead to a misinterpretation of species (Lister and Sher, 2015).

To create a more quantifiable criterion to compare cranial (skull and mandible) and dental (molar and tusk) elements of mammoths, Todd (2010) proposed 77 taxonomic characteristics (33 dental, 32 cranial, and 12 mandible) to determine species. Both Maglio's (1973) and Todd's (2010) methods will be used when measuring Cola and comparing those measurements to other previous literature. These characteristics offer a robust and quantitative method to determine mammoth species and has been used successfully when comparing African and European mammoths. Figure 1.11 displays some of the measurements based on Todd's (2010) methods, as well as a table of the molar measurements for each mammoth taxa being studied based on Maglio (1973).

Goal 2: Determining the time when Cola lived

I will attempt to extract a radiocarbon date from the remains of Cola. We will try to extract a date from Cola's bone but if that is unsuccessful, we will attempt to get an age reading from Cola's molar. Beta Analytics Testing Laboratory will do the extraction. There, they use Accelerator Mass Spectrometry to derive a date. For more about the methods they use, see Appendix A.

Extraction of a radiocarbon date is important because it will put all our observations in geologic context. Questions to be answered include: Did the mammoth live at a time of glacial maximum or was it one of the few remaining mammoths in North America before their final demise? Were mammoths stressed at that time (from anthropogenic or climatic pressures) or did Cola live in a relatively calm period? Depending on the taxonomic results, can we confirm hybridization and, if we can, when did this occur?

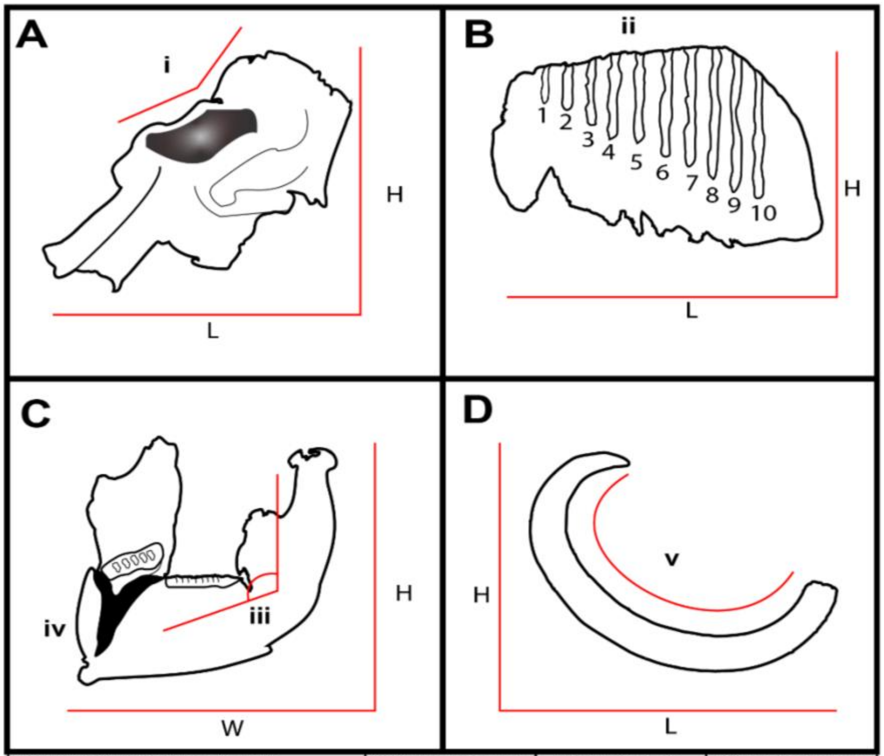
Goal 3: Determining the effect of age on skeletal morphology (ontogeny)

Developmental processes as mammoths age can affect the overall appearance and size of molars and crania. The age of the Cola will be determined using African and Asian Elephant equivalent years using methods from Laws (1966) and Roth and Shoshani (1988) respectively. These methods draw parallels between the known eruption and growth rates of modern elephant molars and distinct ages in their lives and provide an estimate of a mammoth's age at its time of death. Measurements of Cola's molars will be compared to other mammoth remains in previous literature to determine if Cola was young or old when it died. Age profiles of mammoth specimens include juveniles (1-15 years old), sub-adult (16-

24), adult (25-35) and elder (>35; Laws, 1966). The age profile will be compared species interpretation outlined in Roth and Shoshani (1988).

Figure 1.11: Select characteristics shown from Todd (2010). Legend: Length (L) and height (H). A) general shape of a mammoth's skull, measuring features such as the slope of the forehead in relation to the rest of the skull (i); B) molar measurements include enamel plate number (ii, 1-10) as well as the overall shape and curvature of the molar; C) mandible characteristics include the angle between the corpus (horizontal portion of the jaw) and the vertically ascending ramus (iii), and the shape and orientation of the chin (symphysis, iv); D) tusk measurements include the curvature and the growth patterns (v). The table below is a comparison of the established molar measurements (Maglio, 1973) and dimensions of mammoth skeletons (Gillete and Madsen, 1993; Lister, 2017).

N/A*: No values were found reported in literature by the



Maglio (1973) Molar Measurements	Columbian Mammoth	Woolly Mammoth	Jeffersonian Mammoth
Length	N/A	5.9	29-35
Width	8.9-10	8.3	8.3-12.2
Height	15.2-19.7	N/A	19
Enamel Plate Number	20-24	24-28	25-30
Overall Dimensions of Crania, Mandible, and Tusks (cm)			
Height and Length of Skull	99.1 H x 142.3 L	N/A*	N/A*
Height and Width of Mandible	50 H x 80 W	N/A*	N/A*
Length and Diameter of Tusk	N/A	372.2 L x 18.7 D	N/A*

Mammoths, like modern elephants, have six sets of teeth that they wear through in their lives. These teeth make up two upper and two lower molars that are comprised of a series of laterally stacked enamel plates (Figure 1.11) that wear down by the animals grinding their food. By determining what molar set the mammoth had aged into by each tooth's distinct size and shape, and the number of enamel plates lost to wear an accurate assessment of age can be made. A mammoth's skeleton changes over time as it grows older as the animal ages and bones are reformed and fused. Just as mammoth age can affect the shape and wear of molars, age may also alter the appearance of the skull and must be taken into consideration for species identification.

Goal 4: Obtain successful ancient DNA extraction to confirm species of Cola. This will be compared to the evolutionary history of North American proboscideans (phylogeny)

Understanding the taxonomy of North American mammoths is inextricably linked to the overall evolution of the species. Accurate determination of species is required for the establishment of fossil succession, with different mammoths evolving at different times. The proposed taxonomic study will add another data point to tracking the migration of mammoth into the northwestern United States and whether climatic stresses resulted in times when more interbreeding occurred. My results will provide other researchers more key data to help them constrain how mammoths on the North American continent diversified and interacted with each other, and whether these populations were thriving, going extinct, or confined to a geographic region (Fisher, 2018).

Samples of mammoth molars identified as potential *M. jeffersonii* specimens will be sampled and sent to the UCSC Paleogenomics Lab for aDNA extraction. Samples will be processed according to Dabney and others (2013) and sequenced using an Illumina Nextseq 2x150. Samples will then be enriched and analyzed for phylogeny. Results will either refute or confirm taxonomic assignment based on cranial and dental analysis and provide insight into the derived characteristics of North American mammoths.

Goal 5: Establishing the distribution of the studied mammoth taxa on the North American continent and the ecological implications of each (paleobiogeography)

The recent genetic findings that confirmed there were three mammoth species in North America during the Pleistocene is significant for understanding the changing climate as Earth shifted from an ice age to a more transitional interglacial period. These ecological implications help scientists gain a better understanding of where each species lived and how they reacted to changing climate. Woolly Mammoths occupied the mammoth steppe environment in Canada, similar to what most people envision when they think of the ice age. The Columbian Mammoth occupied an open parkland type environment, with sparse trees and sedge bushes, in middle to southern North America. The Jeffersonian Mammoth's range is less understood due to the confusion surrounding its classification as a species, but has been found in wetter, more forested environments along the Canadian/United States border, where the melting glacier provided more water runoff and the ranges between the two other species overlapped (Yansa and Adams, 2012). The Jeffersonian Mammoth's environment is specific to the late Pleistocene to early Holocene, when the climate began to shift. The hybrid species status carries the implication that the two endemic species were interbreeding in an attempt to adapt to an environment neither were suited for. Results of the above for goals will be put in a paleobiogeographical context.

Goal 6: Introducing Cola to the Idahoan community: There is a Mammoth in the Classroom!

On top of learning about the life and possible cause of death of “Cola,” the Soda Springs mammoth, one of the outcomes from this research is to bring our excitement and understanding of science using the mammoth into the surrounding community. With an abysmal national ranking for public education, most students in the state of Idaho do not view higher education as a possibility. Those that attend college, sometimes as the first in their family to do so, are met with additional academic challenges compared to a second- or third- generation college student. Students that succeed in school make a conscious decision to pursue their studies, but with little to no exposure to science, technology, engineering, or mathematics (STEM), they may miss out on the potential to pursue an actual passion in a highly marketable career. One of my thesis goals is to use paleontology, a highly charismatic field of research, to motivate public school students to pursue a degree in a STEM field.

With my original research in this study and references to current literature regarding mammoths, I used information gained from the goals above to create a cohesive narrative presentable to K – 12 classrooms. Information regarding the class’ grade level and background will be supplied by the Stem Access program, including any other program opportunities within the TRiO umbrella that can be given to the students. This outreach will not generate any original research of itself but a way to present my research in a manner that is understandable to students of varying grades that do not have a collegiate background, and develop our oral presentation skills. The age groups targeted are public school classes ranging from elementary – high school age.

This exercise can be accompanied with a 30 – 60 minute lecture to a class with information covering my research on Cola, the general life of mammoths, and the possible death of our excavated mammoth. The presentation will end with information for other possibilities in the TRiO program, and 5 – 10 minutes open for questions. This presentation will include a slideshow presentation highlighting methods used on the mammoth, the results of that research, general mammoth information such as diet and behavior, and pictures to support the information on the slides.

Significance

Mammoths were a keystone species in late Pleistocene ecology, and their extinction during the Holocene transition 11,500 years ago is still not completely understood. The interbreeding of mammoth taxa during this time could be indicative of attempts to adapt to the changing climate, or anthropogenic influences. By establishing a suite of cranial characteristics that more reliably indicate species will aid paleontologists in better constraining the temporal range of mammoth hybridization. Genetic sampling will also add valuable information to an under sampled population and add validity to future morphological taxonomic assignments.

The appearance of the Jeffersonian Mammoth in the fossil record occurred shortly before the End-Pleistocene Megafaunal Extinction, with the earliest specimen dated to the first pulse of Wisconsin glaciation approximately 24 Ka (Wilson, 1967; Kapp, 2002; Yansa and Adams, 2012). This extinction coincides with the retreat of the last ice age continental glacier and is a period where climate change played a major role in the evolving North American biome. In total, 35 mammalian genera went extinct (Gilmour et al., 2015). Mammoths did not survive the changing environment, and better understanding their extinction will help us model modern-day conservation efforts against our own rapidly shifting climate.

Constructing an accurate record of mammoth evolution on the North American continent is necessary to understand overall elephant evolution. The evolution and ultimate demise of mammoths in North America can provide excellent parallels to how modern-day elephants will react. Modern Asian Elephants share a common ancestor with mammoths and are endangered today. As today's warming climate starts driving mass ecological change, this stressed population will have to adapt or perish like their ancestors.

Chapter 2: Piecing together a prehistoric puzzle: Regional inferences of micro- and macroscopic analyses of one of the last hybrid mammoths in mainland North America

(This chapter is currently under review in the Journal of Quaternary International. This is a compilation of work done by undergraduates Kate Brooks, Natalya Usachenko, and Shilah Waters, and my major advisor Dr. Renee Love. For other additions to this publication in review, Kate Brooks has submitted an undergraduate senior thesis to the University of Idaho in May 2021. Her work studied the cause of death and biostratinomy of Cola and is excluded here. My work overlapped with Natalya Usachenko's so our contributions to the paper are included together here with Natalya Usachenko's permission.)

INTRODUCTION

In the Quaternary, 126 - 11.7 Ka, *Mammuthus primigenius* (Woolly Mammoths) and *Mammuthus columbi* (Columbian Mammoths) were endemic to North America. The Pleistocene, Holocene transition occurred 12 - 11.5 Ka and is marked by the Megafaunal Extinction Event, recording the last activity of North American *Mammuthus* (Agenbroad, 2005). This extinction coincides with the retreat of the last ice age continental glacier and is a period where climate change played a major role in the changing North American biome. As the glacier melted, the cold, dry conditions that persisted through the Pleistocene in what is now the United States transitioned into a wetter, more temperate environment typical of modern conditions (Doerner and Carrara, 2001). Megafauna, including mammoths, struggled to adapt, and in total 35 mammalian genera went extinct, with 90% of all mammals over 450

Kg (992 lbs) disappearing from the continent (Gilmour et al., 2015). While the overall driver for the Megafaunal Extinction Event (overkill hypothesis: Miller et al., 1999; Holdaway and Jacomb, 2000; Alroy, 2001; Roberts et al., 2001; Wroe et al., 20046; disease: Edwards, 1967; MacPhee, 1997; rapidly changing climate: Saunders et al., 2010; Yansa and Adams, 2012; Fisher , 2018; or meteorite impact: Firestone et al., 2007; Kennett et al., 2009a; Kennett et al., 2009b; Pinter et al., 2011) remains unclear, the focus of this study provides an insight into one of the last remaining mammoths in mainland North America.

The Pleistocene, Holocene transition marks the end of the Quaternary glaciation. This division of biomes on the continent allowed for multiple mammoth species to cohabitate through niche partitioning and would be subject to dramatic variability between glacial and interglacial conditions towards the end of the Pleistocene (Yansa and Adams, 2012; Lister, 2017). For nearly 80 years, researchers (Yansa and Adams, 2012; Enk et al., 2016; Widga et al., 2017) have debated the validity of a third species: *Mammuthus jeffersonii (*Jeffersonian Mammoth). Recent genetic studies have suggested that the *M. jeffersonii* could either be a *M. primigenius, M. columbi* hybrid (Enk et al., 2011) or a more evolutionarily advanced version of the *M. columbi (*Aguire, 1969; Maglio, 1973; Graham, 1986; Lister, 2017*)*.

A nearly complete mammoth skeleton was excavated from a hydrothermal spring deposit seven miles north of Soda Springs, Idaho (42.747963, -111.546300) in 1966 and is now located at the University of Idaho (UISSM-001-COLA termed 'Cola' herein; Jones and Bowers, 1968; Fig. 2.1, Appendix C). This deposit had been postulated to be Late Pleistocene in age (Malde and Powers, 1962; Jones and Bowers, 1968) based on nearby geologic mapping and seven species of freshwater gastropods that were discovered between 61-91 cm (2-3 ft) above the mammoth remains. Original reconnaissance by R. Jones in 1968 mapped a tufa rim of an ancient discontinuous ‘Pleistocene Spring’ that was about 1 mile in length. Nearly 100 springs have been mapped in the vicinity of Soda Springs and the Aspen Range to the east (Semenza, 2011) and many have been associated with active and extinct accumulations of travertine deposits (Lewicki et al., 2013). The Pleistocene Spring is oriented against the east slope of a north-south oriented fault block, along the trend with China Hat (Welhan et al., 2014; McCurry et al., 2015; Welhan and Breedlovestrout, 2016). The north-south oriented fault block is part of the Paris Thrust fault system within the Sevier fold-and-thrust best in southeastern Idaho (Lewicki et al., 2013) and hydrothermal activity is associated with the Quaternary Blackfoot Volcanic Field (Welhan et al., 2014). Although more bones were searched for in the vicinity, the Pleistocene Spring was the only deposit to contain fossilized bones; the mammoth was discovered six feet in depth.

Although over 50 years have passed since Cola was excavated, a detailed study had never been conducted on the specimen. Here, we perform a collaborative network of studies on the taxonomy and taphonomy of Cola to provide insights into a mammoth hybrid before the final extinction of all mammoths on mainland North America. The focus of this study is to determine the:

1) Absolute date of when Cola lived using radiocarbon dating methods, as well as the paleoenvironmental context of the site of its deposition based on the taxonomic and biostratigraphic reexamination of freshwater gastropod specimens that occurred at the excavation site. The gastropods excavated at the site stratigraphically overlie the mammoth bones and were originally assigned to be Late Pleistocene in age by the US

Geological Survey (pers. comm.) in 1967. The following species were identified: *Valvata humeralis*, *Lymnaea nuttalliana*, *Lymnaea stagnalis appressa*, *Gyraulus parvus*, *Armigar crista*, *Planorbella subcrenata* and *Physa gyrina.*

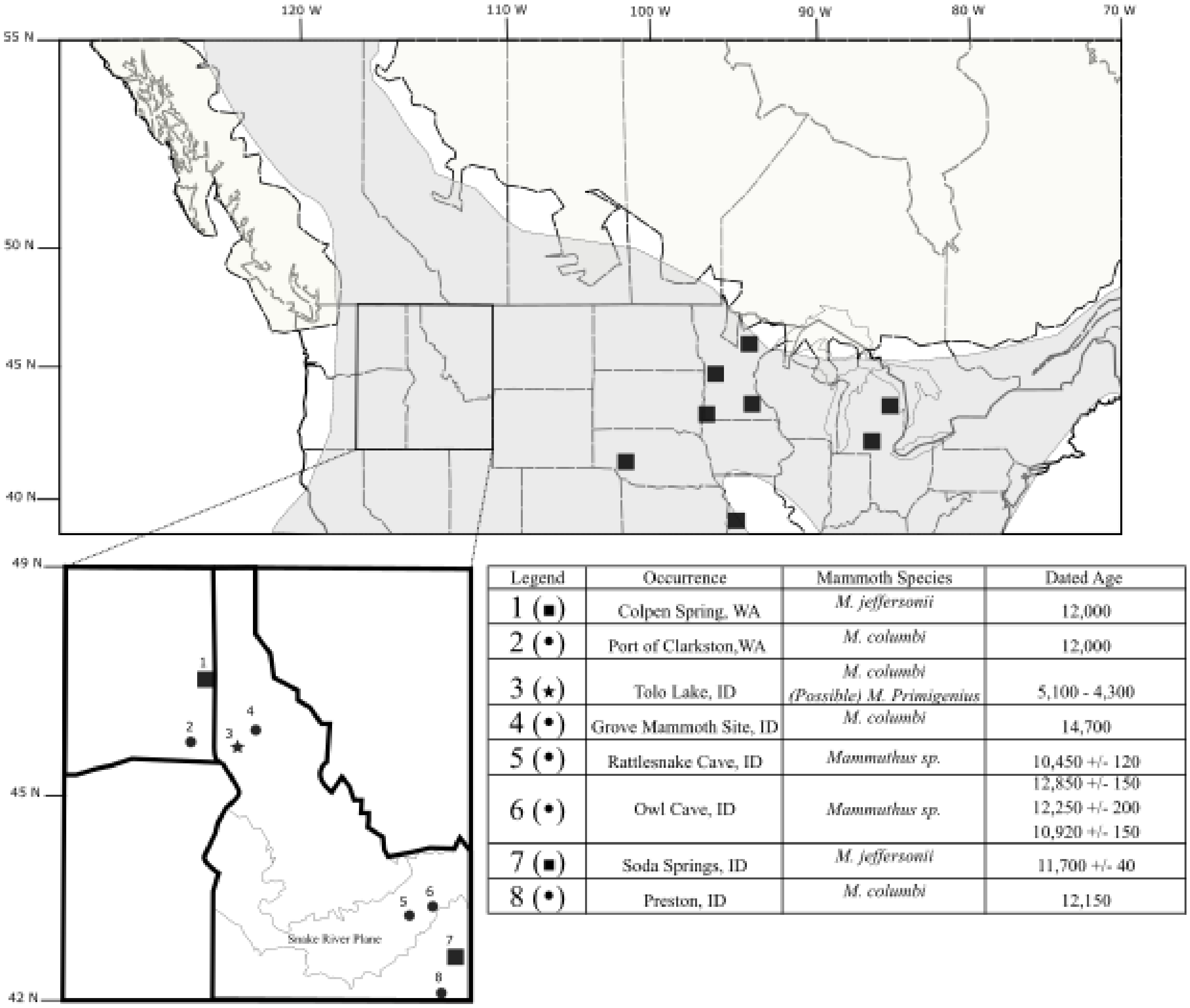


Figure 2.1 Mammoth distribution in North America. Grey shaded area represents the inferred range of mammoths during the Pleistocene – Holocene transition 15-10 Ka and is based off Agenbroad (2005) and distribution of Mammuthus sp. in Faunmap. White shaded areas show the extent of glaciation at this time. Mammoth discoveries attributed to M. jeffersonii are represented with a black square (n). Inset: Mammoth discoveries in Washington and Idaho that have been radiocarbon dated within 15-10 Ka. Descriptions of localities are included. Sites 1-3 are from Sappington (2019) and sites 4-8 are from Agenbroad (2005)

Legend	Occurrence	Mammoth Species	Dated Age
1 (■)	Colpen Spring, WA	*M. jeffersonii*	12,000
2 (•)	Port of Clarkston,WA	*M. columbi*	12,000
3 (★)	Tolo Lake, ID	*M. columbi* *(Possible) M. Primigenius*	5,100 - 4,300
4 (•)	Grove Mammoth Site, ID	*M. columbi*	14,700
5 (•)	Rattlesnake Cave, ID	*Mammuthus sp.*	10,450 +/- 120
6 (•)	Owl Cave, ID	*Mammuthus sp.*	12,850 +/- 150 12,250 +/- 200 10,920 +/- 150
7 (■)	Soda Springs, ID	*M. jeffersonii*	11,700 +/- 40
8 (•)	Preston, ID	*M. columbi*	12,150

2) Estimated age and size of Cola at its time of death using measurements of post-cranial bones and molars. Mammoths wear through six sets of molars in their lifetime, with the last set erupting when they reach maturity between 24 to 32 years of age (Harington et al., 2012). As their molars grow, layers of dentin are deposited, and the number of these dentin layers correlate to the specimen's age in years (Dance, 2018). Proboscideans lose each set of molars at approximately age 2, 6, 15, 28, 43, and 60 to 65 (M1, M2, M3, M4, M5, and M6 respectively). These molar sets are referred to as M1 – M6 in this paper, with M1 correlating to the first dairy molar that erupts, and M6 the final adult molar. A mammoth's first set of molars are only about 1.3 cm (.5 in) long, about the size of those of a human. Their third set is about 15 cm (5.9 in) long, and the final set is about 30 cm (11.8 in) long (Jefferson, 2006).

3) Gender of Cola based on the length of its tusks, degree of epiphyseal fusion in its limb bones, and conditions at the excavation site. Mammoths were sexually dimorphic in body size, tusk length, and rate of skeletal maturation (Haynes, 2017). The tusks of mammoths could reach lengths of 2.4-3.7 m (8-12 ft) on average in males and 1.5-1.8 m (5-6 ft) on average in females (Lister and Bahn, 2007). The epiphyses in the limb bones would typically finish fusing between the age of 30 and 35 in females and between the age of 60 and 70 in males (Haynes, 2017).

4) The taxonomic identification of Cola. Distinction between mammoth species is based on a variety of taxonomic characteristics, primarily the dimensions and morphology of the proboscidean's molars. This taxonomic identification was

confirmed using mitochondrial DNA (mtDNA) analysis of the M4 molar (upper right molar in the 4th molar set).

MATERIALS AND METHODS

Samples of Cola's molar were collected and analyzed by Beta Analytic Testing Laboratory to obtain a $^{14}C/^{14}N$ radiocarbon date. Using a sterilized drill, collagen from the center of the tooth was extracted and placed in a sterile plastic container. The techniques used to measure carbon 14 in the tooth utilized gas proportional counting, liquid scintillation counting, and accelerator mass spectrometry (Appendix A). The stable isotope composition was then used to obtain an accurate estimation of the time of Cola's death and deposition.

The length of the humerus was used to calculate the mammoth's approximate height from foot to shoulder using the equation: Length of Humerus = 0.34 * shoulder height of specimen (Harington et al., 1974). Cola's age range was estimated at its time of death using two methods:

1) Post-Cranial Skeletal Assessment: Age parameters were first determined by the examination of the degree of epiphyseal fusion in the intact proximal and distal regions of the Cola's limb bones. This was cross-referenced with the skeletal growth rates of modern proboscideans (Haynes, 2017).

2) Dentition: The approximate age of the mammoth was also estimated via dental analysis using methods of Roth and Shoshani (1988) comparing *Elephas maximus* (Asian Elephant) molars of known age, which are evolutionarily related to the *Mammuthus* genus, to provide an accurate analogy of mammoth maturation. This method was compared to Laws (1966),

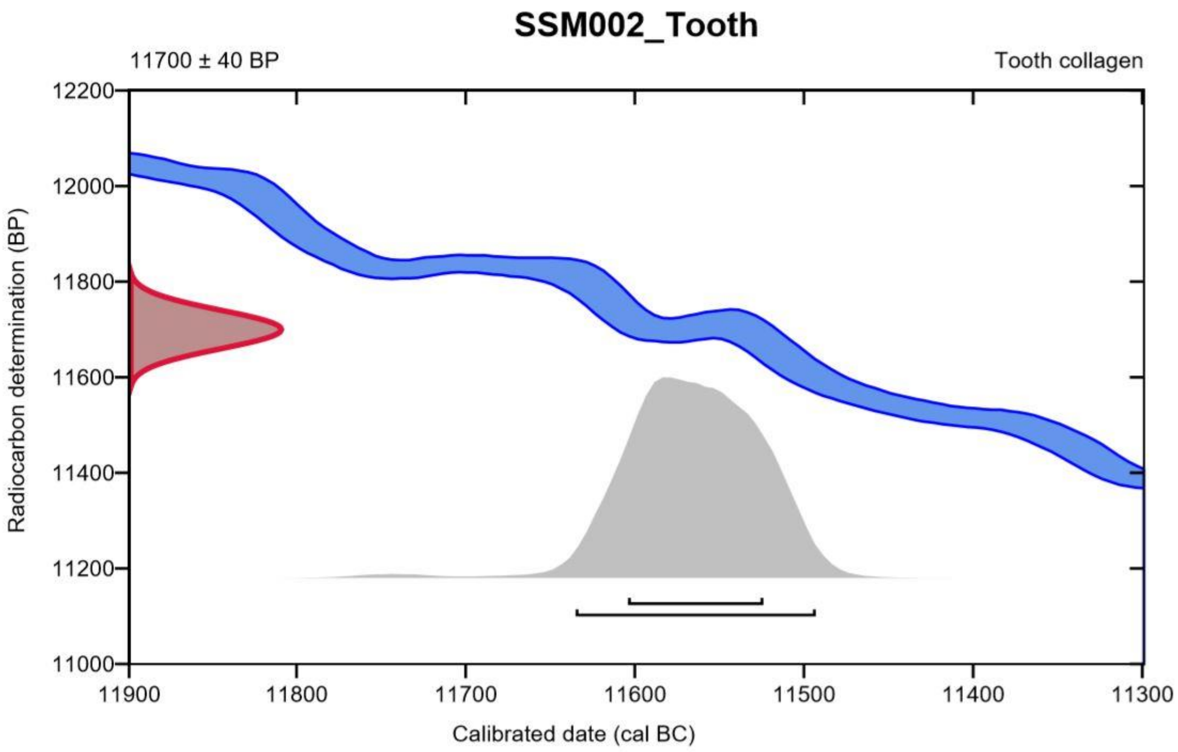
which looks at the molar characteristics of *Loxodonta africana* (African Elephant), a distal relation to mammoths.

Taxonomic identification of Cola was determined two ways: 1) By using measurements of molar characteristics adapted from Maglio (1973) and Lister (2017), and 2) By extracting mtDNA from a tooth sample. Measurements of Cola's molar included length (L), width (W), height of crown (H), enamel plate count (P), lamellar frequency (LF), and hypsodonty index (HI), with all measurements taken in millimeters. The LF was calculated on an average of 6 measurements taken from the upper, middle, and lower portion of the crown on both the lingual and buccal side. The HI was calculated as HI = H/W x 100, or height of the crown as an expression of width standardized to a length of 100 mm (3.9 in). These measurements were obtained using a digital caliper on the upper-right fourth molar (M4). No estimation of missing plates was required due to the presence of the anterior-most root with 5 correlated plates. There are two lower molars, but at the time of this writing, preservation efforts were still ongoing, and they remain cemented into the mandible and are unable to be extracted and described. The M4 was then compared between holotypes or neotypes of *M. primigenius*, *columbi* and *jeffersoni* (Lister and Sher, 2015; Lister, 2017).

Elemental composition analysis provided guidance on where to sample for mtDNA. The anterior talon of the upper fourth molar was sent to the University of California, Santa Cruz Paleogenomics Lab for analysis. Extraction and processing were performed according to Dabney and others (2013). Results were compared to clades described in Enk and others (2016) to assign Cola to a haplogroup. For a more detailed procedure used, please see Appendix B.

Throughout all procedures and sample collection, nitrile gloves were worn to prevent contamination. Necessary care and precautions were always considered including wearing additional PPE such as goggles and face masks when required and sterilizing all sampling equipment and receptacles. When drilling into the bone, the periosteum was discarded to minimize contamination.

Figure 2.2: Conventional radiocarbon age for Cola is 11,700 +/- 40 BP



RESULTS

Date and Inventory

Radiocarbon dating confirmed the Late Pleistocene relative age derived from the intital gastropod identification in 1966 and yielded a date of 11,700 +/- 40 years old (Fig.

2.2). When testing the femur for original material, the results indicated that there was none remaining. Dating results were successful in sampling the molar instead. A total of 249 bones and fragments have since been processed and itemized (Appendix D).

Age and Size

Since the measured length of Cola's humerus was 90.17 cm (35.5 in), the height from foot to shoulder was determined to be 2.65 m (8.7 ft). Cola's tusks were approximately 2.64 m (8.6 ft) long. Since adult *Mammuthus primigenius* and *columbi* reached the height of about 3.35 - 3.96 m (11 - 13 ft), with tusks reaching lengths of about 3.6 - 4.8 m (13 - 16 ft) in males and 1.5 - 1.8 m (5 - 6 ft) in females (Lister and Bahn, 2007), Cola was likely a juvenile or very young adult at the time of its death (Table 2.1, Figure 2.3). Table 2.2 also supports this observation.

The molar characteristics also match the smaller size of mammoth features as indicated in the limb bone and tusk measurements. Due to the distinct appearance of the first three sets of dairy molars, these can be ruled out by morphological comparison of Cola's molars to those presented in Roth and Shoshani (1988). Cola had its first adult molar set. A comparison of measurements between Cola's molars and values listed in Roth and Shoshani (1988; Table 2.1) and Lister (2017; Table 2.3 and Fig. 2.3) display the greatest overlap for the values given for the 4th molar set (M4), or the first set of adult molars. This determination was based off the overlap in values reported for M4's of *E. maximus* (Table 2.2) and the reduced morphometric values of Cola's molar compared to the M6's of different mammoth genera (Figure 2.3; Table 2.6; Lister, 2017). With Cola on its 4th molar set, it was most likely

15 – 28 years of age, but the 6 worn enamel plates on the M4 implies that Cola was probably towards the older end of this estimate, possibly 18 – 28 years old (Table 2.4).

Table 2.1: Comparison between Cola and adult Columbian Mammoth standards of average body size and tusk length (in meters and feet)

Unit Being Measured	**Full Grown Mammoth**	**Cola**	**Implications**
Humerus Length	134.72 cm (4.4 ft)	90.17 cm (2.95 ft)	**Cola was not yet fully grown.**
Height from Head to Shoulder	3.96 m (13 ft)	2.65 m (8.7ft)	
Tusk Length	Female: 1.52-1.83 m (5-6 ft) Male: 3.96-4.88 m (13-16 ft)	2.62 m (8.6ft)	**Cola was a male mammoth since the tusk length already exceeds a female tusk length.**

Table 2.2: Comparison of measurements listed for the 4th molar (upper molars) in Roth & Shoshani (1988) to the characteristics measured on the upper molar of Cola.

Measurements	**Roth & Shoshani**	**Cola**	On average, the measurements of Cola's upper molars most closely align with the measurements of an elephantid's **4th molar set**, suggesting that Cola had been **between 18 and 28 years old**.
Length	150-200 mm	278 mm	
Crown Height	145-185 mm	154 mm	
Molar Width	50-80 mm	82.82 mm	
Plate Count	14-17	19	

The Roth and Shoshoni (1988; Table 2.2) method shows age estimates by correlating the age ranges in which for the fourth molar set is present with the average ages at which the epiphyses finish fusing in both male and female proboscideans (Lister, 1999; Fig. 2.3). Since an analysis of Cola's front and rear limb bones has revealed that none of the epiphyseal plates had yet fully fused at Cola's time of death, together, these age calculations and observations provide an assigned age range of Cola at 18 to 28 years old when it died.

Taxonomy

Description of Crania Characteristics

As part of this thesis, attempts were made at reconstructing the Soda Springs mammoth skull using methods outlined above for the purpose of systematically describing it. Efforts are still underway, and at the time of this writing only 3 portions of the crania have been identified (Figure 2.3). Site photos of Cola's skull prior to fragmentation were used for description.

-Site Photos Analysis:

FIGURE 2.3: SITE PHOTOS OF COLA'S CRANIUM.

While characteristics described based on site photos are tentative, the characteristics observed align with those reported for *M. jeffersonii* in Osborn (1942). The skull appears to be broader and less brachycephalic than *M. primigenius*. The orbital sockets are prominent, and the narial opening appears to be broad and open compared to the narrow opening of *M. primigenius.* The tusk sheaths are also widely divergent distally, with the tusk erupting from the sockets away from the skull. Each of these characteristics either align with observations made from the holotypes of *M. columbi* and *M. jeffersoni*.

-Maxilla:

The maxilla is approximately 60%-70% complete. There are 3 large fragments and 6 smaller fragments have been adhered together (Figures 2.3), and an additional 14 fragments have been identified, but have not been adhered to the larger pieces until more intermediary pieces are found.

-Tusk Sheaths/Premaxilaries

Tusk sheaths are the second most complete portion of the skull currently. Approximately 40%-50% complete, both the proximal the proximal and distal ends of the left and right tusk sheath have been identified (Figures 2.3), but until intermediate pieces are found both are discontinuous. Maximum estimated length of tusk sheaths is 73.5 cm but are presumed to be longer due to missing fragments. Proximal ends of tusk sheaths attach to the front of the maxilla (Figure 2.3), but have not been attached until proper support can be constructed to accommodate the 40-degree slope from the maxilla to tusk sheath transition. In total, 12 fragments have been identified for the proximal end of the tusk sheaths, and 19 fragments have been identified for the distal end of the tusk sheaths (12 fragments for left, 7 for right). An additional 23 fragments have been tentatively identified as tusk sheath material, but their relative position has yet to be discerned. Based on site photos showing the cranium prior to fragmentation (Appendix C), the tusk sheaths are flared and slope down towards the sides. The tusk sockets themselves are rotated anteriorly and point out and down relative to the skull.

Table 2.3: Description of UISSM-001 Tusk Sheath/premaxillaries according to Todd (2010)

(Premaxillaries/Tusk Sheath)		Description
45. Alveolar border of premaxillaries	1	Slopes Down Laterally
46. Premaxillaries	1	Flared Anteriorly
54. Tusk sheaths	0	Rotated Anteriorly
59. Premaxillaries	0	Directed out and Forward

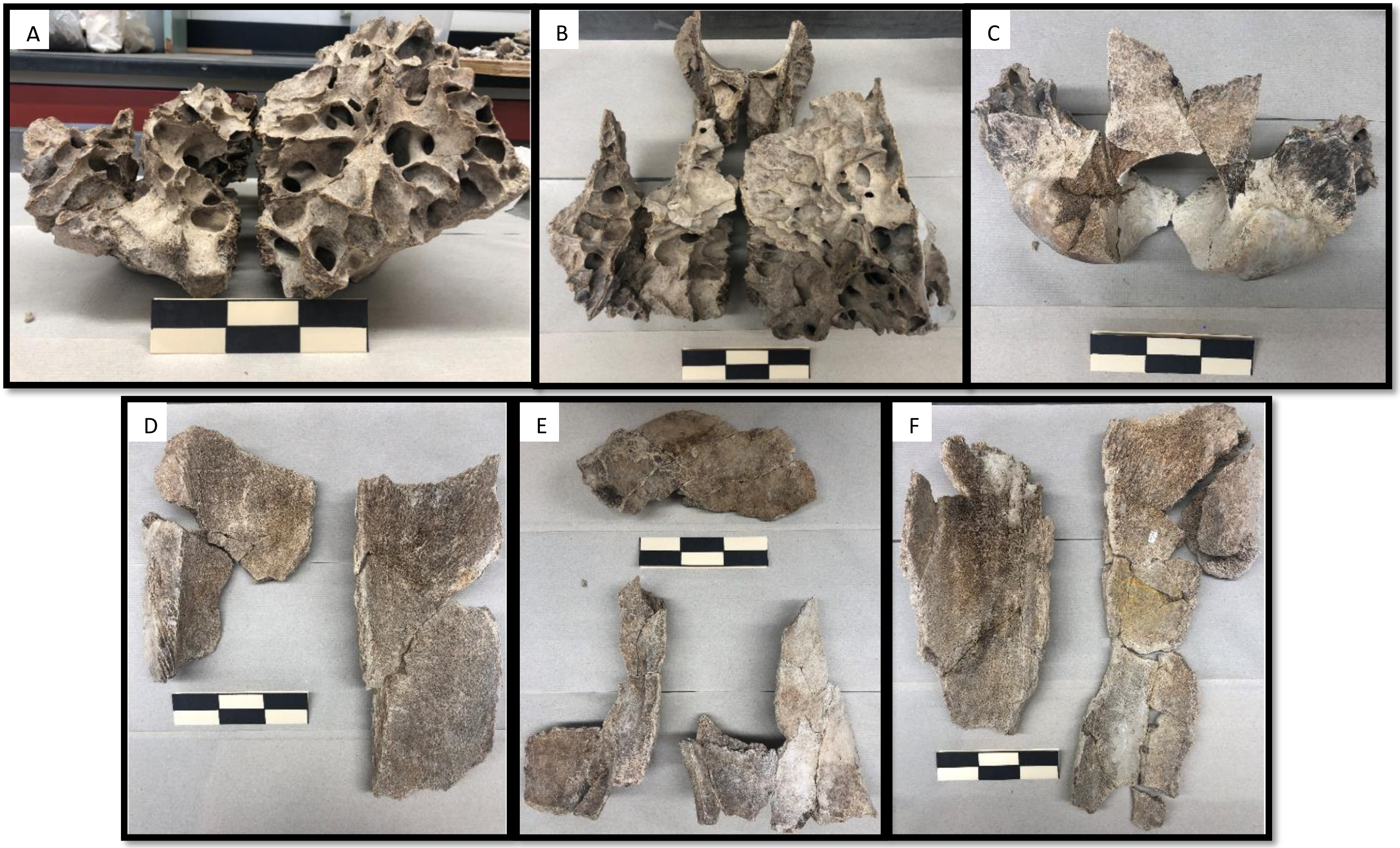
-Occipital

7 fragments of the occipital plate have been identified, and are primarily associated with the occipital condyle (Figure 2.3). The occipital plate is approximately 20% complete. Occipital condyles appear bulbous, bean shaped, and are positioned in line with the end of the tooth.

Table 2.4: Description of UISSM-001 Occipital Condyles According to Todd (2010)

(Crania)	Rank	Description
42. Occipitals	1	Flat
47. Shape of occipital condyles	0	Bean Shaped
56. Position of occipital condyles to tooth row	1	Positioned In line with end of Tooth Row

Figure 2.4: Cranial Elements of Cola. A: Frontal View of Maxila. B: Dorsal View of Maxila. C: Occipitals. D: Distal Portion of Left Tusk Sheath. E: Proximal Portions of Tusk Sheath (Left and Right). F: Distal Portion of Right Tusk Sheath. Scale bar is 15 cm in 5 cm Increments



-Mandible

While requiring some preservation, the mandible of the mammoth is relatively complete, and displays the shorter corpus, high ascending ramus, and downturned symphysis representative of more advanced Proboscidea (Maglio, 1973). Being approximately 90% complete, the mandible displays the best suite of potential taxonomic characteristics (Table 2.5). The mandibular condyles are ovoid in shape and even with each other, with an inward curving ramus. The symphysis is relatively short and the trough is U-shaped. The coronoid process is long and extends to cover the posterior half of the molar. The ramus ascends from the corpus at an acute angle and is even in length with the corpus.

-Other Notes

52 additional fragments have been associated with one or more of each other, but their relative placement and association within the Soda Springs mammoth's skull remains uncertain. In total, 144 fragments have been either identified, or glued to other fragments. Assuming the 826 fragments associated with the mammoth's skull, which was approximately 90%-100% complete at the time of excavation, indicates that approximately 20% of the mammoth's skull has been identified and catalogued. Where applicable, taxonomic characteristics were described according to Todd (2010).

Using photographs of the site (Appendix C) and description of cranial fragments, Cola's skull morphometrics appear to correlate with those reported in Osborn (1942). The anterior narial opening is broad and pronounced at the top and the tusk sheaths are flared and uneven in comparison to those of *M. primigenius.* The acute angle between the corpus and ramus and short, deep symphysis also align with Osborn's (1942) description. While similar to Osborn's (1922) type specimen, the lack of in depth quantitative analysis of cranial morphology and how ontogeny affects skull morphometrics means that attribution of these characteristics to a specific taxa is tentative. Given the degree of overlap in mammoth's molar morphometrics, a more comprehensive study of mammoth crania across ontogenic and geologic time is required.

Table 2.5: Characteristics of UISSM-001 Mandible According to Todd (2010)

(Mandible)	Rank	Description
66. Mandibular condyle shape	1	Oval Shaped
67. Condyle surface	1	Even/Parallel to each Other
68. Ascending rami	1	Curve Inward
69. Mandibular symphysis	1	Directed down
70. Length of mandibular symphysis	2	Short
71. Shape of symphyseal trough	1	U – Shaped
73. Position of coronoid process relative to maximum length of corpus	0	Posterior
75. Angle of ascending ramus relative to corpus	1	Acute angle
76. Height of ascending ramus relative to maximum length of corpus	1	Ramus height equal to corpus length

-Molar Characteristics

The molar characteristics of Cola appear intermediate to *M. columbi* and *M. primigenius.* Cola's overall plate count is similar to the upper limits reported for *M. columbi*, but the lamellar frequency is closer to that of *M. primigenius* (Table 2.6; yellow and green shaded cells). Given that Cola was a sub-adult, subsequent molar sets would show an increase in overall plate count and lamellar frequency (Lister, 2015). Cola's final molar set would most likely display taxonomic characteristics similar to the *M. primigenius* neotype or *M. jeffersonii* holotype. Cola's estimated shoulder height of 2.65 m (8.7 ft), and lack of epiphyseal fusion implying that if it had not died it would have grown larger, implies that Cola is most likely not a woolly mammoth due to their average maximum height of around 3m (9 ft).

According to Article 23.8 of the International Commission on Zoological Nomenclature (ICZN) the use of a taxonomic name to denote a hybrid is considered synonymous to the parental names of both species. While *M. jeffersonii* is not a valid taxon, it is the opinion of this author that it should be retained for the use of this study to denote mammoths whose taxonomic characteristics are intermediary to those reported for *M. columbi* and *M. primigenius* type specimens.

Comparison of Cola to other specimens from southeastern Idaho also yields interesting results (Table 2.7). While Cola is still a sub-adult, its molar morphometrics align with reported values of several American Falls specimens. Despite pre-dating (31.3 Ka +/- 2.3 Ka – 21.6 Ka +/- 700) the Soda Springs locality (11.7 Ka +/- 40), mammoth molars from both displays a high plate count, lamellar frequency, and hypsodonty index. Of note, IMNH 60004/16422 was described by Hopkins (1969) as *M. jeffersonii,* but was later assigned to *M. columbi* by Pinsof (1993) and displays the greatest amount of overlap with Cola's molar characteristics. This supports the assertion that Cola belonged to a regional population whose molar morphometrics are influenced by environmental stressors, and does not necessarily denote separate taxa.

Table 2.6: Molar measurements of Cola compared to the holotypes of the three *Mammuthus* taxa in North America during the Pleistocene-Holocene. Holotype Specimens' Morphometrics Measured from M6 molars.

Collection	**Taxonomy***	**Plate #**	**Molar Length (mm)**	**Crown Height (mm)**	**Molar Width (mm)**	**Enamel Thickness (mm)**	**Lamellar Frequency**
Cola	*M. jeffersonii*	19	278	154 (plate 7), 262.77 (plate 15 [est. 58.06]	82.82 (plate 7)	2.38 (plate 7)	8
AMNH-13707	*M. columbi (holotype)*	19	N/A	197	102	2.0	6.67
ZIN-27105	*M. primigenius (Associated to neotype locality)*	26	N/A	109	N/A	1.6	9.32
AMNH-10457	*M. jeffersonii (holotype)*	31	355	>190	117.5	1.6	8.4

*Holotype Measurements were Obtained from Lister (2017). Measurements for the *M. primigenius* specimen was obtained from Lister and Sher (2015). Yellow highlights are characteristics of Cola that overlap with *M. columbi*, and green *M. jeffersonii*.

Table 2.7: Comparison of UISSM-001 molar characteristics (Maglio, 1973; Lister and Sher, 2015) to reported morphometrics of the American Falls Assemblage (Pinsof, 1993). American Falls specimens have been radiocarbon dated to 31.3 Ka – 21.5 Ka (Agenbroad, 2005). MX/ = Upper Molars; M/X = Lower Molars. Green highlights are characteristics of specimens that overlap with Cola.

Specimen Number	Species	Molar Set	Plate Number	Length	Width	Enamel thickness	Height	Lamellar Frequency	Lamella Length	Hypsodonty Index (HI)	Lamella Length Index (LLI)	Enamel Thickness Index (ETI)
IMNH 48001/216	*M. columbi*	M2/	(Left) 12 (Right) 13	(Left) 243 (Right) 245	(Left) 114.5 (Right) 111.2	(Left) 1.7 (Right) 2.0	(N/A)	(Left) 6.5 (Right) 6.5	(Left) 4.94 (Right) 5.31	(N/A)	(Left) 4.31 (Right) 4.78	(Left) 1.48 (Right) 1.8
IMNH 35015/15113	*M. columbi*	M3/	23	305	87.6	2.4	170.5	7.5	7.5	194.63	8.56	2.74
IMNH 38001/7377	*M. columbi*	M3/	20	283	89.1	2.4	198	7	7	222.22	7.86	2.69
IMNH 35015/16980	*M. columbi*	M1/	10	97.5	45.7	1	70.2	11e	10.25	153.61	22.43	2.19
IMNH 35015/16883	*M. columbi*	M2/	16	194	60.1	1.8	114.1	8.5	8.24	189.85	13.71	3

IMNH 65003/24687	*M. columbi*	M2/	12	182.1	78.1	1.5	106.6	6	6.59	136.49	8.44	1.92
IMNH 81009/30892	*M. columbi*	DP/2	3	16.7	11.6	(N/A)	(N/A)	(N/A)	17.96	(N/A)	154.81	(N/A)
IMNH 81009/30892	*M. columbi*	DP/3	8	63.8	28.7	1.2	(N/A)	(N/A)	12.53	(N/A)	43.66	4.18
IMNH 35015/16123	*M. columbi*	DP/3	9	61.3	28.9	1.5	(N/A)	(N/A)	14.68	(N/A)	50.8	5.19
IMNH 35004/287	*M. columbi*	M/1	10	121.3	50.1	1.1	(N/A)	10	8.24	(N/A)	16.45	2.2
IMNH 35015/18149	*M. columbi*	M/1	9	119.3	45.7	1.1	(N/A)	9	7.5	(N/A)	16.41	2.41
IMNH 49001/300	*M. columbi*	M/2	12	226	79.5	2.8	136.7	6	5.31	171.95	6.68	3.52

IMNH 65003/32220	*M. columbi*	M/2	11	172.8	73.3	1.5	73	5.5	6.37	99.59	8.69	2.05
IMNH 35015/16911	*M. columbi*	M/3	13	220	86.1	2.2	(N/A)	6	5.91	(N/A)	6.84	2.56
IMNH 48001/85	*M. columbi*	M/3	10	196	80.5	3.2	(N/A)	6	5.1	(N/A)	6.34	3.98
IMNH 58004/2592	*M. columbi*	M/3	20	257	80.5	2.7	163.8	7	7.78	203.48	9.66	3.35
IMNH 60004/16422	*M. columbi*	M/2	(Left) 8 (Right) 8	(Left) 107 (Right) 107	(Left) 77.8 (Right) 83.9	(Left) 1.9 (Right) 2.4	(N/A)	(Left) 8 (Right) 8	(Left) 7.47 (Right) 7.47	(N/A)	(Left) 9.6 (Right) 8.9	(Left) 2.44 (Right) 2.86
IMNH 60004/16422	*M. columbi*	M/3	(Left) 13+ (Right) 14+	(Left) 163+ (Right) 171+	(Left) 76.5 (Right) 76.4	(Left) 2.1 (Right) 3.0	(N/A)	(Left) 8 (Right) 8	(Left) +7.98 (Right) +8.19	(N/A)	(Left) 10.43 (Right)10.72	(Left) 2.74 (Right) 3.93
UISSM – 001-COLA	*M. jeffersonii*	M1/	19	278	82.82	2.38	154	8	6.83	185.95	8.25	2.87

Table 2.8: Comparison of Mammoth Morphometrics for Regional Populations. All measurements except those reported for SE Idaho are from Widga, et al. (2017). N = Sample size, P = Plate number, L = Length, H = Height, W = Width, ET = Enamel Thickness, LF = Lamellar Frequency, LL = Lamella length, HI = Hypsodonty index, LLI = Lamella length index

Mammoth Species	‘Cola’ *M. jeffersonii*	*M. columbi (American Falls, Idaho)*	*M. columbi (Great Plains)*	*M. columbi (Mexico/Southwest)*	*M. columbi (West Coast)*	*M. columbi (eastern US)*	*M. jeffersonii (eastern US)*	*M. primigenius*
N	1	7	43	42	4	16	27	79
P	19	16.5	21	19.4	18	19.8	23.4	25.2
L	278	227.86	278.1	285.7	166	340	285.4	280.9
H	154	177.43	189.1	205.4	170	228.4	178.1	168.5
W	82.82	82.39	101.8	97.6	82	106.47	101.6	95.7
ET	2.38	2.54	2.1	2.7	(N/A)	2.6	2	1.6
LF	8	7	6.8	6.6	6.1	6.2	7.6	8.4
LL	6.83	7.07	14.9	15.4	16.5	16.2	13.5	12.1
HI	206.78	206.78	189.6	213.7	205.9	218.5	178	181.5
LLI	8.25	8.63	13.8	15.7	20.5	14.7	13.5	12

FIGURE 2.5 ANALYSIS OF MOLARS AND TUSKS. A: VIEW OF COLA'S LOWER LEFT JAW. B: CHARACTERISTICS OF MAMMOTH MOLARS SHOWING PLATE, LAMALLAR FREQUENCY, AND ENAMEL THICKNESS (MODIFIED FROM ROTH AND SHOSHANI, 1988). C-D: ASSESSMENT OF MOLAR PARAMETERS. E-F: TUSK MEASUREMENTS

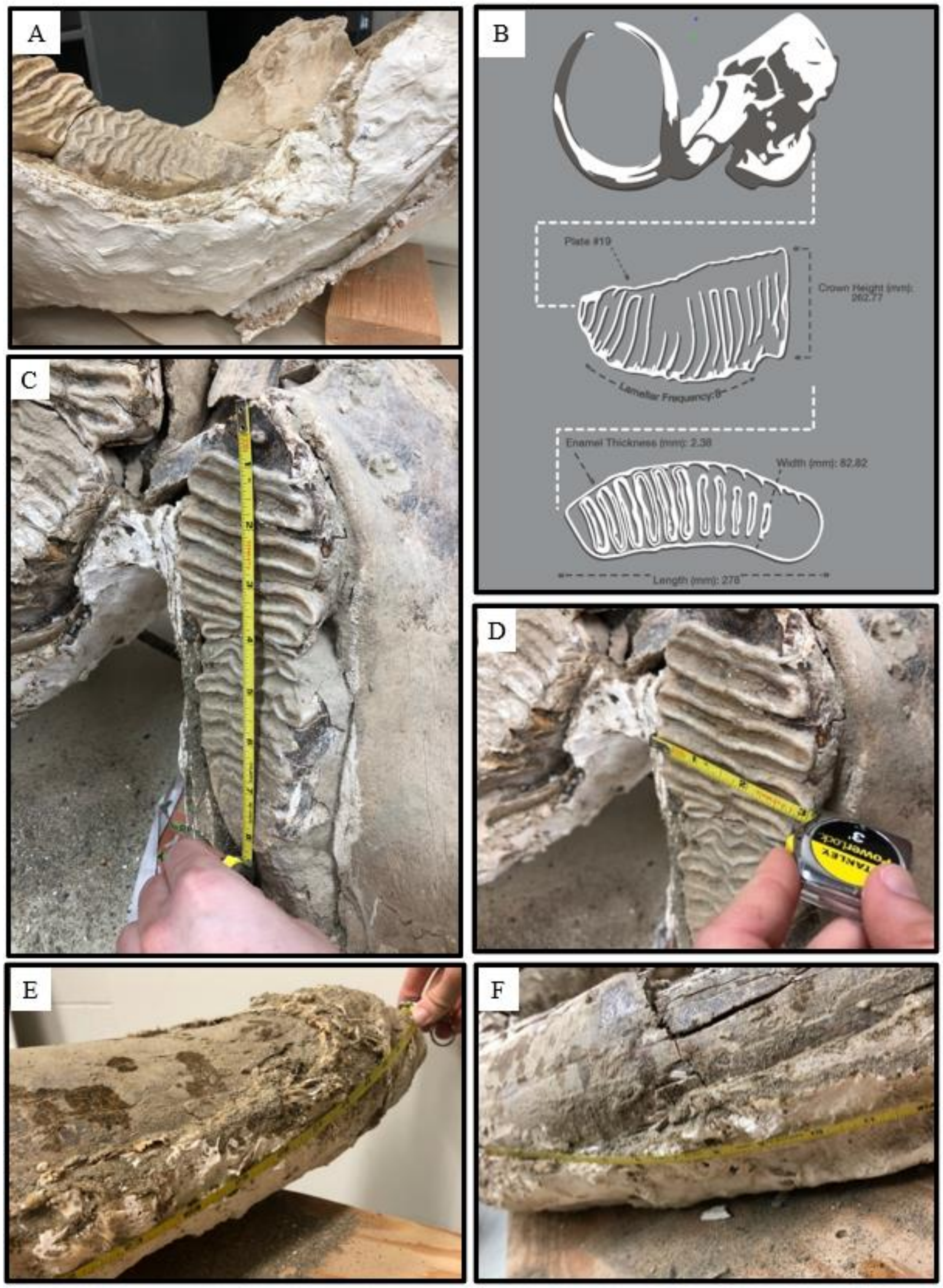


Table 2.9 Age (in years) at which proboscideans lose each set of molars, according to Laws (1966)

Molar Set	**Age of Proboscidean**	**Context**
1	2	Cola's size and tusk length suggests it was older than 6 years, but younger than 30. This is confirmed by the lack of complete fusion in the limb bones (Fig. 2.4). Measurements of the molars suggest that Cola was on its 4th molar set and provides an **estimated age of 18-28 years old.**
2	6	
3	13-15	
4	28	
5	43	
6	65	

DISCUSSION

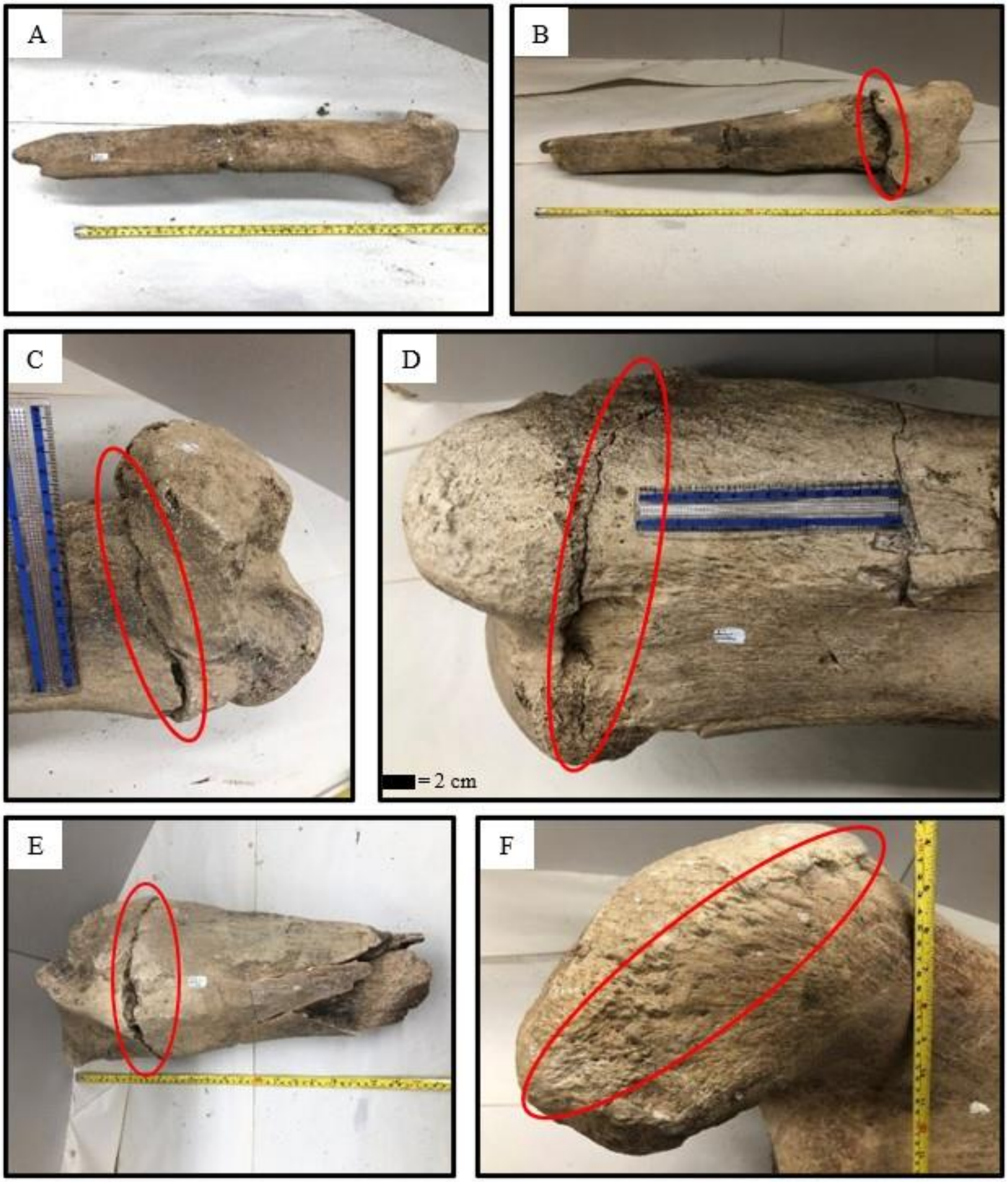
Taxonomy

It is possible that Cola was a *M. jeffersonii* from the molar measurements but since there is overlap in the measurement parameters (Table 2.6), there was also a possibility that it was a *M. columbi*. This study highlights the uncertainty in taxonomic assignment of North American mammoths using molar measurements. While Cola displays a higher lamellar frequency similar for those reported for the type specimen of *M. jeffersonii* and neotype of *M. primigenius*, the plate number is still characteristic of *M. columbi*. While these characteristics were used to make the taxonomic assignment, the amount of overlap in value ranges presented for each taxa's molar measurements causes uncertainty. This issue is compounded based on the ontogenetic determination that Cola was most likely a sub-adult based on molar and post-cranial skeletal characteristics.

Molars display different characteristics that are dependent on the tooth's state of wear and the age of the mammoth and can lead to misinterpretation of a mammoth's species (Lister and Sher, 2015). This issue is compounded due to taxonomic characteristics established from type specimens are related to the last adult molar set (M6). Cola was determined to be on its first set of adult teeth, or the 4th molar set (M4), and a direct comparison to type specimens could yield an incorrect taxonomic assignment. Mammoths, like elephants, experience a serial progression towards more derived molar characteristics in subsequent molar sets (Roth and Shoshani, 1988), and it is possible that Cola would display a higher degree of advancement if it had reached maturity.

It has also recently been proposed that mammoths occupying certain biogeographic ranges also display variability between members of the same species. While most mammoth occurrences in Idaho have not been taxonomically described according to current morphometrics, Widga and others (2017) observe biogeographic variation between mammoth occurrences in the western and eastern United States. Mammoth occurrences of the Great Plains, west coast, and southwest are typified by molars that display more basal characteristics in their overall plate count and enamel thickness. Mammoth occurrences from the midwest to the east coast, however, appear more derived, with higher plate counts and thinner enamel. While a more detailed description of mammoth collections from Idaho, and by extension the Pacific Northwest is required, it appears that Cola displays characteristics similar to other western United States populations of *M. columbi* (Widga et al., 2017).

Figure 2.4 Assessment of epiphyseal fusion in limb bone fragments with scale. Epiphyses circled in red. A: Full view of proximal radius. B: Full view of distal radius. C: Enhanced view of distal radius (red). D: Enhanced view of proximal humerus. E: Full view of distal region of ulna. F: Enhanced view of proximal region of ulna

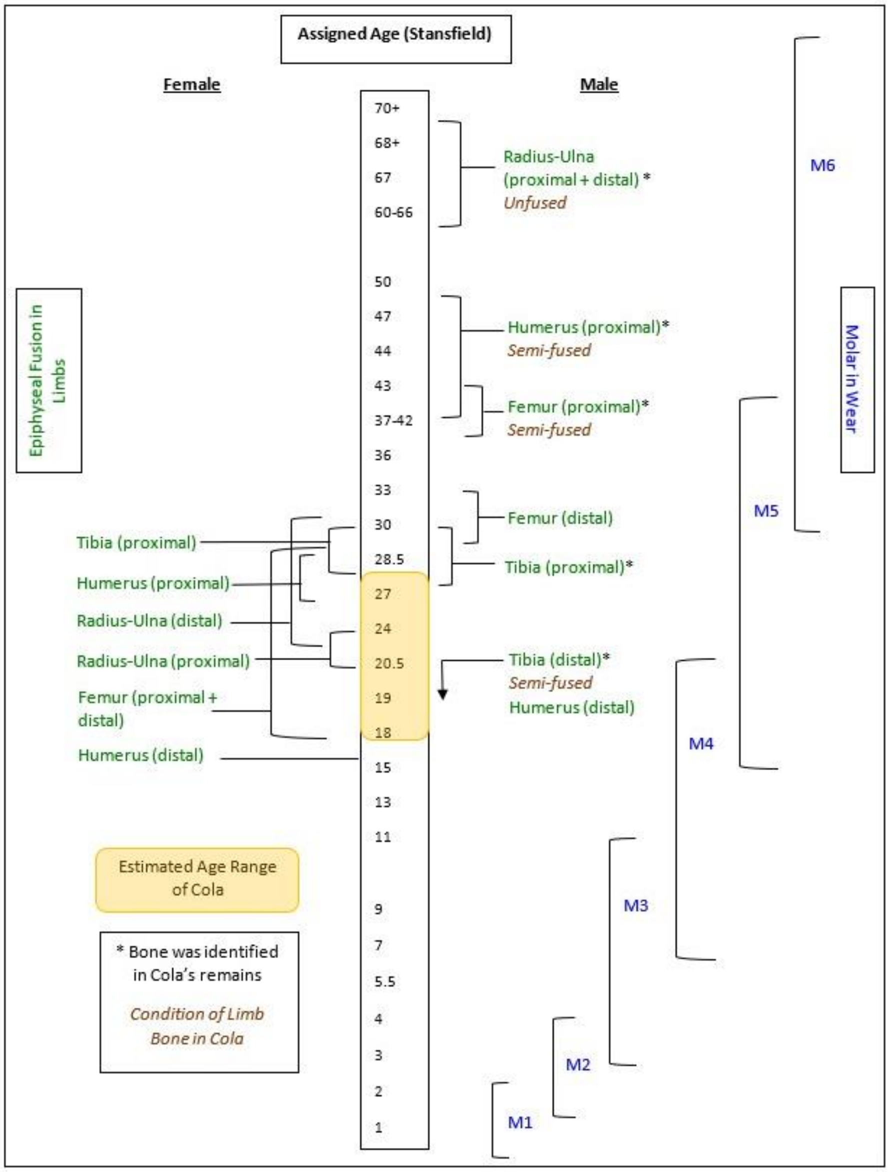


Gender Determination

Although determining with certainty whether Cola was male or female was challenging because the pelvis was severed before excavation, the lengths of the tusks suggest that Cola was male. Although Cola was not fully grown, its tusks were already rather large; the most complete one was measured to be about 2.64 m (~8.6 ft) long. While the tusks of male *M. columbi* have been known to reach lengths of 3.9 m - 4.8 m (12 - 16 ft), on average, they were not much longer than those of *M. primigenius*, which were typically between 2.4 and 3.7 m long (8 - 12 ft). The tusks of females, on the other hand, were typically only 1.5 - 1.8 m (5 - 6 ft) long (Lister and Bahn, 2007). With this knowledge, it can likely be concluded that Cola was a male mammoth since its tusks were already longer than those of the average female even prior to adulthood. There is additionally a higher statistical probability that Cola had been male based on the dominance of male mammoth remains in the fossil record.

Cola's remains included only the skeletal bones found at the site. Mammoths, much like modern elephants, tended to live and travel in groups, therefore, when mammoth remains are discovered, they typically belong to multiple mammoths and are located in close proximity to one another. It would typically be uncommon for a mammoth to be solitary, unless they are males. Modern male elephants are known to disperse from their main family units between the ages of 10 and 15, after which they roam alone or in small groups of other males with looser social bonds compared to those of females (Meyer, 2006). Assuming male mammoths exhibited similar behavior, it would perhaps make more sense that Cola's remains were found relatively isolated from the remains of other mammoths if it had been a male. The nearby Mammoth Site in South Dakota exhibits this point well with approximately 60 individual mammoths excavated and only one determined to be female (Haynes, 2017).

Figure 2.5 Age estimation for Cola based on a correlation of the condition of its epiphyses with prior correlations between molar wear and epiphyseal fusion in male and female specimens of *Loxodonta africana* (modified from Haynes, 2016). Overlap of the age estimate with the fifth molar set (M5) is not being considered in the scope of this paper since measured parameters of Cola's molars aligned most closely with the M4 of the elephantids in other studies, and due to implied phenotypic discrepancies between *Mammuthus* and *Loxodonta*



Age Determination

Evidence suggests that Cola was under the age of thirty because the epiphyses of its limb bones had not finished fusing at the time of death (Fig. 2.4). The epiphyses of male proboscideans finish fusing between 35 and 45 years of age (Lister, 1999; Haynes, 2017). The proximal region of the femur does not finish fusing until the male is about 40 years old, and the proximal region of the humerus does not finish fusing until the male is around 45 years old (Haynes, 2017; Fig. 2.5). Based on the dental measurements, Cola was most likely on its 4th molar set. Given Cola's estimated shoulder height of 2.65 meters (~8.7 ft), and the six worn enamel plates, Cola was most likely a male in his late teens or early twenties: between 18-28 years old.

Because the tusk has a more homogenous anatomy than the tooth and given that the tusk is highly and easily fragmented at this point in time, little to no recoverable organic materials are left in the tusk. The degradation of proteins, lipids, and genetic materials in the bones have likely mirrored that of the tusk. The tooth, on the other hand, demonstrated more promising results of biomolecular preservation. The heterogeneity of elemental composition of the tooth may be explained by the protective barrier of enamel disrupting fossilization and degradation of the interior tooth (Trueman and Martill, 2002; Kendall et al., 2018).

Hybridization

Genetic testing of Cola's molar revealed that this mammoth belonged to the haplogroup F population of North American mammoths. Haplogroup F is the more primitive group of mammoths, associated with their initial migration to the continent approximately 1.5 Ma (Figure 2.6). This is consistent with sampling from mammoths of the Great Plains and West Coast (Enk, et al., 2016), most likely due to radiation from Idaho and Montana. The presence of MtDNA from *M. primigenius* in all Late Pleistocene clades also implies introgression between all populations in North America.

Cola's relationship to previously sampled specimens assigned to *M. jeffersonii* implies hybridization*,* but a more comprehensive genetic analysis would be required to confirm. While some specimens of *M. jeffersonii* have been confirmed as hybrids, it is not likely that all specimens are. Due to the large amount of introgression and gene flow between migrating populations of mammoths there is no clear delineation between mammoth species. Most specimens from Enk and others (2016) study were also sampled from the Great Lakes region, where there is clear paleontological evidence for the presence of *M. primigenius* and *M. columbi* in the region. Without fossil evidence for the range overlap between the two species in Idaho, Cola most likely represents a Columbian mammoth whose advanced taxonomic characteristics are a result of environmental pressures.

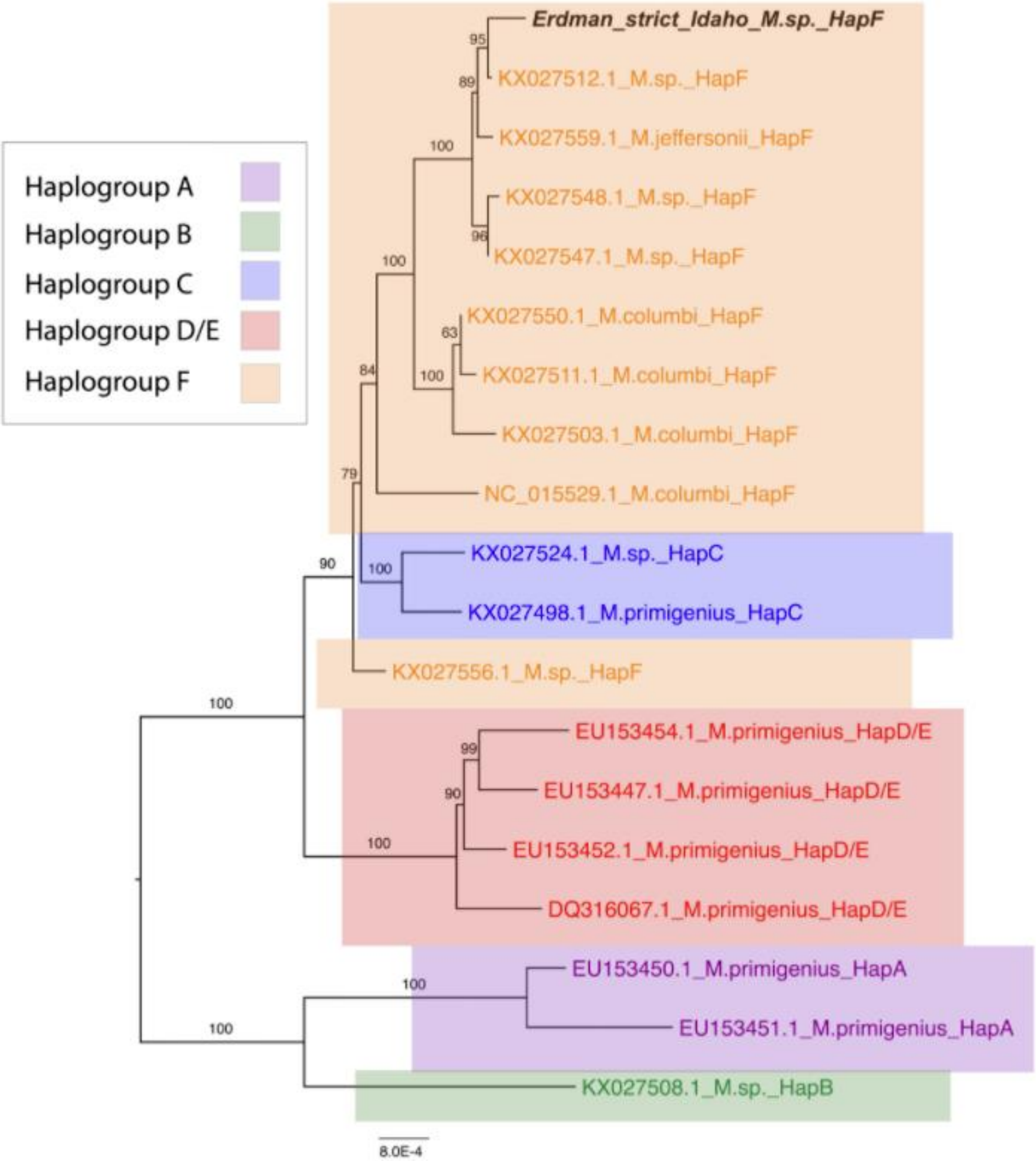
Paleoecology and Paleobiogeography

Cola's depositional age of 11, 700 +/- 40 years places Cola approximately 200 years before the Pleistocene to Holocene transition, and concurrent with the End Pleistocene Megafaunal Extinction event. This places Cola within the last 500 – 1000 years before the official extinction of mammoths on continental North America.The primary driver for this extinction is still debated, although a combination of climate change and anthropogenic influences appears to be the most likely cause (Fischer, 2018). Palynological records (Doernner and Carrara, 2001) indicate a transition from a colder, sedge brush dominated landscape to a higher concentration of spruce and pine and more temperate conditions similar to modern day during this time. It is possible that *M. columbi* and *M. primigenius* began interbreeding in Idaho in an attempt to adapt to the changing environment, but at this time a more comprehensive taxonomic and paleoecological study would need to be undertaken to confirm this.

While the exact driver for mammoth interbreeding in Idaho remains unclear, Cola aids our understanding of mammoths in Idaho at the end of their reign on the continent. Recent work by Widga and others (2017) indicates that mammoths across the continent were comprised of regional populations that underwent frequent introgression. It is possible that certain molar morphometrics used in taxonomic identification of North American mammoths are indicative of environmental pressures on these regional populations.

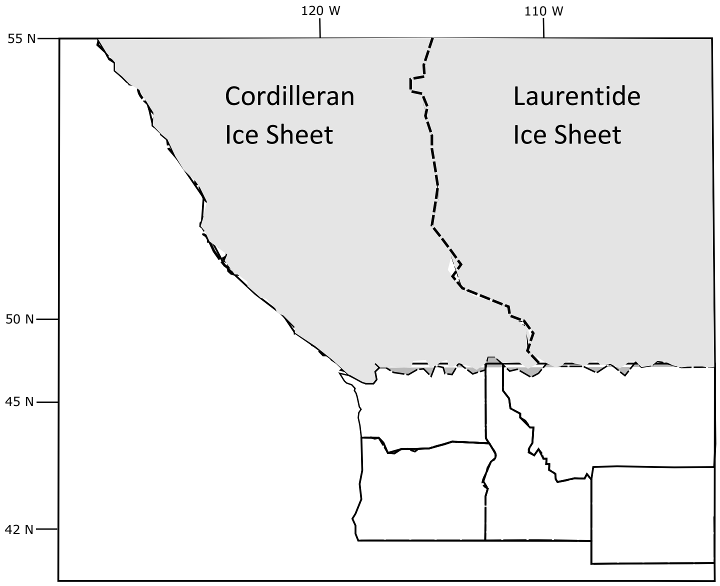
M. jeffersonii may be an outdated taxonomic term based solely on molar morphometrics, as recent genetic studies have shown that Late Pleistocene North American mammoths frequently introgressed with one another. Material described as *M. jeffersonii* most likely represents a regional variant of *M. columbi,* but it is the opinion of the author that this assignment still has use to denote populations were geneflow across both endemic North American mammoth species is present (Fig. 2.6).

FIGURE 2.6 MAXIMUM LIKELIHOOD TREE OF COLA'S (ERDMAN_STRICT_IDAHO_M.SP_HAPF) MTDNA FROM 100 RAXML BOOTSTRAP REPLICATES. COLA'S MTNDA ALIGNS STRONGLY WITH HAPLOGROUP F, WHICH INCLUDES *M. COLUMBI*, *M. JEFFERSONII,* AND UNIDENTIFIED MAMMOTH SAMPLES



Idaho has one of the oldest recorded evidence of mammoth migration into North America. Potassium – argon dating of a mammoth molar excavated from Bruneau, Idaho provided a depositional age between 1.3 – 1.5 Ma (Everden et al., 1964; Agenbroad, 2005). The molar's fragmentary nature makes taxonomic identification difficult however. The Bruneau mammoth does give evidence that Idaho and Northwestern Montana acted as a sweepstake route during this time, as mammoths moved between the Cordilleran and Laurentide ice sheets during interglacial periods (Figure 2.7).

FIGURE 2.7: EXTENT OF GLACIATION DURING THE LATE PLEISTOCENE BEGINNING APPROXIMATELY 2.5 MA



With the exception of the Bruneau mammoth, most excavated specimens in Idaho date to the end of the Pleistocene, from approximately 31.3 Ka – 10.4 Ka (Agenbroad, 2005). The earliest evidence besides the Bruneau mammoth is the American Falls assemblage.

Located along the Snake River plain, the American Falls assemblage contains two fossiliferous horizons. The first is a 15 – 16m gravel bed that overlies the Crystal Spring basalt, and has been radiocarbon dated to 210 Ka – 76 Ka (Pinsof, 1992). The second horizon unconformably overlies the Lacustrine Member and has been radiocarbon dated to 33 Ka – 21 Ka.

With over 5000 fossils excavated across the Sangamon and Wisconsin glacial periods, the American Falls assemblage provides the best paleoecological evidence of the Late Pleistocene. Based on palynological evidence (Bright, 1982) and faunal distribution of fossils (Guthrie, 1982; Guthrie, 1990), four distinct habitats were present in Late Pleistocene Idaho: aquatic/riparian, grassland/step, woodland/brushland, and montane/boreal. These habitats supported a complex megafaunal community including mammoths and mastodons, with niche partitioning allowing for coexistence.

The general paleoecology of southeastern Idaho was a combination of montane/boreal at higher altitudes and grassland around American Falls. Woodlands of juniper, maple, fur, and pine occurring in foothills around mountain ranges, and an aquatic community surrounding the ancestral Snake River (Pinsof, 1992). Colder, wetter conditions persisted throughout the region during the Sangamon, but transitioned to more modern climatic conditions during the end of the Pleistocene. This transition produced an overall reduction in the grassland/step and woodland/brushland environments.

This change in ecology could have driven introgression between *M. columbi* and *M. primigenius* as more grassland gave way to an arid/step environment. *M. primigenius* migration into the area would also have been facilitated by the reduction of the Cordilleran and Laurentide ice sheets post Wisconsin glaciation approximately 25 Ka – 21 Ka. While there is no definitive evidence for *M. primigenius* in Idaho, Tolo Lake offers some tantalizing evidence. During reconstruction of the lake near Grangeville, the lake was drained and the remains of potentially 200 mammoths were discovered. Over the limited time for excavation provided, two mammoths were excavated. One was a mature *M. columbi* and the other, while being mature, was smaller in overall size than a typical Columbian mammoth, and is potentially *M. primigenius* (Akersten et al., 1996; Sappington, 2019), but genetic testing has yet to be applied to refute or confirm this assignment.

From taphonomic analysis, possible trample marks are present, but no rodent or carnivore gnaw-marks, suggesting the mammoths floated far enough offshore to be relatively undisturbed. Dating of the Tolo Lake fossils remains tentative, with pollen evidence suggesting deposition of 4.6 m of lacustrine sediments across a warm-cold-warm interval during the Wisconsin. Radiocarbon dating of bone and carbonate at the site yielded a depositional age of 5.1 Ka – 4.3 Ka, but has been presented as potentially erroneous due to the presence of mammoths post-dating the Megafaunal Extinction event (Sappington, 2019). Unfortunately no research has been conducted since the 1994 field season when excavation stopped and the lake was filled back in with water, and further studies need to be undertaken to make any substantial inferences based on the fossil assemblage.

Apart from Tolo Lake and the Soda Spring mammoth, specimens dating near the end of the Pleistocene are less abundant in Idaho (Figure 2.1). Sites such as Owl and Rattlesnake caves, contemporaneous to Soda Springs (Figure 2.1) have unearthed *Mammuthus sp.*

fragments, but none provide an indication of taxonomy. In Washington, mitochondrial analysis has been utilized on remains excavated from Port of Clarkston and Colpen Springs, with the Colpen Springs mammoths indicating hybridization (Karpinski, 2014; Gough et al., 2017; Sappington, 2019).

Parallels between the paleoecology of Idaho and the Great Lakes Region can be drawn. Mastodons and mammoths are observed occupying similar niches in each locality, with mammoths supported by grassland and aquatic flora (Pinsof, 1992; Yansa and Adams, 2012). Mastodons of Idaho differ from their Great Lakes relatives in preferring high altitude, spruce dominated forests over browsing from scattered forests and wetlands around the lakes in the region (Pinsof, 1992; Yansa and Adams, 2012). Both communities probably faced the same ecological stressors as the climate warmed approximately 14.6 Ka – 12.9 Ka (Bjorck et al. 1998; Yansa and Adams, 2012) with the reduction of grassland environments pushed mammoths and mastodons in competition of resources.

CONCLUSION

Here, it was determined that the UISSM-001-COLA specimen was most likely a male mammoth approximately 2.65 m (8.7 ft) tall, between 18-28 years old, living 11,700 +/- 40 years ago. Cola was one of the last mammoths to live on mainland North America apart from potential refugia environments such as the Great Lakes (Yansa and Adams, 2012). Cola represents an interesting discovery near the end of mammoths’ reign in North America. While the implications of mammoth hybridization are still not completely understood, it might represent interactions between distinct mammoth populations in response to the changing climate of the time. Whether this interbreeding was a direct result of climatic pressures remains unclear, but Cola provides direct evidence of *M. primegenius* and *M. columbi* interaction in an environment that was beginning to resemble modern conditions. Cola's death and subsequent exceptional preservation provides paleontologists with information about a key component to the ecosystem of Idaho, where mammoth studies have been relatively sparse. Further studies into other mammoth occurrences in the Pacific Northwest will undoubtedly reveal more about the paleoecological and population dynamics of one of the Cenozoic's most eponymous taxa.

Chapter 3: Lesson Plan for deciphering mammoth taxa based on molar characteristics

The Story of Cola, and Mammoths of North America

A “Mammoth” Discovery in Idaho

During the summer of 1966, geologist Robert Jones and Archeologist Alfred Bowers were called to excavate a mammoth from the El Paso Products phosphate mine near Soda Springs, Idaho. While digging a ditch, a bulldozer struck the mammoth’s pelvis, which led to its discovery. While the mammoth remains were initially housed at the University of Idaho, in the early 1990’s Jones donated them to the Palouse Discovery Center where it remained in storage and, was for a limited time on display. Then in 2019 the University of Idaho retained the remains once again.

It was not until the Discovery Center donated the fossil to the University of Idaho that the mammoth could be studied in detail and earn its nickname Cola. Despite having been excavated over 50 years ago, Cola still had many questions surrounding it, one of the most major being “what mammoth species was it?”

Mammoth Species of North America

While you probably already know the Woolly Mammoth, it may surprise you to learn that during the late Pleistocene (the time period that Cola lived in), there were in fact several different mammoth species:

- Woolly Mammoths

The famous woolly mammoth is well understood since we have found mummies frozen in Russian permafrost that still have skin and hair! This species is smaller than the others, reaching 8-10 feet tall at the shoulders, and had a coat of thick hair to protect it in the snow-covered environments it lived in. These mammoths lived primarily in the glacier-covered Canada, but have been found in the more northern areas of the United States.

FIGURE 3.1: ARTIST’S INTERPRETATION OF THE WOOLLY MAMMOTH. FROM OBSERVATIONS OF MODERN DAY ELEPHANTS, PALEONTOLOGISTS HYPOTHESIZE THAT MAMMOTHS LIVED IN HERDS OF FEMALES AND YOUNG, WHILE THE MALES WANDERED AROUND IN A PRIMARILY SOLITARY LIFE. IMAGE FROM: S-MEDIA-CACHE-AK0.PINIMG.COM

- **Columbian Mammoths**

  Less well known than the Woolly Mammoth, the Columbian Mammoth, was actually the dominant mammoth species in the United States and even into Mexico. Larger than the Woolly Mammoth with a 12 ft. shoulder height, the Columbian Mammoth was covered in a fine coating of thin fur similar to today's elephants. It did not need as much insulation as the Woolly Mammoth because it occupied the warmer open grasslands in the U.S. and Mexico at this time.

FIGURE 3.2: ARTIST'S INTERPRETATION OF A HERD OF COLUMBIAN MAMMOTHS. THESE MAMMOTHS LIVED IN AN AREA WITH LESS SNOW AND GLACIATION, AND AS SUCH HAD ACCESS TO FOOD THAT LET THEM GROW LARGE, WITH A FEW HAVING REACHED 15 FEET TALL! IMAGE FROM: MEDIAD.PUBLICBROADCASTING.NET

- **Jeffersonian Mammoths**

This final mammoth was a mystery to paleontologists for the longest time. Only appearing in the late Pleistocene, these mammoths displayed characteristics similar to both Woolly and Columbian Mammoths. It was not until scientists were able to conduct genetic analysis on this mammoth to determine that it was actually a hybrid between the two! Paleontologists are still unsure about why the Columbian and Woolly Mammoth were interbreeding, but it could be linked to their extinction in North America.

FIGURE 3.3: ARTIST'S INTERPRETATION OF A JEFFERSONIAN MAMMOTH. NOTICE HOW SIMILAR IT LOOKS TO THE COLUMBIAN MAMMOTH, WHICH IS WHY IT REQUIRED DNA ANALYSIS TO DETERMINE THIS MAMMOTH'S RELATIONSHIP TO THE REST.

IMAGE FROM: WWW.COBBLEARNING.NET

How do we determine a Mammoth's Species?

While reading about mammoth species in North America you might begin to wonder, how do paleontologists figure out all this information about mammoth species from fossilized bones? While some advances are made from extraordinarily preserved animals, paleontologists can actually determine a mammoth's species solely from their teeth.

Mammoths have four teeth in their mouth, two molars in the upper jaw, and two molars in the lower jaw. While humans only have two sets of teeth throughout their life, mammoths had 6, and are the most likely part of the animal to get fossilized. We analyze several different characteristics of mammoth teeth to determine the species:

-Length

The overall length of the molar itself.

-Width

How wide the molar is. This measurement is usually taken on the top surface of the molar which actually grinds the food, known as the occlusal surface.

-Height

The height of the molar, from the root of the tooth to the top. The height changes across the tooth as most molars are worn at an angle from mammoths grinding their teeth together. Three measurements are usually taken, and can be reported at the position you took it, or an average of the three.

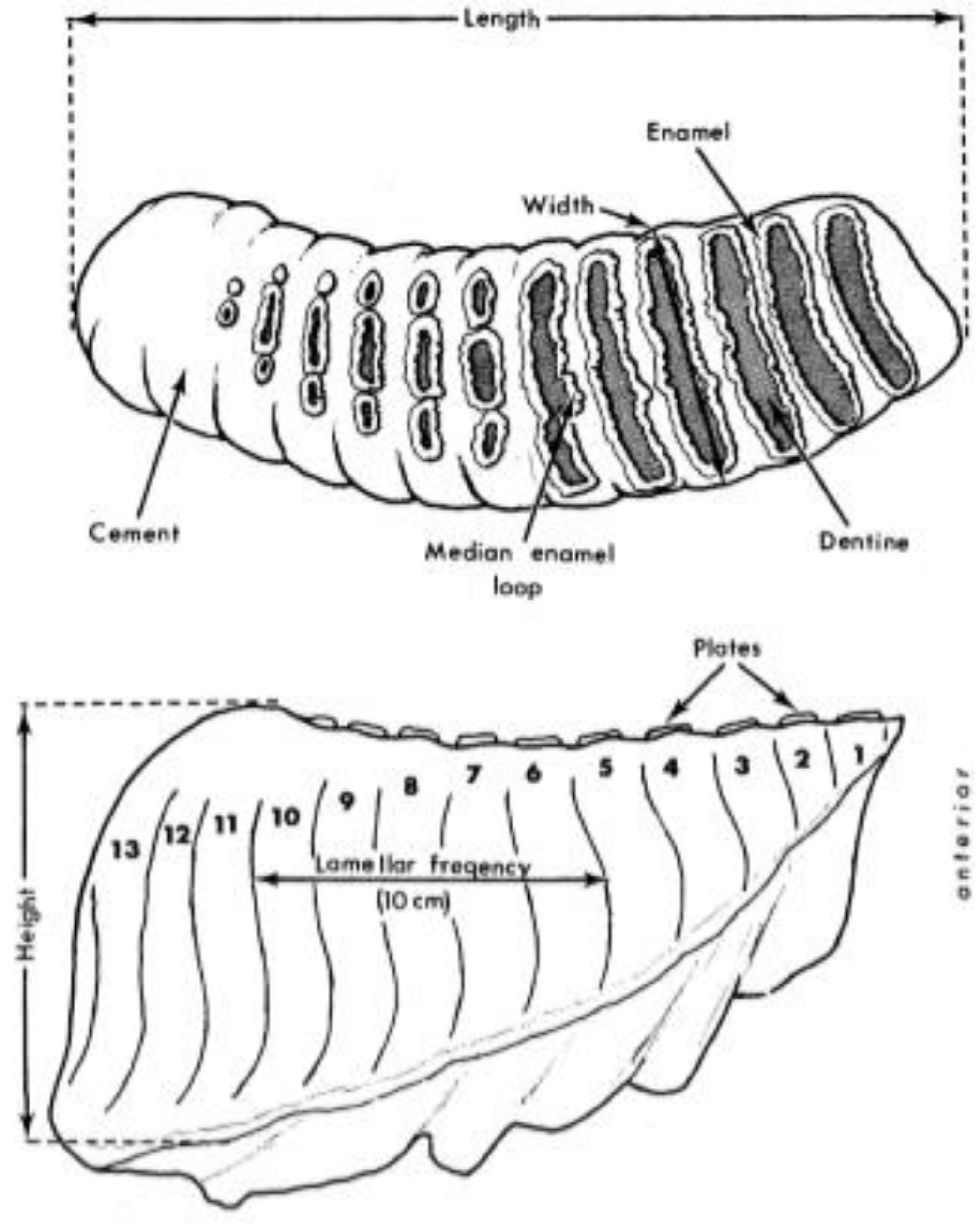
-Enamel Plate Number

Mammoth teeth are comprised of compressed plates of enamel, the hard part of teeth used to chew food. These plates are stacked one in front of the other, and the overall number of these plates present in a molar gives us an idea of the mammoth's species, as well as diet. The enamel plate number is measured by counting the number of enamel plates preserved in the molars, although some may be worn down from chewing and may need to be estimated.

-Lamellar Frequency

The lamellar frequency is the number of enamel plates measured within 10 cm. This measurement tells paleontologists how closely packed the tooth is, and again can help us gain insight about the mammoth's diet.

FIGURE 3.4: EXAMPLE OF THE CHARACTERISTICS USED TO DETERMINE A MAMMOTH'S SPECIES (MAGLIO, 1973)



Mammoth Taxonomy Exercise

Now it's time for you to be a paleontologist! Using this handout as a guide, examine the image/3D model of Cola's molar and determine what species of mammoth it was. This examination of an animal's characteristics to determine what species it belonged to is actually what paleontologist practice and call taxonomy.

Work with the group assigned to you to measure and fill out the table below. Once you have your measurements filled out, discuss with you're the classmates in your group what mammoth species you think it is.

Table 3.1: Cola's Molar Characteristics

Molar Measurements	
Length (cm)	
Width (cm)	
Height (cm)	
Enamel Number	
Lamellar Frequency	

Question 1. Did your group all have the same molar measurements as you? How did they differ?

Question 2. If your group did not reach a consensus on species, why did they not?

Table 3.2: Molar Characteristics of North American Mammoth Species

	Woolly Mammoth	Columbian Mammoth	Jeffersonian Mammoth
Length (cm)	**15 - 18**	**28.5 - 34**	**29 -30**
Width (cm)	**7.5 - 8.5**	**8 - 13**	**8 - 11**
Height (cm)	**11 - 22.5**	**15 - 19**	**14 - 20**
Enamel Number	**24 - 30**	**20 - 24**	**19 - 30**
Lamellar Frequency	**5 - 7.5**	**5 - 7**	**7 - 9**

Question 3. Based on your molar measurements, what species of mammoth do you think Cola belongs to? Why?

At this time we will get back together as a class to discuss each what each group concluded looking at Cola's molar.
Question 4. Is there a variety of answers among the groups for Cola's species? Explain.

Question 5. What was the other groups' reasoning for what species they assigned the molar to? Were these reasons contrary to your own?


5 cm
10


5 cm
10 cm

Presentation for the Lesson Plan

The Story of Cola and Mammoths of North Americ

JON ERDMAN

1

Discovering Cola

- During the summer of 1966, geologist Robert Jones and Archeologist Alfred Bowers were called to excavate a mammoth from the El Paso Products phosphate mine near Soda Springs, Idaho. While digging a ditch, a bulldozer struck the mammoth's pelvis, which led to its discovery.

2

- Over the next 53 years, the mammoth would remain in storage
- The mammoth was donated to the University of Idaho, and earned its nickname "Cola"

Fig. 3: Fragments of Cola's legs

Fig. 4: Cola at the University of Idaho

3

Woolly Mammoth

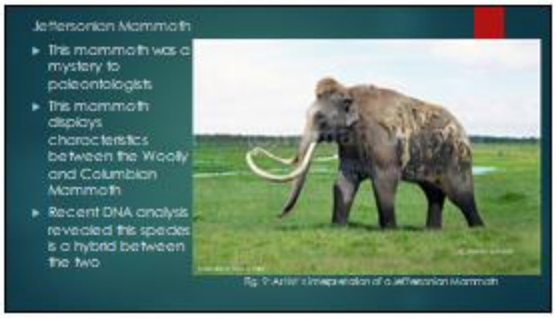
- Smallest of the mammoth species
- Thick covering of hair on entire body
- Found in Canada, and the northernmost parts of the United States

4

Columbian Mammoth

- Largest of the mammoth species
- Occupied warmer open grassland environments
- Some specimens reached up to 15 feet tall

5



Jeffersonian Mammoth

- This mammoth was a mystery to paleontologists
- This mammoth displays characteristics between the Woolly and Columbian Mammoth
- Recent DNA analysis revealed this species is a hybrid between the two

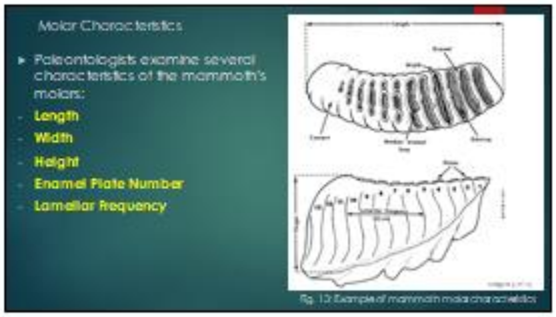
Fig. 9: Artist's Interpretation of a Jeffersonian Mammoth

6

Taxonomy

- How paleontologist determine the features that aid in determining what species a fossil belongs to is called taxonomy
- With mammoths, paleontologists use their teeth
- Mammoths shed six sets of molars throughout their life, making them relatively common

Figs. 10 – 12: Example of fossilized mammoth molars



Molar Characteristics

- Paleontologists examine several characteristics of the mammoth's molars:
- Length
- Width
- Height
- Enamel Plate Number
- Lamellar Frequency

Fig. 13: Example of mammoth molar characteristics

References

- Figure 5 Retrieved From [illegible]
- Figure 6 Retrieved From [illegible]
- Figure 7 Retrieved From [illegible]
- Figure 8 Retrieved From https://upload.wikimedia.org/wikipedia/commons/thumb/6/62/Columbian_mammoth.JPG/1200px-Columbian_mammoth.JPG

References (Cont.)

- Figure 9 Retrieved From [illegible]
- Figure 11 Retrieved From [illegible]
- Figure 12 Retrieved From [illegible]

"The Story of Cola and North American Mammoths" Lesson Plan

Name: Jonathan Erdman	**Date:** 12/03/2019
Subject: Paleontology	**Topic:** Mammoth Taxonomy

The big idea(s) or essential question(s)

Students should be able to identify the differences in North American mammoth species and the skeletal characteristics paleontologists use to tell them apart.

State of Idaho and/or common core standards addressed (please state grade level; provide an alternative to adjust for lower/higher grades):

For 8th grade:

LS4-HS- 1. (Communicate scientific information that common ancestry and biological evolution are supported by multiple lines of empirical evidence).

Students will be looking at and comparing the similarities/differences of extinct mammoth species to discuss possible evolutionary relationships.

LS4-HS-2. Construct an explanation based on evidence that the process of evolution primarily results from four factors: (1) the potential for a species to increase in number, (2) the heritable genetic variation of individuals in a species due to mutation and sexual reproduction, (3) competition for limited resources, and (4) the proliferation of those organisms that are better able to survive and reproduce in the environment.

Students will learn about the two primary mammoth species in North America, and discuss the potential of interbreeding and the alteration of physical characteristics to adapt for changing ecology.

For 12th grade:

LS4-HS- 1. (Same as above).

LS4-HS-2. (Same as above).

Objectives (what the students will be able to do as a result of the lesson)

(TSWBAT = The students will be able to…) Explain for each grade

TSWBAT (8th Grade)	Explain the evolutionary relationship of North American and common ancestry. They will also be able to differentiate these species based on their dental characteristics
TSWBAT (9th Grade)	Same as above.

Materials Resources: Text/Technology/Didactics needed for lesson

- PowerPoint presentation

- Handout

- Printed Photos of mammoth molars

- 3d printed mammoth molar(s) (optional)

Relational Resources: Community Resources/Family Resources

Activities/procedures (include anticipated time for each)

Introduction/activator

- Introduce myself to the classroom, give personal background and when/where Cola was discovered.

Class activity sequence (what you/students will do)	**Class activity sequence (why you will do them)**
- Give an approximately 10 minute long presentation covering the following subjects: **1)** Where Cola was discovered, tie in with local geology and paleontology in the state of Idaho itself. **2)** Cola's 53 year research history, highlight paleontology being conducted at the University of Idaho (U of I), and the advanced technological projects undertaken by the U of I's Virtual Technology and Design program. **3)** Introduce the class to the two accepted mammoth species that roamed	- This will give the class the background necessary to complete the interactive class

North America during the Late Pleistocene (Woolly and Columbian Mammoths), as well as the potential Woolly/Columbian hybrid, the Jeffersonian Mammoth.	activity.
4) Explain the determination of mammoth species primarily by molar characteristics set forth in Maglio (1973), modified after Osborn (1942).	
5) Transition from explanation to interactive problem.	
Interactive Portion of Lesson	
- Children will team up in groups determinable by class size and available 3D models.	
- Each group will have one 3D printed molar, handouts, and a ruler/tape measure.	- Students will be in a small enough group to encourage participation
- Work with class to determine height, length, plate number, and enamel thickness of molar by counting the enamel plates as described from presentation and using a ruler to measure characteristics in centimeters.	- These are the characteristics the students will use to determine mammoth species
- Students will document their measurements and observations (such as number of worn enamel plates) and create a table of those measurements.	
- Students will compare their measurements on average molar characteristics for each of the 3 species (Woolly, Columbian, Jeffersonian) from the table of characteristics in their handouts. They will construct a hypothesis on which species the molar belongs to.	- Documentation of measured characteristics, easy to compare to species characteristics from handout
- Class will reconvene after a 10 minutes and as a whole will discuss which species they chose and why. Molar characteristics show a degree of overlap with the Columbian Mammoth in plate count, but has thinner enamel characteristic of the Woolly, a range of answers for species is expected.	

-Finish exercise discussing the issues encountered in determining species. The same issues encountered by the class in determining species is the same experienced by paleontologists studying mammoths, leave with potential to study crania characteristics. This will highlight my research as well as show class that there are still mysteries surrounding prehistoric animals so similar to modern elephants.	- Allows class to assert their hypothesis on species and support their hypothesis in a discussion - This will emphasize that a diligence in studying characteristics of fossils is required for paleontology, as well as transition into an interesting new concept on how to determine mammoth speciation

Closure/reminders

Thank class for participation, if time available open up for questions.

Reminders: More than one mammoth species roamed North America, and their molars are the primary determinant in species assignment, although there are some limits to this method.

Assessment (how you will know students met the objectives - include rubrics)

Students should be able to quantitatively describe the differences in mammoths (overall size, molar characteristics described in PowerPoint/handout). Students should recognize the relationship between mammoth species due to the similarities in overall body plan and dentition.

Accommodations/differentiation (how will you give multiple options and meet the needs of varied learners?)

The number of molar characteristics required to compare between mammoth species can be expanded or reduced to accommodate younger learners or those with varied educational needs.

Laminated mammoth molar picture handouts can also be drawn on with highlighters or wipe of markers of varying colors to show specific characteristics.

Grading Rubric

Criteria	Exceeds	Meets	Approaches
Mammoth Biogeographic Distribution	Students correctly identifies the geographic location and ecology of each mammoth species	Student correctly identifies some ranges, ecologies, or some combination of the two for each mammoth species.	Student incorrectly identifies most or all of mammoths' ranges and ecology.
Mammoth Taxonomy	Student knows the molar morphometrics of each species, and can make taxonomic assignments based on observations.	Student knows some of the molar morphometrics, and can make a taxonomic assignment with reference or further study of material.	Students do not know the taxonomic characteristics of any mammoth species.
Mammoth Taxonomy Discussion	Students engage in discussion about their taxonomic assignment. Students recognize the possibility of different assignments based on same characteristics.	Students engage in discussion about their taxonomic assignment.	Students do not engage in discussion.

Chapter 4: Conclusion and Future Research

This research was conducted during the worldwide pandemic of COVID-19. It was the author's original intent to compare the measurements and data derived from Cola to other mammoth specimens at museum sites across North America. Due to the pandemic, museums were closed to any outside visitors or researchers who wanted to study their collections. Future work would be to compare the holotype and neotype specimens at museums regarding crania and molar characteristics (Appendix E). The comparison of these would confirm or refute whether Todd's (2010) parameters can be used in North America when assessing the taxonomy of the *M. primegenius, M. columbi,* and *M. jeffersonii.* DNA analysis is costly and not feasible at times if original material is not present. It would be useful to be able to measure crania and molar to decipher taxonomic assignment.

Here, I was able to determine that Cola lived 11,700 +/- years before present with AMS radiocarbon dating methods, in the last final stages of the reign of mammoths on mainland North America. This is the timeframe for the last glacial retreat in North America and Jeffersonian hybridization observed in the fossil record (Pichardo, 2001). It is debated when the last large mammoth (excluding pigmy mammoths) existed, but this date is within a thousand years or less of the megafaunal extinction event. Thus far, specimens of *M. jeffersonii* have only been found in deposits dated during this glacial retreat, approximately 19 – 11.5 Ka, coinciding with the megafaunal extinction that wiped out mammoths and other large mammals on a planet-wide scale (Haynes, 2002).

While the megafaunal extinction most likely had multiple drivers, the changing environment certainly played a role in North American mammoth taxonomy, if not their demise on the continent. Due to the influence ontogeny, stress, and diet play in affecting molar shape, specimens must be put into as complete a paleontological context as can be obtained. Mammoth finds in the Pacific Northwest represent a unique long-lived population that most likely utilized Idaho as a migratory corridor to access the United States. The unique ecology of the area certainly influenced their molar shape, and constructing regional datasets across a larger temporal range in the Pacific Northwest will aid understanding the role biogeography and paleoecology have on mammoth molar morphometrics.

DNA analysis confirmed that we either have a *M. columbi* or *M. jeffersonii* but it is still debated in the current literature whether introgressive radiation (Widga et al., 2017) caused many forms of *M. jeffersonii,* and if *M. jeffersonii* should be included as a subspecies of *M. columbi (M. c. jeffersonii).* Cola was a sub adult (18-28 years old), not fully grown, and was a male at its time of death.

In addition to the goals above, I have also included 'There's a Mammoth in the Room' lesson plan to help make this study more understandable and accessible to K – 12 aged students. Future studies of this specimen will help to better constrain the paleogeographic distribution of this mammoth hybrid species and the interaction between *M. columbi* and *M. primigenius* in western North America.

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Appendix A: Methods for Radiocarbon Dating at Beta Analytic Testing Laboratories

(Taken from Beta Analytics website at www.radiocarbon.com)

The Accelerator Mass Spectrometry (AMS) technique for radiocarbon dating accounts for a substantial number of the analysis requests Beta Analytic receives each day. There can be considerable advantages to using the AMS technique in many dating applications, making it possible to extend radiocarbon dating into many new areas of research. AMS also permits applications in important situations that cannot be dated by the radiometric dating technique.

AMS Lab Procedure

The AMS measurement is done on graphite produced by hydrogen reduction of the CO2 sample over a cobalt catalyst. The CO2 is obtained from the combustion of the sample at 800°C+ under a 100% oxygen atmosphere. The CO2 is first dried with methanol/dry ice then collected in liquid nitrogen for the subsequent graphitization reaction. The identical reaction is performed on reference standards, internal QA samples, and backgrounds to ensure systematic chemistry.

The analytical result ("BP" or "pMC") is obtained by measuring sample C14/C13 relative to the C14/C13 in Oxalic Acid II (NIST-4990C) in one of Beta Analytic's multiple in-house particle accelerators using SNICS ion source. Quality assurance samples are measured along with the unknowns and reported separately in a "QA report". The radiocarbon dating lab requires results for the QA samples to fall within expectations of the known values prior to accepting and reporting the results for any given sample.

The AMS result is corrected for total fractionation using machine graphite d13C. The d13C reported for the sample is obtained by different ways depending upon the sample material. Solid organics are sub-sampled and converted to CO2 with an elemental analyzer (EA). Water and carbonates are acidified in a gas bench to produce CO2. Both the EA and the gas bench are connected directly to an isotope-ratio mass spectrometer (IRMS). The IRMS performs the separation and measurement of the CO2 masses (44, 45, and 46) and calculation of the sample d13C.

Guaranteed Agreement Between Samples and Reference Standards

The client's samples are included in a "full wheel" of graphite targets, including backgrounds, modern and known-age standards prepared by Beta Analytic. These additional materials undergo the same chemical pretreatments and graphite syntheses as do the client's samples. This is indispensable for precision radiocarbon dating. They are interspersed throughout the accelerator wheel to provide reference measurements for the age calculations and verifications. Only with rare exception that it is acceptable to analyze unknowns prepared separately from the reference standards.

AMS Dating Advantages

- It can be used to radiocarbon date one milligram of carbon or less.
- The small sample size needed for analysis may permit a more selective sampling.
- The small sample requirement often allows a stronger pretreatment than would otherwise be possible.
- The small sample taken often means that a portion of the original material can be archived.
- Statistical error is better for older and smaller samples.
- Measurement is quasi-simultaneous between reference standards and unknowns.

Appendix B: Methods for DNA extraction from UCSC Paleogenomics Lab

(Taken from UCSC Paleogenomics Lab)

Following the initial assessment of the sample's preservation, we used the single-stranded library (following Kapp et al. *in review)*[1] for a hybridization-based target enrichment approach to generate a high coverage mitochondrial genome. We used custom megamammal baits described in Kirillova et al. (2017)[2], followed the myBaits v4.01 protocol[3], and hybridized the megamammal baits at 65°C for 36 hours described by Vershinina et al (2019)[4]. The enriched library was sequenced on an Illumina NextSeq 2x150 run targeting ½ million raw reads.

Following sequencing, we used Seqprep2[5] to trim the raw reads of adapters, merge reads that overlapped by 15 bases or more, and discard reads shorter than 28 base pairs. We combined the merged and unmerged reads and converted the files from fastq format to fasta format using FASTX_ToolKit[6]. Next, we collapsed identical sequences with PRINSEQ_lite[7] into a final fasta file. We aligned the final duplicate filtered fasta file to the *M. primigenius* mitochondrial reference genome (GenBank accession: NC_007596.2) and called a consensus sequence using MIA[8].

The final consensus sequence was called after 3 iterations at 348-fold average coverage which we then filtered two different ways based on depth of coverage. We used a relaxed filter (minimum of 3x coverage at every base, with ⅔ of reads agreeing to call the position) and a strict filter (minimum of 10x coverage at every base, with 9/10 of the reads agreeing before calling the position). Due to the incredibly high coverage, the relaxed and strict filters yielded no significant change in the assembly quality.

We aligned the strict converge filtered fasta to other previously published mammoth mitochondrial genomes representing all described clades in order to identify where this sample fell within known mammoth mitochondrial diversity. The sequences were aligned using muscle and a maximum likelihood tree built with RAxML with 100 bootstrap replicates. I've attached the tree to this email. Each major mammoth clade is colored according to the described clades in Enk et al. 2016[9].

The mammoth molar that you sent to us sits in a strongly supported clade with Clade I or Haplogroup F mammoths, which includes both *M. columbi, M. jeffersonii,* and unresolved *M. sp*. It is important to note that the tree we generated identifies which haplotype your molar is, but more comprehensive analyses should be done if you would like a figure that is of publication quality.

References

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From the Phase 1 report -

We used a dremel to subsample a piece of the mammoth molar and powdered the subsample to prepare it for DNA extraction. Next, we extracted DNA from the powdered bone using a protocol optimized for highly degraded and fragmented DNA (https://www.pnas.org/content/110/39/15758). Afterward, we quantified the extracted DNA, performed a single stranded library preparation using an in-house protocol, and amplified the library for sequencing. The library was sequenced on an Illumina Nextseq 2x150 run targeting 1 million raw reads.

*Following sequencing, each read was trimmed of adapters and overlapping paired reads were merged and filtered for complexity. We aligned the filtered reads to the African elephant nuclear genome (*Loxodonta africana*, GenBank accession number: GCF_000001905.1), and the mammoth mitochondrial genome (*Mammuthus primigenius*, GenBank accession: NC_007596.2). We aligned to African elephant nuclear genome, rather than mammoth, because it is a close living relative with a high-quality genome assembly. That being said, the true estimate of endogenous (target) DNA will be slightly higher than what we’ve reported due to divergent reads that are not able to map to the African elephant. The mammoth molar had roughly 19% of reads aligning to the African elephant and 0.8X coverage of the mammoth’s mitochondrial genome.*

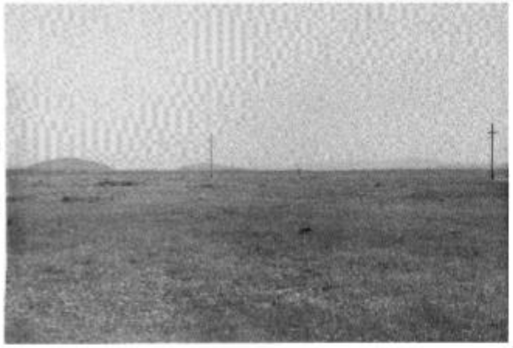
Appendix C: Excavation Site Photos from 1966


DISTAL END FEMUR
TIBIA
DISTAL END, FEMUR
DITCH

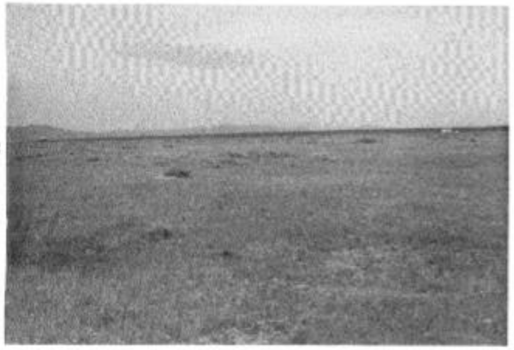

FRAG. OF PELVIS?
DISTAL
TIBIA
PROX
HUMERUS
PROX
HUMERUS
DISTAL
VERT

0

1



2



3

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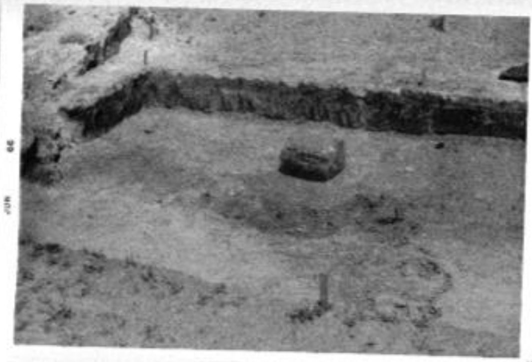

10

11

12

13

14

14

15

16

17

SKULL

MOSTLY FOOT BONES ; DISTAL END HUMERUS , FEMURS

LOWER JAW

LOWER JAW & TUSKS + VERTEBRAE


PELVIC FRAG
TIBIA
DISTAL END FEMUR
DISTAL END FEMUR

Mammoth Spinose Process:

Sample #	Scan ID (If Applicable)	Bone ID	% Intact	Measurements	Other Comments
SMS001	1-4	Vertebrae (Portion)	20		
SMS002	2-2	Lumbar Vertebrae	80		
SMS003	2-13	Vertebrae (Portion)	20		
SMS004	2-16	Sacrum	50		
SMS005	1-5	Atlas	100		
SMS006	2-12	Vertebrae (Portion)	10		
SMS007	1-16	Vertebrae (Portion)	40		Possible Lumbar Vertebrae
SMS008	2-17	Vertebrae (Portion)	50		Possible Caudal (tail) Vertebrae
SMS009	1-2	Lumbar Vertebrae	60		
SMS010	1-8	Vertebrae (Portion)	20		
SMS011	1-18	Vertebrae (Portion)	60		Possible Cervical, Thoracic Vertebrae

SMS012	1-11	Vertebrae (Portion)	40		Possible 7th Thoracic Vertebrae
SMS013	1-10	Vertebrae (Portion)	5		
SMS014	2-1	Vertebrae (Portion)	15		
SMS015	1-20	Vertebrae (Portion)	10		
SMS016	1-19	Thoracic Vertebrae	70		
SMS017	2-3	Vertebrae	55		
SMS018	1-14	Thoracic Vertebrae	50		
SMS019	1-12	Vertebrae (Portion)	25		
SMS020	1-15	Vertebrae (Portion)	10		
SMS021	1-7	Vertebrae (Portion)	5		
SMS022	2-6	Vertebrae	90		Possible Caudal (Tail) Vertebrae

Ribs:

Sample #	Scan ID (if possible)	Bone ID	% Intact	Measurements (L/W)	Other Comments
R001	9-21	Rib	N/A (so far)	26cm/ 7cm	Marks, root etching
R002		Rib	N/A (so far)	27cm/ 6cm	marks, grooves
R003		Rib	N/A (so far)	10cm/ 4.5cm	
R004	3-22	Rib	N/A (so far)	16cm/ 7cm	marks, root etching
R005	3-11	Rib	N/A (so far)	14cm/ 9cm	marks, possible carnivore punctures
R006		Rib	N/A (so far)	13cm/ 8cm	root etching, marks, rodent knaw marks?
R007	3-1	Rib	N/A (so far)	16.5cm/ 7.5cm	rot etching, rodent gnaw marks
R008		Rib	N/A (so far)	11.5cm/ 7cm	marks, root etching, rodent gnaw marks
R009		Rib	N/A (so far)	21.5cm/ 5cm	marks (cuts? scavengers?)
R010		Rib	N/A (so far)	12cm/ 5cm	
R011	3-25	Rib	N/A (so far)	15cm/ 6.5cm	
R012	3-7	Rib	N/A (so far)	14.5cm/ 7.5cm	
R013		Rib	N/A (so far)	10.5cm/ 4cm	
R014	3-2	Rib	N/A (so far)	25.5cm/ 7cm	
R015		Rib	N/A (so	22.5cm/ 6cm	

			far)		
R016	9-18	Rib	N/A (so far)	11.5cm/ 9cm	
R017		Rib	N/A (so far)	10cm/ 5-7cm	
R018		Rib	N/A (so far)	7.5cm/ 7.5cm	
R019		Rib	N/A (so far)	12cm/ 6cm	
R020		Rib	N/A (so far)	9cm/ 3.5cm	
R021		Rib	N/A (so far)	7cm/ 4.5cm	
R022		Rib	N/A (so far)	17cm/ 4.5cm	
R023		Rib	N/A (so far)	13cm/ 5cm	
R024		Rib	N/A (so far)	17cm/ 6cm	(2 pcs.)
R025		Rib	N/A (so far)	11cm/ 6cm	marks? cuts? scavengers?
R026		Rib	N/A (so far)	33cm/ 4cm	(2 pcs.)
R027		Rib	N/A (so far)	17cm/ 3.5cm	**(fits R028)***
R028	9-12	Rib	N/A (so far)	27cm/ 3.5cm	**(fits R027)***
R029		Rib	N/A (so far)	14cm/ 3.5cm	
R030	9-6	Rib	N/A (so far)	33.5cm/ 4.5cm	
R031	3-5	Rib	N/A (so far)	33cm/ 5cm	

R032	9-16	Rib	N/A (so far)	31cm/ 5cm	
R033		Rib	N/A (so far)	14.5cm/ 3.5cm	
R034		Rib	N/A (so far)	11cm/ 3.5cm	
R035		Rib	N/A (so far)	26cm/ 4.5cm	(2 pcs.) marks
R036		Rib	N/A (so far)	36.5cm/ 5.5-4cm	(2 pcs.) marks
R037		Rib	N/A (so far)	29.5cm/ 5cm	(2 pcs.) marks
R038		Rib	N/A (so far)	27cm/ 5-4cm	marks
R039		Rib	N/A (so far)	17.5cm/ 4cm	
R040		Rib	N/A (so far)	9cm/ 4cm	
R041	3-18	Rib	N/A (so far)	26cm/ 5-4.5cm	cuts*
R042	3-16	Rib	N/A (so far)	28.5cm/ 5.5-4-3	marks
R043	3-12	Rib	N/A (so far)	34cm/ 6-5cm	marks
R044	9-14	Rib	N/A (so far)	13.5cm/ 5.5cm	marks*
R045		Rib	N/A (so far)	19cm/ 4.5cm	marks
R046		Rib	N/A (so far)	9.5cm/ 5cm	
R047		Rib	N/A (so far)	19.5cm/ 5.5-5cm	marks
R048		Rib	N/A (so	10.5cm/ 4.5cm	marks*

			far)		
R049		Rib	N/A (so far)	24.5cm/ 4.5-4cm	
R050		Rib	N/A (so far)	14cm/ 5-4.5cm	
R051		Rib	N/A (so far)	11cm/ 4.5cm	marks
R052		Rib	N/A (so far)	11cm/ 5-4cm	weird ossification/growth on bone
R053		Rib	N/A (so far)	9cm/ 4.5cm	rodent gnaw marks
R054		Rib	N/A (so far)	46.5cm/ 3.5-3cm	(3 pcs.)
R055		Rib	N/A (so far)	55.5cm/ 4-3.5cm	(4 pcs.) root etching
R056		Rib	N/A (so far)	16cm/ 7cm	marks, root etching
R057		Rib	N/A (so far)	21.5cm/ 8cm	marks?
R058		Rib	N/A (so far)	23.5cm/ 4cm	(2 pcs.)
R059		Rib	N/A (so far)	10cm/3.5cm	
R060		Rib	N/A (so far)	12cm/3cm	
R061		Rib	N/A (so far)	5cm/ 4.5cm	
R062		Rib	N/A (so far)	9.5cm/ 3.5cm	
R063		Rib	N/A (so far)	9cm/ 2.5cm	marks
R064		Rib	N/A (so far)	6cm/ 2.5cm	

R065		Rib	N/A (so far)	7cm/ 3cm	root etching
R066		Rib	N/A (so far)	6cm/ 5cm	
R067		Rib	N/A (so far)	9.5cm/ 4cm	
R068		Rib	N/A (so far)	7cm/ 5cm	marks
R069		Rib	N/A (so far)	9cm/ 3cm	rodent gnaw marks
R070		Rib	N/A (so far)	5.5cm/ 3cm	marks
R071		Rib	N/A (so far)	16cm/ 3-.5cm	
R072		Rib	N/A (so far)	13cm/ 5-4cm	ossification
R073		Rib	N/A (so far)	13.5cm/ 3.5cm	marks, rodent gnawing
R074		Rib	N/A (so far)	8cm/ 4cm	marks
R075		Rib	N/A (so far)	6cm/ 3.5cm	
R076		Rib	N/A (so far)	6.5cm/ 3.5cm	
R077		Rib	N/A (so far)	11cm/ 3.5cm	ossification, marks**
R078		Rib	N/A (so far)	8cm/ 3.5cm	marks
R079		Rib	N/A (so far)	11cm/ 3-2.5cm	
R080		Rib	N/A (so far)	13cm/ 3cm	ossification
R081		Rib	N/A (so far)	8cm/ 2.5cm	marks

R082		Rib	N/A (so far)	8cm/ 3cm	marks
R083		Rib	N/A (so far)	4cm/ 3cm	marks
R084		Rib	N/A (so far)	10cm/ 3.5cm	marks, root etching
R085		Rib	N/A (so far)	7cm/ 2.5cm	marks*, cuts*
R086		Rib	N/A (so far)	6.5cm/ 2.5cm	
R087		Rib	N/A (so far)	7cm/ 4cm	
R088		Rib	N/A (so far)	9cm/ 3cm	
R089		Rib	N/A (so far)	11.5cm/ 3.5cm	
R090		Rib	N/A (so far)	12cm/ 2.5cm	marks
R091		Rib	N/A (so far)	8cm/ 4cm	marks
R092		Rib	N/A (so far)	6cm/ 2.5cm	marks
R093		Rib	N/A (so far)	6cm/ 3cm	marks
R094		Rib	N/A (so far)	7cm/ 3cm	marks, tool???***
R095		Rib	N/A (so far)	9cm/ 3.5cm	root etching
R096		Rib	N/A (so far)	6cm/ 1.5cm	
R097		Rib	N/A (so far)	4cm/ 3cm	
R098		Rib	N/A (so far)	6.5cm/ 4cm	

R099		Rib	N/A (so far)	15.5cm/ 4.5cm	
R100		Rib	N/A (so far)	14cm/ 3.5cm	
R101		Rib	N/A (so far)	12cm/ 3.5cm	
R102		Rib	N/A (so far)	22.5cm/ 4cm	
R103		Rib	N/A (so far)	8cm/ 5cm	
R104		Rib	N/A (so far)	12cm/ 4cm	
R105		Rib	N/A (so far)	24cm/ 3.5cm	
R106		Rib	N/A (so far)	14.5cm/ 3.5cm	
R107		Rib	N/A (so far)	11cm/ 2cm	
R108		Rib	N/A (so far)	9.5cm/ 3.5cm	root etching
R109		Rib	N/A (so far)	9.5cm/ 3cm	marks
R110		Rib	N/A (so far)	8cm/ 2cm	
R111		Rib	N/A (so far)	5.5cm/ 3cm	
R112		Rib	N/A (so far)	6.5cm/ 4cm	
R113		Rib	N/A (so far)	15.5cm/ 4cm	marks
R114		Rib	N/A (so far)	7cm/ 4.5cm	marks
R115		Rib	N/A (so far)	16.5cm/ 4.5cm	

R116		Rib	N/A (so far)	10cm/ 4.5cm	
R117		Rib	N/A (so far)	17cm/ 3.5cm	root etching
R118		Rib	N/A (so far)	9.5cm/ 4.5cm	marks
R119		Rib	N/A (so far)	11cm/ 4cm	
R120		Rib	N/A (so far)	10cm/ 3.5cm	
R121		Rib	N/A (so far)	8cm/ 3cm	
R122		Rib	N/A (so far)	9cm/ 4cm	marks, ossification
R123		Rib	N/A (so far)	16.5cm/ 5.5cm	marks
R124		Rib	N/A (so far)	6cm/ 3.5cm	
R125		Rib	N/A (so far)	11.5cm/ 5cm	marks, ossification
R126		Rib	N/A (so far)	6cm/ 3cm	termite burrowing*
R127		Rib	N/A (so far)	15.5cm/ 4cm	root etching
R128		Rib	N/A (so far)	7cm/ 2cm	marks
R129		Rib	N/A (so far)	10.5cm/ 4cm	marks
R130		Rib	N/A (so far)	5cm/ 3-2cm	marks
R131		Rib	N/A (so far)	11cm/ 4cm	
R132		Rib	N/A (so far)	6.5cm/ 2.5cm	root etching

R133		Rib	N/A (so far)	9cm/ 4.5cm	marks
R134		Rib	N/A (so far)	4.5cm/ 3.5cm	
R135		Rib	N/A (so far)	8cm/ 3.5cm	marks
R136		Rib	N/A (so far)	6.5cm/ 3.5cm	
R137		Rib	N/A (so far)	10cm/ 4cm	marks, *termite burrowing*?*
R138		Rib	N/A (so far)	10cm/ 3.5cm	*termite burrowing*?*
R139		Rib	N/A (so far)	8.5cm/ 2.5cm	
R140		Rib	N/A (so far)	12.5cm/ 3.5cm	
R141		Rib	N/A (so far)	11.5cm/ 4cm	marks, reodent gnawing
R142		Rib	N/A (so far)	13cm/ 3cm	root etching

Cranium:

Sample #	Scan ID (If Applicable)	Bone ID	% Intact	Measurements	Other Comments
SMC001	11-36	Cranium (Portion)	15		Portion of maxilla, part of upper right molar cavity
SMC002	11-45	Cranium (Portion)	15		Maxilla fragment, glued to SMC001
SMC003	11-46	Cranium (Portion)	15		Maxilla fragment, to be glued to SMC001
SMC004	11-4	Cranium (Portion)	15		Maxilla fragment, glued to upper left molar cavity
SMC005	11-30	Cranium (Portion)	95		Occipital Condyle
SMC006	11-24	Cranium (Portion)	95		Bridge between occipital condyles
SMC007	11-15	Cranium (Portion)	15		Fragments of maxilla glued to SMC001
SMC008	11-16	Cranium (Portion)	5		Possibly a fragment of tusk sheath
SMC009	11-17	Cranium (Portion)	5		Possibly a fragment of tusk sheath
SMC010	11-18	Cranium (Portion)	2		Possibly a portion of ear bone
SMC011	11-19	Cranium (Portion)	20	204 mm (Length) X 88 mm (Width)	Possibly a zygomatic arch fragment
SMC012	11-21	Cranium (Portion)	10		Fragment of either paraetal or occipital, possibly related to SMC013
SMC013	11-27	Cranium (Portion)	15		Either paraetal or occipital fragment, 2 unscanned fragments to glue together
SMC014	11-41	Cranium (Portion)	5		Possibly maxillary, zygomatic arch, or paraetal ridge
SMC015	11-43	Cranium (Portion)	10		Possibly paraetal
SMC016	11-44	Cranium (Portion)	10		Possibly paraetal ridge
SMC017	11-38	Cranium (Portion)	10		Possibly fronto-paraetal fragment
SMC018	11-40	Cranium (Portion)	10		Highly honeycombed possibly fronto-paraetal

SMC019	11-8	Cranium (Portion)	2		Small Fragments (<5cm), possibly maxillary
SMC020	11-6	Cranium (Portion)	10		Either paraetal or occipital fragment
SMC021	11-42	Cranium (Portion)	10		Possible tusk sheath
SMC022	11-35	Cranium (Portion)	25		Zygomatic arch
SMC023	11-12	Cranium (Portion)	10		Possible paraetal
SMC024	15-1	Lower Jaw/Mandible	80	Length: 76.2 cm Width: 50.8 cm	Mandible complete but highly fragile, reinforce before removing from cling wrap
SMC026	15-2	Right Tusk	90	Length: 228.6 cm	Highly fragmented, do not remove plaster jacket without reinforcement
SMC027	15-3 (possibly)	Left Tusk	90		Highly fragmented, do not remove plaster jacket without reinforcement
SMC028	15-1	Lower Left Molar (M1)	100		
SMC029	15-1	Lower Right Molar (M1)	100		
SMC030		Upper Left Molar	100		

Front Legs:

Sample #	Scan ID (If Applicable)	Bone ID	% Intact	Measurements	Other Comments
SSMFL 1	7_1	Ulna	75	Length (cm): 66.04	

SSMFL 2	7_2	Humerus	90	Length (cm): 38.10	
SSMFL 3	7_3	Radius	85	Length (cm): 63.50	
SSMFL 4	7_4	Ulna	30	Length (cm): 45.72	
SSMFL 5	7_5	Ulna	30	Length (cm): 59.63	
SSMFL 6	7_6	Ulna	80	Length (cm): 58.42	
SSMFL 7	8_1	Humerus	90	Length (cm): 90.17	
SSMFL 8	8_2	Humerus	70	Length (cm): 46.99	
SSMFL 9	8_3	Radius	95	Length (cm): 50.80	
SSMFL 10	8_4	Radius	45	Length (cm): 19.05	
SSMFL 11	8_5	Radius	50	Length (cm): 22.86	
SSMFL 12	8_6	Humerus	90	Length (cm): 20.32	
SSMFL 13	8_7	Radius	95	Length (cm): 21.59	
SSMFL 14	8_8	Radius	15	Length (cm): 10.16	
SSMFL 15	8_9	Radius	20	Length (cm): 20.32	

Rear Legs:

Sample #	Scan ID (If Applicable)	Bone ID	% Intact	Measurements (length)	Other Comments
SMRL001	4-1	Femur(distal)	40%	51cm	Distal end of the femur, some fragmentation around the break
SMRL002		Femur(distal)	50%	73cm	Distal end of the femur, has been previously glued toegether
SMRL003	4-5	Femur	15%	45cm	Possible fragment of 4-1 femur
SMRL004	4-6	Femur	15%	41cm	Possible fragment of 4-1 femur
SMRL005	4-7	Femur	15%	44.5cm	Possible fragment of 4-1 femur
SMRL006	5-1	Tibia	40%	30.5cm	Marries with SMRL007
SMRL007		Tibia	20%	33.7cm	Glue shows that it was pieced together most likely with SMRL006
SMRL008	5-2	Tibia3	40%	37cm	Missing the distal growth plates and the proximal portion
SMRL009	5-6	Tibia 4	30%	34cm	Distal end of the Tibia could marry with SMRL007
SMRL010	4-8	Patella 1	100%	15.4cm	
SMRL011	5-4	Pelvis 1	10%	35.6cm	Possible iliac crest, or tuber ischii
SMRL012	5-3	Pelvis 2	15%	33.8cm	Possible iliac crest
SMRL013	6-6	Pelvis 3	10%	29.6cm	Possible pubis, previously glued

SMRL014	6-4	Pelvis 4	10%	28.7cm	possible pubs or tuber ischii
SMRL015	5-5	Pelvis5	10%	26.8cm	Previously reconstructed
SMRL016	6-11	Pelvis 6	10%	20.3cm	
SMRL017	6-12	Pelvis 7	5%	17.7cm	
SMRL018	6-5	Pelvis 8	5%	18cm	
SMRL019	4-2	Pelvis 9	5%	20.4cm	Parts have ben broken either during transportation or handling, kept in the wrap
SMRL020	6-9	Pelvis 10	5%	14.6cm	
SMRL021	5-7	Pelvis 11	10%	28.3cm	
SMRL022	6-13	Pelvis 12	5%	23cm	
SMRL023	6-1	Pelvis 13	5%	19.5cm	
SMRL024	6-10	Pelvis 14	5%	21cm	Has been glued in the past
SMRL025	6-7	Pelvis 15	5%	20.5cm	Has been glued in the past

Forefeet:

Sample #	Scan ID	Bone ID	% Intact	Perservation Quality	Measurements: Length and Width (cm)	Other Comments
SMF009		Cuneiform	80	Longated feature of bone missing.	L: 10.5 W: 9	Fragmented piece glued on; missing part of bone structure
SMF010		Magnum	50	Large portion fragmented and missing	L: 8 W: 10.5	50% missing; cracks running throughout entire bone
SMF011		Unciform	96	Very intact. Some slight fragmentation	L: 15.5 W: 10.5	Fragmented on posterior and some dark discoloring
SMF013		Trapezium	96	Very intact; little fragmentation	L: 9 W: 5	Some discoloration. Fragmented on distal end.
SMF014		Scaphoid	96	Few cracks and fragmentation.	L: 16 W: 4	Some discoloration. Ruggose texture on promixal end.
SMF016	14-8	Cuneiform	98	Well perserved. Sediment possibly glued on	L: 19 W: 7	Small cracks on proximal end and middle section
SMF017	14-7	Lunar	90	Previously fragmented and reglued at dorsal	L: 13.5 W: 8	Large fracture reglued; other small cracks on distal end
SMF018	14-11	Trapezium	98	Little fragmentations and small cracks	L: 9 W: 4.5	Rugose texture. Discoloring from lacker previsouly used on bone.

SMF019	14-3	Pisiform	98	Very intact. Discoloration from glue.	L: 15 W: 7	Very rugose texture throughout structure
SMF020	14-4	Magnum	98	Very intact. White powder discoloring?	L: 10.5 W: 7.5	Small cracks throughout. White powder discoloring. Sediment possibly glued to bone.
SMF021	14-6	Trapezoid	98	Very intact. Some discoloring from lacker	L: 11 W: 6	Small cracks and possible cut marks on proximal end.

Hindfeet:

Sample #	Scan ID	Bone ID	% Intact	Perservation Quality	Measurements: Length and Width (cm)	Other Comments
SMF001		Calcaneum	98	Half appears to be covered in lacker. Light detiration.	L: 24 W: 19	Only half is covered in substance. Pale white coloring; yellow-brownish on half
SMF002		Calcaneum	97	Largeg crack at bottom of distal end of bone. Cracks between distal and proximal.	L: 24 W: 18	Cracks running to and from distal and proximal position of bone.

SMF003		Astragalus	65	Fragmented; around half of bone missing	L: 9 W: 7	Bone fragmented and missing almost hald of structure. Identifing more difficult; Bone ID possibly wrong
SMF004		Navicular	75	Fragmentation left of anterior view	L: 13 W: 4.5	Fragmented: approx. 25% missing from structure. Smore cracks. Sediment possibly glued to bone.
SMF005		External Cuniform	98	Lacker covering proximal with sediment	L: 10.5 W: 6.5	Some cracks running on dorisal side; one running along proximal end. Yellowing from lacker.
SMF006		External Cuniform	96	Broken and reglued. Large cracks present.	L: 11 W: 7	Reglued toward front posterior. Large crack on dorisal. Sheen from lacker.
SMF007		Internal Cuniform	98	Very intact. Discoloration from lacker.	L: 8 W: 5	Some cracks on distal end. Dark yellowing.
SMF008		Internal Cuniform	96	Fragmented and glued near posterior.	L: 7.5 W: 5.5	Fragmented and glued near posterior end. Sediment possibly glued to bone from lacked.

SMF012		Astragalus	98	Very intact	L: 17.5 W: 8	Small cracks on distal end. Discoloration on proximal end.
SMF015		Cuboid	98	Well preserved. Some small cracks present	L: 14.5 W: 5	Cracks on distal side. Discoloration from lacker.
SMF022		Navicular	50	Possible half of a navicular	L: 11.5 W: 5	Only half of bone present: Bone ID possibly wrong as identification was more difficult. What is preserved, has little damage and minimal cracking

Toes:

Sample #	Scan ID	Bone ID	% Intact	Perservation Quality	Measurements: Length and Width (cm)	Other Comments
SMF023	14-9	Metacarpal	98	Almost completely intact. Little detiroration.	L: 18.5 W: 6.5	Little cracking or damage. Some discoloration. Possible third metacarpal
SMF024	14-1	Metacarpal	90	Fragmented toward proximal end	L: 21 W: 5.5	Small cracks throughout. Fragmented toward proximal end. Possible second metacarpal

SMF025	14-2	Metacarpal	96	Very intact. Minimal detiroration.	L: 19 W: 6	Crack running along ridge of distal end. Possible third metacarpal
SMF026	10 44	Metacarpal	90	Fragmented and reglued	L: 20 W: 6	Glued by previous researcher
SMF027		Metacarpal	96	Only one noticable large crack	L: 19.5 W: 7	Discoloration from lacker. Crack toward proximal end

Appendix E: Recommended Museum Collections for Future Work

Collection	Mammoth Species	Material	Excavation Locality	Collections Location	Age	Dating Method
Smithsonian	*M. primigenius, M. columbi, M. boreus (M. primigenius?)*	5 Skulls; 3 Woolly (1 highly fragmentary), 1 Columbian, 1 "boreus"	*M. Primigenius* are from Siberia *M. columbi* is from Florida *M. boreus* is from Ohio	10th St. & Constitution Ave NW Washington DC, 20560	Specimens are all listed as either Pleistocene or Quaternary in age.	N/A
American Museum of Natural History (AMNH)	*M. primigenius, M. columbi, M. jeffersonii, M. imperator* *M. meridionalis*	21 *M. columbi* (including holotype), 4 *M. jefferosoni* (including holotype), 61 *M. primigenius*	*M. columbi* primarily collected from Texas and Florida *M. jeffersoni* primarily collected from Texas *M. primigenius* primarily collected from Alaska	200 Central Park W New York, NY, 10024	Specimens are listed as either Pleistocene or Quaternary. Some Columbian Mammoth specimens are listed as Tertiary (65 - 2.5 Ma) but the excavation locality is not listed, and I suspect they are from outside the United States	N/A

Georgia College and State University	*M. columbi* from Brunswick Canal, GA (Type Locality)	Not Listed	Brunswick Canal, Georgia (Type locality of *M. columbi*)	231 W. Hancock St. Milledgeville, GA, 31061	Pleistocene Fauna, w/the Brunswick Canal locality dated 19,840 - 22,240 bp.	Relative Dating
University of Michigan Museum of Natural History	Possibly a large collection of *M. primigenius* and *M. jeffersoni*	Not Listed	(Possibly) Great Lakes Area, MI	Biological Sciences Building 1105 North University Avenue, Ann Arbor, MI, 48109-1085	(Possibly) Late Pleistocene	Dating pulled from Yansa & Adams (2010)
Burke Museum	*M. primigenius, M. columbi*	30 *M. primigenius* specimens; assorted ribs, long bones, vertebra, and 2 mandibles. 56 *M. columbi* specimens: 1 partial skeleton, 1 complete skeleton, 1 mandible 377 total attributed to *Mammuthus sp.* With 11	*M. primigenius* are from Alaska *M. columbi* are from the Touchet Formation, WA *Mammuthus sp.* From various localities including Alaska, King County	4300 15th Ave NE, Seattle, WA	Collections are listed as Quaternary or Pleistocene in age. Touchet Formation is listed as 16,450 -12,500 in age.	Relative? (I wiki'd it, but it lists the formation as concurrent to Missoula and Bonneville floods, but I can look into possible absolute dating)

		additional skulls, 4 mandibles, and 1 partial mandible not attributed to a specific taxon.	Washington, and undefined 'United States'			
Museum of Natural and Cultural History	*M. primigenius, M. columbi*	73 specimens, primarily unidentified; 2 mandibles and 1 skull in collection (*Mammuthus sp.*), all other collections various molar and limb bones	Alaska and Oregon	1680 E 15th Ave, Eugene, OR, 97403	Specimens are listed as Quaternary and Pleistocene in age.	N/A
University of California Museum of Paleontology	M. primigenius, M. columbi	348 specimens; 43 *M. primigenius* (1 skull, 4 mandibles, 2 tusks), 57 *M. columbi* (3 skulls) and 8 unidentified skulls attributed to	*M. primigenius* are from Alaska *M. columbi* are from Sacramento and Alameda County, California	1101 Valley Life Sciences Building, Berkeley, CA, 94720-4780	Alameda locality is Irvingtonian in age, Sacramento and Alaskan localities are Rancholabrean in age.	N/A

		Mammuthus sp.				
La Brea Tar Pits & Museum	*M. columbi*	Not listed on the website, but presumed to be a large amount (>100)	All are excavated from La Brea	5801 Wilshire Blvd., Los Angeles, CA, 90036	Collection spans between 10,000 - 20,000 years old	Radiocarbon dating of the specimens
Natural History Museum of Los Angeles	*M. columbi, M. primigenius, M. meridionalis, M. exilis*	Only fragmentary mandibles and tusks listed for *M. primigenius,* 1 *M. columbi* skull and fragmentary mandibles and tusks. Of note, fragmentary skulls of *M. exilis* and *M. meridionalis*	All are excavated from California	900 Exposition Blvd., Los Angeles, Ca, 90007	Collections are all listed as Rancholabrean in age	(Maybe) Radiocarbon, most likely relative dating
BYU Museum of Paleontology	*Mammuthus sp.*	No database is available online	All specimens are from Utah	1683 North Canyon Road, Provo, UT 84602-3300	Specimens are listed as 15,000 years old in age on the website	**N/A**

Denver Museum of Nature and Science	*M. columbi,* (Maybe) *M. primigenius, Mammuthus sp.*	16 Skulls, some with associated skeleton are listed; 8 *M. columbi* (6 fragmentary), rest are attributed to *Mammuthus sp.,* but one is from an alaskan locality so it is possibly *M. primigenius*	All except for 1 Alaskan skull are from either Weld or Jefferson County, Colorado	2001 Colorado Blvd., Denver, CO, 80205	All specimens are listed as Quaternary or Pleistocene in age	**N/A**
Idaho State University Natural History Museum	*M. columbi,* (possible) *M. primigenius*	7 complete mammoth skulls	Collections are from Idaho localities	698 E Dillon St., Pocatello, ID, 83201		

Appendix F: Taxonomy

The systematic framework listed below was adapted from; Maglio (1973). This framework represents morphological and geographical similarities, as well as evolutionary relationships where applicable.

Genus: *Mammuthus* Burnett, 1830

Synonymy:

Mammuthus Burnett, 1830: p. 352 (for *E. primigenius*).
Dicyclotheriumn R. Geoffroy St.-Hilaire, 1837: p. 119 (for *E. primigenius*).
Cheirolites von Meyer, 1848: p. 286 (for *E. primigenius*).
Archidiskodon Pohlig, 1888: p. 138 (for *E. meridionalis*).
Parelephas Osborn, 1924: p. 4 (for *E. jeffersonii*).

Type Species: *M. primigenius* Blumenbach, 1799

Included Species:

M. primigenius Blumenbach, 1799
M. subplanifrons (Osborn), 1928
M. africanavus (Arambourg), 1954
M. meridionalis (Nesti), 1825
M. armeniacus (Falconer), 1857
M. imperator (Leidy), 1858, 1957
M. columbi (Falconer), 1857, 1922.

Description:

Diverse group of proboscideans that range from medium-large sized species, as well as dwarfs. Taxonomic characteristics range dependent on the species stratigraphic range. These characteristics are listed from primitive to advance. M3 plate number 8-27; plates transition from thick and widely spaced, to thin and closely packed; Lamellar frequency 3.0-11.0; enamel thickness 5.5-1.0 mm. Enamel transitions from smooth to heavily, minutely folded; crown height 75%-300% greater than molar width. Cranium features for primitive species include a short symphysis, corpus, and coronoid. Condyles are recessed; anterior parietal shortened and posterior portion expanded. In all species Skull tall and convex on the side (depressed temporally); eye sockets widely spaced, with an anterior parietal ridge projecting and an optical plan directed downward in primitive species, upwards in more advanced. Tusk sheaths are closely spaced, and tusks long and spiraled.

Species: *M. subplanifrons* Osborn, 1928

Synonymy:

Archidiskodon subplanifrons Osborn, 1928: p. 672, fig. 1.
Archidiskodon andrewsi Dart, 1929: p. 711, fig. 14.
Archidiskodon proplanifrons Osborn, 1934: p. 10, fig. 2.
Archidiskodon planifrons nyanzae MacInnes, 1942: p. 86, pl. 7, fig. 9; pl. 8, fig. 1.
Mammuthus (*Archidiskodon*) *scotti* Meiring, 1955: p. 189, pls. 1-4, text figs. 1-8.
Stegolophodon sp., Singer and Hooijer, 1958: pp. 1-3, figs. 1-4.

Holotype: MMK 3920 (McGregor Memorial Museum, Kimberley): Fragmentary M_3

Description:

Primitive molar characteristics; broad with thick, widely spaced, 7-9 enamel plates. Lamellar frequency 2.5-4.5; enamel is smooth and 3.5-5.5 mm thick. Crown is 60%-90% taller than it is wide and forms 4-6 molar columns, with the worn enamel figure forming a continuous loop and strong median folds. Cranial features include a long symphysis and corpus, and a tall and narrow ramus. Specimens have been excavated from Early Pliocene beds in Eastern and Southern Africa, and are believed to be one of the more basal representatives of the genera.

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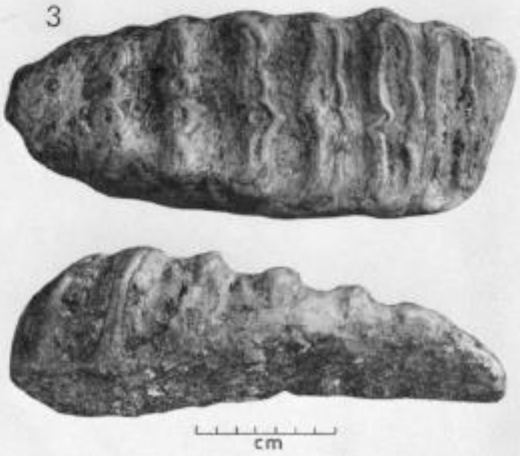

Species: *M. africanavus* Arambourg, 1952

Synonymy:
Elephas africanazus Arambourg, 1952: p. 413, pl. 1, fig. 2; text fig. 1.
Elephas meridionalis, Pomel, 1895: p. 13, pl. 1, fig. 3.
Elephas planifrons, Deperet and Mayet, 1923: p. 120, pl. 4, fig. 7.
Loxodonta africanava, Coppens, 1965: p. 348, pls. 5-8; pl. 9, figs. 1-6.

Holotype: MNHN 1950-1-12: Right M_3

Description:

Smaller representative of the genera, with moderately wide molars and thick enamel plates. Plates number 9-12 in M3 and are spaced moderately apart. Enamel thickness 2.5-4.0 mm; lamellar frequency 3.6-5.6 and crown height (-)10%-20% (sometimes 40%) greater than molar width. Anterior of enamel plate is smooth, while the posterior is folded and wears into median loops. Enamel slopes towards the crown on the side of the plate. Cranial features characteristic of genera. Specimens excavated form middle-late Pliocene beds.

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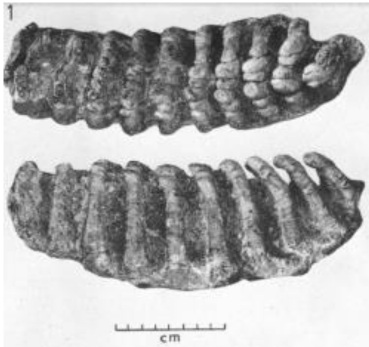

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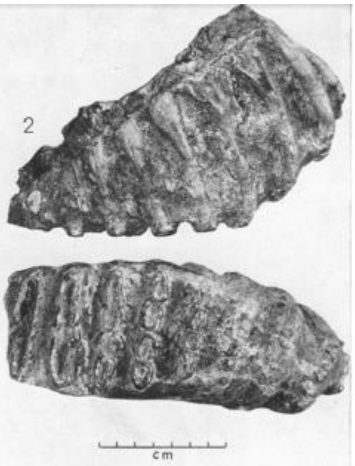

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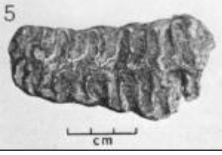

Species: *M. meridionalis* Nesti, 1825

Synonymy:

Elephas meridionalis Nesti, 1825: p. 211, pl. 1, figs. 1, 2.

Elephas antiquus Falconer and Cautley (in part), 1845-1849: pl. 14B, figs. 1, 17, 18; pl. 42, fig. 19; pl. 44, fig. 19.

Elephas lyrodon Weithofer, 1889: p. 79; 1890: p. 172, pl. 3, fig. 2; pl. 4, fig. 2; pl. 5, fig. 1; pl. 6, figs. 1-2.

Elephas planifrons, Deperet and Mayet, 1923: pp. 101-120, pl. 4, figs. 1-6, 8; pl. 5, figs. 1-5; text figs. 4-15. *Elephas planifrons rumanus* Stefanescu, 1924: p. 179. Original figure (as *E. cf. meridionalis*) in Athanasiu, 1912 (1915): pl. 17, fig. 4.

Holotype: IGF 1054: Skull with left and right M^3's (Lectotype)

Description:

Another *Mammuthus* species with broad molars and relatively thick enamel (2-4 mm). Enamel plate number more advanced, 11-14, with a crown height 10%-60% greater than molar width. Lamellar frequency 3.5-7.7; worn enamel figures more advanced than previously described species, with minor median folds only present in some specimens. Dorsal portion of skull expanded, with the anterior portion of the parietals concave transitioning to flat or convex moving dorsally. Tusk sheaths closely spaced and flaring, with massive tusks displaying twisting characteristic of the genera. Specimens occur in middle Pliocene-early Pleistocene and, given the phylogenetic span of approximately 1 million, divided into three separate evolutionary stages:

A) M. meridionalis - Laiatico Stage

Specimens excavated from beds in the Netherlands bearing an average 11-12 enamel plates on the M3. Specimens of this stage have a low crown height and lamellar frequency (3.5-4.0). Enamel plates are thick, with an enamel thickness of 3.5-4.0 mm. Enamel is sometimes weakly folded.

B) M. meridionalis - Montavarchi Stage

Specimen excavated from beds in Italy and Grenada and displays characteristics most closely in line with the specific description given above. Enamel is sometimes folded on the median portion of the plate.

C) M. meridionalis - Bacton Stage

Specimens that occur in from beds in Algeria and Germany, and displays the most advanced characteristics of the species. Upwards of 14 enamel plates on M3 molars, and a crown height 140%-160% greater than molar width. The enamel is relatively thin, and some differences in cranium characteristics, but are not elaborated upon in Maglio (1973).

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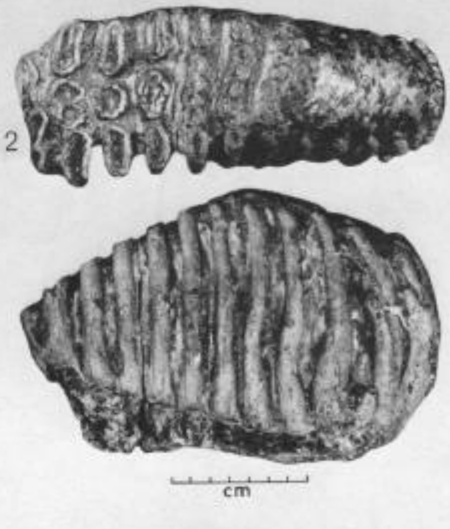

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Species: *M armeniacus* Falconer, 1857

Synonymy:

Elephas armeniacus Falconer, 1857: p. 319; 1863: p. 74, pl. 2, fig. 2.
Elephas trogontherii Pohlig, 1885; p. 1027; 1888: p. 193, fig. 79; p. 195, fig. 82.
Elephas intermedius Jourdan, 1891: p. 1013.
Elephas nestii Pohlig, 1891: p. 303; Osborn, 1942: p. 1059, fig. 941.
Elephas wiistii Pavlow, 1910: p. 6, pl. 1, figs. 1, 2.
Elephas antiquus trogontheroides Zuffardi, 1913: p. 130, pl. 9 (III), figs. 6a and 6b.
M. trongontherii

Holotype: BM 32250-52: Two M^{3}'s, and fragmentary lower molar

Description:

More advanced characteristics than previous *Mammuthus* species. Molars are narrower, with 15-21 thin enamel plates closely spaced. Lamellar frequency of 8.0 for M3 and finely folded with many small open loops. Crown height ranges from 40%-200% greater than molar width. Enamel thickness 1.5-3.0 mm and lacking a posterior median fold. Cranial characteristics representative of the genera, with an elevated parietal plane above the occipitals. Optical and mandibular plane directed more down than out, with tusk sheaths directed downwards as well. Specimens have been excavated from Middle Pleistocene beds in Europe, and are believed to be an intermediary species between *M. meridionalis* and *M. primigenius*.

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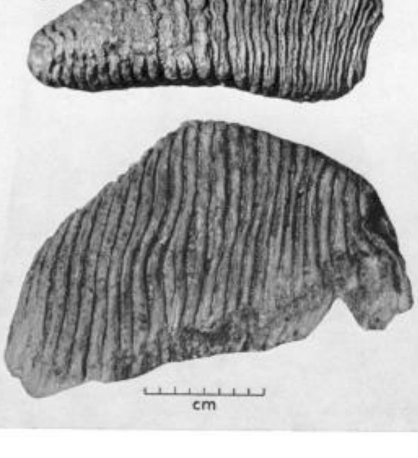

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Species: *M. primigenius* Blumenbach, 1803

Synonymy:

Elephas primigenius Blumenbach, 1803: p. 697.
Elephas mammonteus G. Cuvier, 1799: p. 21, pl. 5, fig. 2; pl. 6, fig. 1.
Elephas mammouth Link, 1807: p. 3845.
Elephas primaevus Blumenbach, in Adams, 1808: p. 152.
Elephas jubatus Schlotheim, 1820: p. 4.
Elephas paniscus Fischer de Waldheim, 1829a: pp. 285, 289.
Elephas periboletes Fischer de Waldheim, 1829a: pp. 285, 290, pl. 18, fig. 1.
Elephas pygmaeus Fischer de Waldheim, 1829a: pp. 285, 292, pl. 18, fig. 2.
Elephas campylotes Fischer de Waldheim, 1829a: pp. 285, 291.
Elephas kamenskii Fischer de Waldheim, 1829b: p. 276.
Mammut sibricum von Meyer, 1832: p. 64.
Elephas brachyramphus Brandt, 1832: p. xi. Figured by Tilesius, 1815: pl. 10.
Elephas giganteus Brandt, 1833. Figured by Breyne, 1741: pl. 1, figs. 1, 2.
Elephas commutatus Brandt, 1833. Figured by Cuvier, 1825: pl. 9, fig. 7 and p. 179.
Elephas stenotaechus Brandt, 1833: p. xiii.
Elephas platytaphrus Brandt, 1833: p. xiv. Figured by Cuvier, 1825: pl. 9, figs. 5 and 6.
Elephas macrorynchus Morren, 1834: p. 23, pl. 2, figs. 1-4.
Elephas odontotyrannus Eichwald, 1835: p. 723, pl. 63, figs. 1, 2.
Dicyclotherium primigenius R. Geoffroy Saint-Hilaire, 1837: p. 119, fig. 1.
Elephas americanus De Kay, 1842: p. 101, pl. 32, fig. 2.
Elephas kamensis de Blainville, 1845: p. 202.

Holotype: Zoological Institute of the Museum of the University of Gottinge: Left M_3 (Lectotype)

Description:

The eponymous Woolly Mammoth displays some of the most advanced taxonomic characteristics of the proboscideans. Smaller in size than most mammoths, *M. primigenius* averages 8-12 feet at shoulder height. Molars are narrow, with closely packed, thin enamel plates. Plate number ranges from 20 to 27, resulting in a lamellar frequency of 7-12 from M1-M3. Crown height is 50%-150% greater than molar width, with an enamel thickness of 1-2 mm. Worn enamel figure is irregular, and enamel is heavily folded with many tiny open loops. Crown displays wide intervals of cement between enamel plates.

Cranium features are similar to *M. trongontherii*, with an elevated parietal region that is compressed longitudinally. The anterior and posterior are concave, and the lateral sides of the skull are convex. Occipitals meet at the forehead at a right angle, and tusk sheaths are directed downwards. This species is widespread during the middle Pleistocene, with specimens being excavated from beds in Europe, Asia, and North America.

North American Mammoths

Species: *M. meridionalis* Nesti, 1825

Synonymy:
Elephas meridionalis Nesti, 1825: p. 211, pl. 1, fig. 1, 2.
Archidiskodon hayi Barbour, 1915: p. 129, figs. 1, 3.5d.
Archidiskodon haroldcooki Hay, 1928: p. 33; Hay and Cook, 1930: pl. 3, fig. 1; pls. 13, 14.
Archidiskodon meridionalis nebrascensis Osborn, 1932: pp. 1- 3, figs. 1-3.

Holotype: Same as European species

Description:
Taxonomic characteristic similar to the Bacton evolutionary stage previously described.

Species: *M. imperator* Leidy, 1858

Synonymy:
Elephas imperator Leidy, 1858: p. 2; 1869, pl. 25, fig. 3.
Elephas exilis Stock and Furlong, 1928: p. 140; Stock, 1935: p. 210; fig. 6.
Archidiskodon sonorensis Osborn, 1929: p. 18; fig. 18.

Holotype: USNM 185: Fragmentary M^3

Description:
Originally believed to be a separate species of mammoth, *M. imperator* is now considered a junior synonym of *M. columbi*. The more primitive members of *M. columbi* originally ascribed to this species is very large, with a large heavy mandible and 16-19 enamel plates in broad molars. These characteristics progress to the more advanced characteristics observed in *M. columbi* specimens.

Species: *M. columbi* Falconer, 1857

Synonymy:
Elephas columbi Falconer, 1857: p. 319; 1863: p. 43, pl. 1.
Elephas jeffersonii, Osborn, 1922: p. 11, fig. 10.
Elephas roosevelti Hay, 1922: p. 100. Figured in Osborn, 1942: fig. 968.
Elephas washingtonii Osborn, 1923: p. 4; 1942: p. 1101, figs. 972, 975, 893B and BI.
Parelephas progressus Osborn, 1924: p. 4; 1922, figs. 11, 12.
Elephas eellsi Hay, 1926: p. 154, figs. 1, 2.
Elephas floridanus Osborn, 1929: p. 20, fig. 20.

Description:

North American specimens have been excavated from Late Pleistocene beds, and display some of the most advanced proboscidean features alongside *M. primigenius*. Molars are narrow, with 18-20 thin, closely packed molar plates.

Species: *M. jeffersonii*

Description:
This is a *Mammuthus* species that displays taxonomic characteristics that are intermediary between the more primitive *M. columbi* and *M. primigenius*. This mammoth displays molar characteristics such as: 20-30 closely packed enamel plates; enamel thickness 3.0-15 mm; and a lamellar frequency of 5-9. Once believed to be a junior synonym to *M. columbi*, recent genomic studies conducted by Enk, et al. (2016) has proposed that this species is actually a hybrid between *M. columbi* and *M. primigenius*. This hybrid occurred around the latest Pleistocene, during the Rancholabrean NALMA. *M. jeffersonii* is proposed to represent its own geographic ecological niche, occupying areas previously covered by the receding glacial sheet at this time.

Species: *M. primigenius*

Synonymy:
Elephas primigenius Blumenbach, 1803: p. 697.
Elephas jacksoni Mather, 1838: p. 96, fig. A (p. 363).
Elephas americanus DeKay, 1842: p. 101, pl. 32, fig. 2.

Description:
Same taxonomic characteristics as Eurasian species, *M. primigenius* is present on the North American continent from the Rancholabrean NALMA up to the megafaunal extinction that occurred approximately 11,700 Ka.