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New mammutids (Proboscidea) from the Clarendonian and Hemphillian of Oregon – a survey of Mio-Pliocene mammutids from North America

By W. von Koenigswald[1], C. Widga[2], and U.B. Göhlich[3]

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[1]Universität Bonn, Institut für Geowissenschaften – Paläontologie, Nussallee 8, D 53115 Bonn, Germany
[2] Center of Excellence in Paleontology, East Tennessee State University, Johnson City, TN 37614 USA
[3] Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung, Burgring 7, 1020 Wien, Austria

Orcid numbers:
W. v. Koenigswald https://orcid.org/0000-0002-0109-0736
C. Widga https://orcid.org/0000-0002-2961-0078
U.B. Göhlich https://orcid.org/0000-0002-9553-3488

Corresponding author:
Wighart v. Koenigswald - mail address: koenigswald@uni-bonn.de

Author Contributions

WvK, CW, and UBG conceived and designed the study, performed the investigation, analyzed the data, prepared figures and tables, authored or reviewed drafts of the paper, approved the final draft.

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CONTENTS

CONTENTS

CONTENTS

FIGURES

TABLES

PLATES

ABSTRACT

A survey of Miocene-Pliocene Mammutidae from North America is provided. Two important but undescribed specimens from Unity (Clarendonian) and Hermiston (Hemphillian) are reported, and a previously described mandible from Black Butte (Clarendonian) is revisited. The Unity specimen, a maxilla with a tusked longirostrine mandible, represents *Zygolophodon proavus*. Upper and lower tusks are well developed. Mammutid species are best characterized by traits of the mandible, the upper tusks and lower and upper dentitions. However, they are rarely preserved in a single individual, as in the Unity specimen. A second mammutid mandible from the nearby, stratigraphically similar Black Butte locality has a short, tuskless symphysis and was described as "*Mammut (Pliomastodon) furlongi*". We question the independence of this species, because both types of mandibles are coeval in several Eurasian localities. The widespread geographic and stratigraphic co-occurrence of different mandible types cannot be explained through a phylogenetic model alone. Therefore, we discuss whether these parallel mammutid occurrences can be interpreted as resulting from species diversity, intraspecific variability, pathological abnormities, or as a sex-linked morphological difference.

The Hermiston maxilla from the upper Hemphillian represents *Mammut matthewi*. The large upper tusk differs from *Z. proavus*. The morphology of the mandible, however, remains unknown, thus its precise evolutionary stage is uncertain. The maxillary molars of the Hermiston specimen are larger than in *Z. proavus* however, we observe a high degree of variability in the size of mammutid molars so this character alone is not indicative of a specific evolutionary stage.

The relatively small number of localities with informative specimens and the conservative dental morphology of mammutids throughout the Miocene and Pliocene obscures the potential occurrence of synchronous North American taxa. Our results favor the interpretation of a continuous and endemic evolution from *Zygolophodon* to *Mammut* and make an independent immigration of the genus *Mammut* from Eurasia less probable. Therefore, the genus name *Mammut* should be avoided for Eurasian mammutids.

Keywords: *Mammutidae, Proboscidea, North America, Biostratigraphy, Miocene, Sex- linked morphological difference*

INTRODUCTION

Mammutidae are a family of the proboscidean Elephantimorpha TASSY & SHOSHANI, 1997 (in Shoshani et al., 1998). Originating in Africa, they expanded through Eurasia and colonized North America during the Middle Miocene (Saunders, 1996; Prothero et al., 2008). They are characterized by zygodont molar morphology, which is extremely conservative throughout their evolutionary history. Due to this morphological conservativism, taxonomic differentiation during the Neogene is difficult to establish on the basis of molar morphology alone.

However, some evolutionary trends are observed within Neogene mammutids, e.g. shortening of the symphysis with partial reduction of the mandibular tusks, large and curved upper tusks, and the loss of an enamel band. Highly variable dental morphology of Late Pleistocene *Mammut americanum* (KERR, 1792), (King & Saunders, 1984; Green, 2006) cautions against the over-interpretation of subtle differences in Neogene forms. Tooth morphology and measurements alone are insufficient for discriminating the evolutionary stages of different lineages within the Mammutidae. More complete specimens of early Mammutidae are required to illustrate the coherence of characters between the cranium and mandible.

Mammutidae are best known from the many skeletons of *M. americanum* that document an exceptional diversification during the late Pleistocene (Allmon & Nester, 2008; Fisher et al., 2014; Karpinski et al., 2020; Widga et al., 2017a; Zazula et al., 2014). During the Miocene and Pliocene, however, the record of fossil mammutids is inadequate, both in terms of the number of specimens and in the geographical distribution of mammal bearing localities across the North American continent. Most occurrences are of isolated molars or fragmentary portions of mandibles. Complete mandibles are rare, and only three complete maxillae have been published to date. Due to morphologically conservative molars, upper tusks and the symphyseal region of the mandibles have been the primary vehicle to characterize different taxa. Many species, however are based on single elements that provide insufficient diagnostic detail (e.g., Cope, 1889; Osborn, 1936; Hibbard, 1944) and thus cannot be productively compared to other localities. As a result, North American mammutids have experienced significant taxonomic pruning in recent decades (Lambert & Shoshani, 1998). The scenario accepted by most modern studies follows Saunders (1996) and Lambert & Shoshani (1998), although these scenarios may underestimate the possible diversity of synchronous species.

Remains of Neogene Mammutidae are often rare and incomplete with several species known only from isolated molars. Several mandibles of type specimens lack any associated information about the upper dentition. Therefore, the Unity and Hermiston crania are welcome exceptions. Nevertheless, anatomical detail remains limited due to poor preservation, so we consider any quantitative phylogenetic approach to be premature. Here we give a short stratigraphic survey of the occurrences of Miocene Mammutidae.

MIOCENE MAMMUTIDAE IN NORTH AMERICA

During the late **Hemingfordian** North American Land Mammal Age (i.e., NALMA; 20.6-16.3 Ma), *Zygolophodon* VACEK, 1877 emigrated from Asia via the Bering land bridge (Tobien, 1977). The oldest evidence of *Zygolophodon* in North America is a fragmentary cheek tooth from Massacre Lake (NV), dated 16.5-16.4 Ma (Morea, 1981; Prothero et al., 2008). Material that is more informative comes from the Barstovian Pawnee Creek site (CO; Frick, 1933). The species *Zygolophodon proavus* COPE, 1873 (including *Miomastodon brevidens* COPE, 1889 and *Miomastodon merriami* OSBORN, 1921) is the only mammutid in North America during the **Barstovian** NALMA (16.3-13.6 Ma). From the **Clarendonian** NALMA (13.6-10.3 Ma) comes a very informative specimen from Unity (11-12 Ma) representing *Z. proavus*. It is one of the main objects of this paper and is compared to the mandible of "*Mammut furlongi*" SHOTWELL & RUSSELL, 1963, which comes from the nearby Black Butte locality and is of the same stratigraphic age.

According to the general scheme of Saunders (1996), the genus *Mammut* (= *Pliomastodon* OSBORN, 1926) emerged from *Zygolophodon* (= *Miomastodon* OSBORN, 1922) with *M. matthewi* OSBORN, 1921 during the **Hemphillian** NALMA (10.3-4.9 Ma). The type specimen of *M. matthewi*, however, is extremely poor (Osborn, 1921). Characters of *Mammut*, such as enlarged upper tusks and a shortened mandibular symphysis, are not preserved together in any single locality from the Hemphillian. *Mammut* (*Pliomastodon*) *nevadanum* STOCK, 1936 shows enlarged upper tusks but has no preserved mandible. No other mandibles are available from this period, thus, the transition from *Zygolophodon* to *Mammut* is poorly documented. Many American paleontologists (e.g. Osborn, 1936; Saunders & Tassy, 1989) have postulated an endemic evolutionary transition, whereas European researchers (Schlesinger, 1917; 1922; Fejfar, 1961; Kubiak, 1972; Tobien, 1977; 1986; 1996) have discussed the genus *Mammut* as an immigrant from Eurasia.

Several mammutid species from the **Blancan** NALMA (4.9-1.8 Ma) were initially established: *Pliomastodon vexillarius* MATTHEW, 1930, *Pliomastodon raki* FRICK, 1933, *Pliomastodon cosoensis* SCHULTZ, 1937, and *Pliomastodon adamsi* HIBBARD, 1944. These were attributed to *Pliomastodon* and later the entire genus was synonymized with *Mammut* (Shoshani and Tassy, 1996). Some of them are regarded either as (potentially) valid or synonymized with *Mammut americanum*. One of the earliest reported examples of *M. americanum* comes from the early Blancan Ringold Formation in Washington (Gustafson, 1978). There is a range of morphological variability, possibly even a degree of taxonomic diversity in North American mammutids from the Blancan, but at the current time, small sample sizes do not provide much taxonomic resolution.

During the Quaternary, two species of *Mammut* are present, *M. americanum* KERR, 1792 and the recently described *Mammut pacificum* DOOLEY et

Table 1. Miocene and Pliocene mammutid taxa and their synonymized names used in this paper

Stratigraphic abbreviations: BA-Barstovian; BL- Blancan, CL – Clarendonian, HH – Hemphillian; PL - Pleistocene

Originally described mammutid species	Type locality and Stratigraphy	In this paper
Mammut adamsi HIBBARD, 1944	Saw Rock (KS), BL	*Mammut matthewi*
Elephas americanus KERR, 1792	Big Bone Lick (KY), PL	*Mammut americanum*
Tetrabelodon brevidens COPE, 1889	Deep River (MT), BA	*Zygolophodon proavus*
Pliomastodon cosoensis SCHULTZ, 1937	Coso Mountains (CA), BA	*Mammut cosoensis*
Mammut (Pliomastodon) furlongi SHOTWELL & RUSSELL, 1963	Black Butte (OR), CL	*“Mammut furlongi”*
Mastodon matthewi OSBORN, 1921	Thompson Quarry 1 (NE), HH	*Mammut matthewi*
Mastodon merriami OSBORN, 1921	Virgin Valley (NV), BA	*Zygolophodon proavus*
Pliomastodon nevadanus STOCK, 1936	Thousand Creek Beds (NV), HH	*Mammut nevadanum*
Mammut pacificus DOOLEY Jr et al. 2019	Hemet (CA), PL	*Mammut pacificum*
Mastodon proavus COPE, 1873	Pawnee Creek (CO), BA	*Zygolophodon proavus*
Mastodon raki FRICK, 1933	Truth or Consequences (NM), BL	*Mammut raki*
Pliomastodon sellardsi SIMPSON, 1930	Brewster (FL), HH	*Mammut matthewi*
Pliomastodon vexillarius MATTHEW, 1930	Elephant Hill (CA), BL	*Mammut matthewi*

al., 2019. The former is found throughout much of North America, while the latter is geographically restricted to the western part (Dooley et al., 2019; McDonald et al., 2020). Mammutids persisted in North America until the end of the Pleistocene, but never emigrated to South America (Lucas & Alvarado, 1991). See Table 1 for a list of mammutid species used in this paper.

THE PROJECT

While working on a mammutid skeleton from Germany (Koenigswald et al., 2022); we discovered online an undescribed Miocene mammutid cranium with mandible from Unity (OR) that is on exhibit at the Oregon Museum of Science and Industry (OMSI) in Portland. During efforts to access this important specimen, we learned of another undescribed Miocene mammutid maxilla from Hermiston (OR) in the Paleontology collection at the University of Oregon, Eugene (OR). This collection also houses the type mandible of “*Mammut furlongi*” SHOTWELL & RUSSELL, 1963 from Black Butte (OR). These three specimens from Oregon, Unity, Black Butte, and Hermiston, were the starting point for the current project which grew to become a survey of the Miocene and Pliocene Mammutidae from North America. Although detailed, this survey remains limited in scope. This study makes clear that further revision of Miocene and Pliocene Mammutidae in North America is needed and clarifies key questions to be answered with future research efforts.

INVESTIGATED MATERIALS AND METHODS

MATERIALS

Several genera and species have been proposed for Barstovian, Clarendonian, and Blancan mammutid fossils. Names of Barstovian taxa have generally been synonymized with *Z. proavus* (e.g.

Lambert & Shoshani, 1998) while mammutids from the Hemphillian and Blancan have been generally assigned to *M. matthewi*. However, stratigraphic position often influenced the assignment of specimens to specific taxa. To avoid preconceptions and promote clarity, we use locality names for the identification of the different specimens instead of calling them by their original or synonymized species names. This is justified because all discussed localities are monospecific, often with only a single individual.

This paper focuses on the **Unity** cranium (OMSI 1946.02.1026) and the **Black Butte** (UO F 10291/2) mandible. Both specimens are from the Clarendonian. We also discuss a maxilla recovered near **Hermiston** (UO F 7024) that dates to the late Hemphillian. These fossils were investigated in person at OMSI and UO.

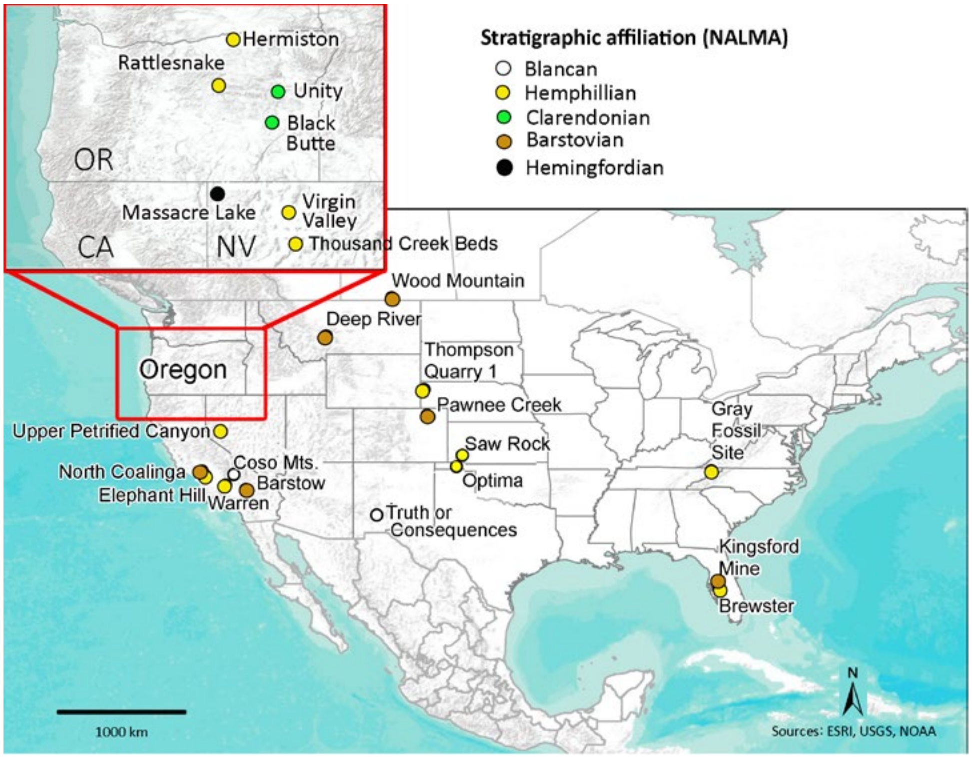
Additional data from Mio-Pliocene mammutids were collected in person, acquired through correspondence with museum staff, or gathered from the literature.

The following sites represent the **Barstovian**: Deep River (MT), Virgin Valley (NV), North Coalinga (CA), Kingsford Mine (FL), Wood Mountain (SK-CDN), Barstow (CA), and Pawnee Creek (CO). Two sites are assigned to the **Clarendonian**: Unity (OR) and Black Butte (OR). The **Hemphillian** is represented by Thomson Quarry 1 (NE), Thousand Creek Beds (NV), Rattlesnake Creek Beds (OR), Upper Petrified Canyon (NV), Hermiston (OR), Optima (OK), Brewster (FL), Warren (CA), and the Gray Fossil Site (TN). The **Blancan sample includes** Saw Rock (KS), Truth or Consequences (NM), Elephant Hill (CA), and Coso Mountains (CA).

Selected Eurasian Miocene and Pliocene sites provided mammutid mandibles with brevirostrine and gracile symphyses for comparison: Yanghecun (CN), Laogou (CN), Mikulov (CZ), Wolkersdorf (AT), Vialette and Fauverney (FR).

Locality details, their stratigraphic position, available material, and relevant collections are given in each section to avoid repetition. The North American localities are mapped in Fig. 1, and Fig. 2 provides a stratigraphic framework for this dataset.

Figure 1. Location of significant mammutid sites in the Miocene and Pliocene of North America. Localities are color coded according to their stratigraphic position. - Map data © ESRI (World Terrain Base).



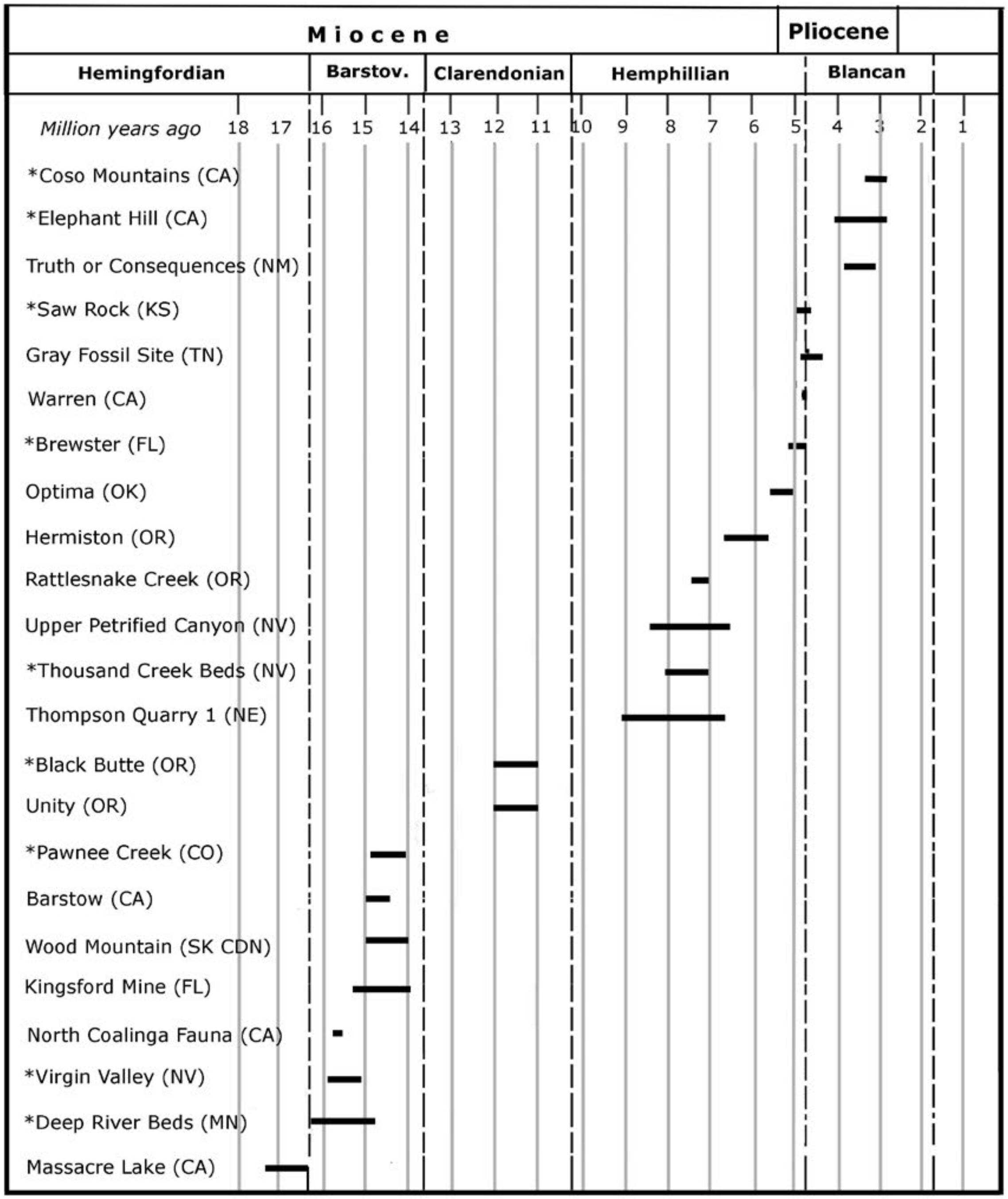


Figure 2. Approximate stratigraphic age ranges of significant Miocene and Pliocene mammutid sites. *Type localities: Coso Mountains: *Pliomastodon cosoensis (= Mammut cosoensis)*; Elephant Hill: *Pliomastodon vexillarius (= Mammut vexillarius)*; Saw Rock: *Mammut adamsi (= Mammut matthewi)*; Brewster: *Pliomastodon sellardsi (= Mammut matthewi)*; Thousand Creek Beds: *Pliomastodon nevadanus (= Mammut nevadanum)*; Thompson Quarry 1: *Mammut matthewi*; Black Butte: “*Mammut furlongi*”; Pawnee Creek: *Miomastodon proavus (= Zygolophodon proavus)*; Virgin Valley: *Mastodon merriami (= Zygolophodon proavus)*; Deep River: *Tetralophodon brevidens (= Zygolophodon proavus)*. – Refer to Table 1 for the author names. - References for the stratigraphic placement are indicated in the text description of each locality.

For the numerical ages of the boundaries between the North American Land Mammal Ages (NALMA) and the Eurasian zones of the Mammals Neogene (MN) zones we follow Hilgen et al. (2012).

METHODS

The primary characters of interest are the upper and lower molars (morphology, number of loph(id) s, and measurements), the mandible (the length of the symphysis, and the presence or absence of mandibular tusks), the maxilla (the orientation of the tooth rows), and upper tusks (presence or absence of an enamel band, curvature, and orientation).

Measurements taken include molar length and width in order to calculate length/width ratios, which roughly reflect specimen shape. All measurements were collected using digital and vernier calipers, following Göhlich (1998).

In most sites, only upper or lower molars are present, and thus a direct comparison of measurements is impossible. If one set of molars is missing, we predict an approximate length of the missing elements by using the relationship between the upper and lower M3/m3. The ratio for the length of upper and lower molars was estimated from the complete cranium and mandible of *Zygolophodon* (Unity, OR), Pliocene *Mammut* sp. (Gray Fossil Site, TN) and late Pleistocene *Mammut* (Boney Spring, MO; Saunders 1977). This relationship is (M3 = m3 x 0.939) or (m3 = M3 x 1.06). This calculated ratio between the length of upper and lower 3rd molars allows estimation of missing molar lengths.

In some cases, latex molds of studied specimens (molar crowns) were made. Reference casts are housed in the ETMNH, the NHMW and the IGPB. Specimens from Unity, Black Butte and Hermiston were 3D scanned with an Artec Eva structured light scanner. Proboscidean remains are large, and present unique challenges to 3D scanning due to the history of preparation and mounting. To reflect uncertainty in reconstruction and accessibility of specimen surfaces, all models were rendered without hole-filling. Molar casts were 3D scanned with an Artec Space Spider. Textured and un-textured 3D models are available in OBJ and STL format in the Morphosource.org project directory (https://www.morphosource.org/projects/00000C814).

ABBREVIATION FOR COLLECTIONS

AMNH – American Museum of Natural History, New York; **CIT –** California Institute of Technology, Pasadena (now housed at the LACM); **COL** - Colorado Museum of Natural History (now DMNS); **CMNH –** Carnegie Museum of Natural History, Pittsburgh, PA; **DMNS –** Denver Museum of Nature and Science (formerly EDP); **ETMNH** – East Tennessee State University Museum of Natural History, Gray, TN; **ETSU –** East Tennessee State University, Johnson City, TN; **FAM –** Frick Collection at the AMNH; **GIOTC –** Gansu Industrial Occupational Technology College, China; **GPM –** Gansu Provincial Museum, Lanzhou, China; **IGPB** – Institut für Geowissenschaften der Universität Bonn (Paläontologie), Bonn, DE; **JODA –** John Day Fossil Beds National Monument (casts at ETMNH); **KUVP –** University of Kansas Vertebrate Paleontology, Lawrence, KS; **LACM –** Los Angeles County Museum of Natural History, Los Angeles, CA; **ML –** Musée d'Histoire Naturelle, Lyon, FR; **MZM –** Moravian Museum Brno, CZ; **NHMW** – Naturhistorisches Museum, Wien, AT; **NMC –** National Museum of Canada, Ottawa, CDN; **OMSI –** Oregon Museum of Science and Industry, Portland, OR; **RAM –** Raymond Alf Museum, Claremont, CA; **RSM –** Royal Saskatchewan Museum, Regina, CDN; **UF –** University of Florida, Gainesville, FL; **UF/FGS –** Florida Geological Survey collection, now at UF; **UMORF –** University of Michigan, Online Repository of Fossils; **UO –** University of Oregon, Eugene, OR; **WSC –** Western Science Center, Hemet, CA.

ABBREVIATIONS USED IN STRATIGRAPHIC CONTEXT

BA – Barstovian; **BL –** Blancan; **CL –** Clarendonian; **HE –** Hemingfordian; **HH –** Hemphillian; **Ma –** Mega-annum; **MN –** Neogene Mammal zones in Eurasia; **NALMA** - North American Land Mammal Ages; **PL –** Pleistocene

ANATOMICAL ABBREVIATIONS

dext – right (dextra); **DP, dp** - deciduous upper and lower premolars; **I, i –**upper and lower tusks;

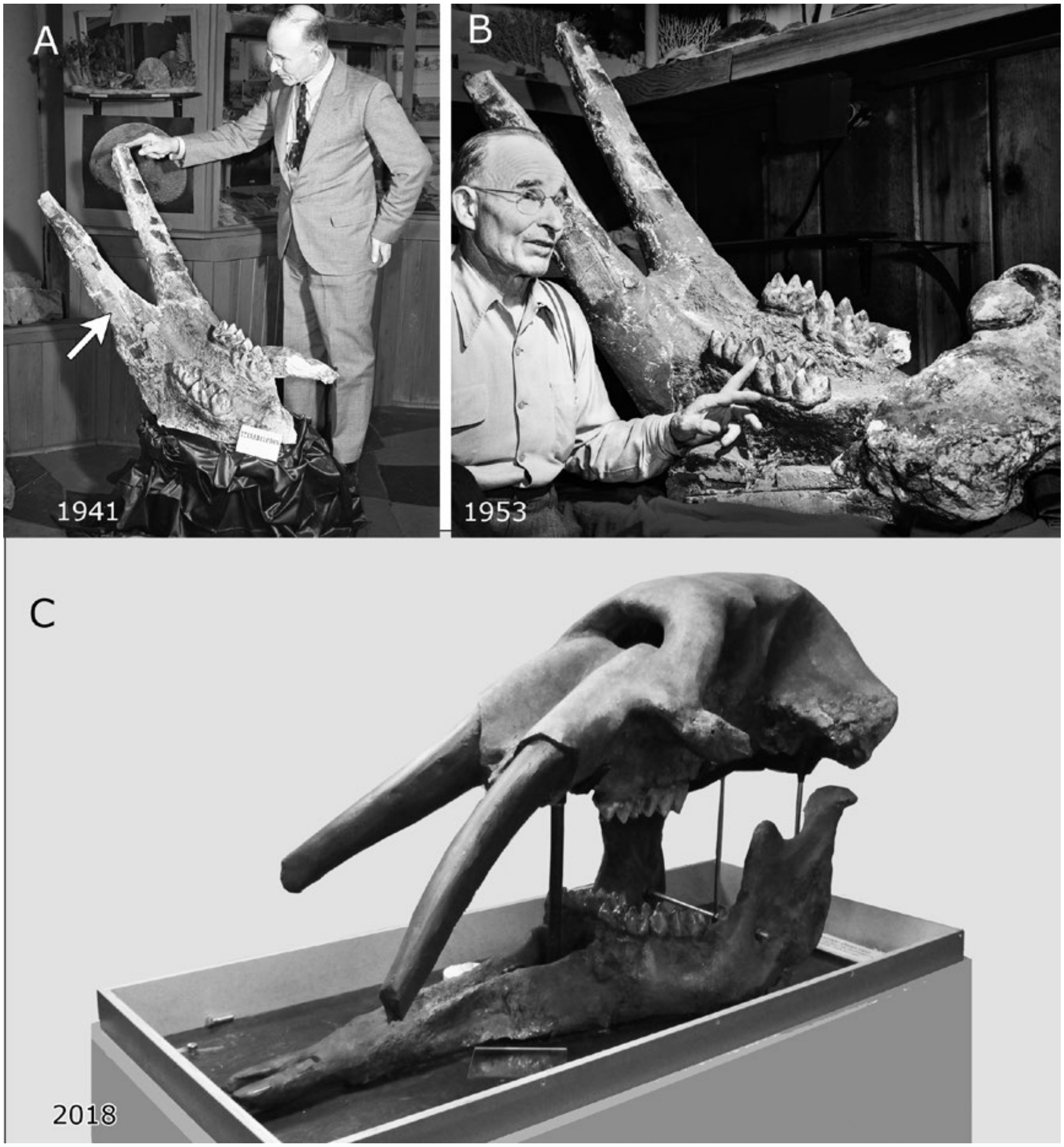


Figure 3. Cranium of *Zygolophodon proavus* from Unity (OR) "Hancock's Mastodon". (A) Unprepared skull showing tusks with Alonso Hancock in 1941. The white arrow points to the enamel band. (B) Press photo from 1953, Hancock with cranium after the visit of G.G. Simpson. (C) The cranium was reconstructed and is exhibited with its mandible (Fig. 5C) in the Oregon Museum of Science and Industry, Portland OR. (OMSI 1946.02.1026). Photos (A) and (B) are property of the Oregonian Publishing Co., used with permission.

inf – lower; **M, m-** upper and lower molars; **sin –** left (sinistra); **sup –** upper.

GEOGRAPHICAL ABBREVIATIONS

AT – Austria; **CA –** California**; CDN –** Canada; **CO –** Colorado; **CZ –** Czech Republic; **DE –** Germany; **FR –** France; **FL –** Florida; **KS –** Kansas; **KY –**Kentucky; **MT –** Montana; **MO –** Missouri; **NE –** Nebraska; **NV –** Nevada; **OR –** Oregon; **SK –** Saskatchewan; **TN –**Tennessee.

RESULTS

Systematic Paleontology

Proboscidea ILLIGER, 1811

Elephantimorpha TASSY & SHOSHANI, 1997, in Shoshani et al. 1998

Mammutidae HAY, 1922

Zygolophodon VACEK, 1877

ZYGOLOPHODON PROAVUS (COPE, 1873)

Unity – "Hancock's Mastodon"

Locality: about 4 km NE of Unity, Baker County, Oregon (Retallack, 2004: fig. 1 point 8; 44°27'N 118°W)

Stratigraphy: Ironside Fm., equivalent to Juntura Fm., Clarendonian (Retallack, 2004; 2009)

Published figures: Orr & Orr 1999; Retallack 2004: figs. 6

In this paper: Figs. 3-11

Specimen: The skull of "Hancock's Mastodon" (OMSI 1946.02.1026) consists of an almost complete mandible with left and right m2-m3 and a long symphysis with lower tusks; the dorsal part of the cranium is largely reconstructed; the premaxilla, the maxilla with M2-M3, and the basicranium are preserved (Fig. 3). In their current state, (Fig. 3C) the upper and lower tusks seem largely restored or even completely replaced by casts (perhaps they were broken in the past), but the historic photos clearly show that they were originally preserved. This specimen is on display at the Oregon Museum of Science and Industry (OMSI) in Portland. Historical photos also provide important information about the condition of this skull prior to restoration (Fig. 3A and B).

HISTORICAL NOTE ABOUT "HANCOCK'S MASTODON" FROM UNITY

"Hancock's mastodon" was excavated in 1941, but has been largely overlooked by researchers working on North American mammutids (e.g., Madden & Storer, 1985; Saunders, 1996; Shoshani & Tassy, 1996; Lofgren & Anand, 2011). Alonzo Wesley Hancock (1884-1961), a postman from Portland, OR was an ambitious fossil hunter, especially in the area of John Day Basin. By the late 1950s, he had accumulated ~10,000 fossils in his collection. In 1941, Hancock along with the paleobotanist Chester Arnold (1901-1977) from the University of California (and later University of Michigan), discovered and excavated a partial proboscidean cranium with both upper tusks near Unity in Baker County (Fig. 3). Initially it was regarded as "*Tetrabelodon*" and stored for years in Hancock's personal collection (Orr & Orr, 1999; Allen, 2005). George Gaylord Simpson visited the Hancock collection in January 1953, recognized that the cranium represented a rare Miocene mammutid, and after comparing to his notes in New York, wrote a letter to Hancock stating that the fossil probably represents *"Miomastodon merriami. It is the best specimen of that genus or species that ever has been collected, it is therefore of outstanding scientific importance and I know that you appreciate the desirability of protecting it and of seeing that it is permanently preserved."* G.G. Simpson also drew media attention to the remarkable fossil. The New York Times (March 26, 1953) mentioned the find, and *Time*, the weekly news magazine (April 6, 1953) also discussed it, including a photo of Hancock presenting the fossil cranium. In his letter, G.G. Simpson encouraged Hancock to revisit the site. The same year Hancock returned to the locality and collected a complete mandible *"about 15 feet from the spot that the skull had been discovered earlier"* (Orr & Orr, 2009: 210). The mandible was figured in a short note in the "Newsletter of the Geological Society of the Oregon Country" (1953, 19/7: 77).

Although the cranium, Simpson's visit, and the subsequent discovery of the mandible (Fig.4.) was reported in the newsletter of the Geological

Society of the Oregon Country (1953), the find was neglected and generally ignored by researchers focused on fossil proboscideans. Hancock died in 1961 and willed his collection of fossils to the Oregon Museum of Science and Industry in Portland (OMSI). In 1990, the fossil collection was transferred to the Department of Earth Sciences at the University of Oregon in Eugene as a permanent loan, with the exception of some fossils kept at OMSI for exhibition. "Hancock's Mastodon" is on display and is the most prominent specimen of the materials retained by OMSI. It is not clear from the collection documents who organized the restoration and partial reconstruction of the cranium, or when and where it was performed. We recognized that the two broken parts of the skull, the maxilla and the occiput as reconstructed, are not in the correct anatomical position. The reconstruction of the upper part of the cranium is freehanded (see below).

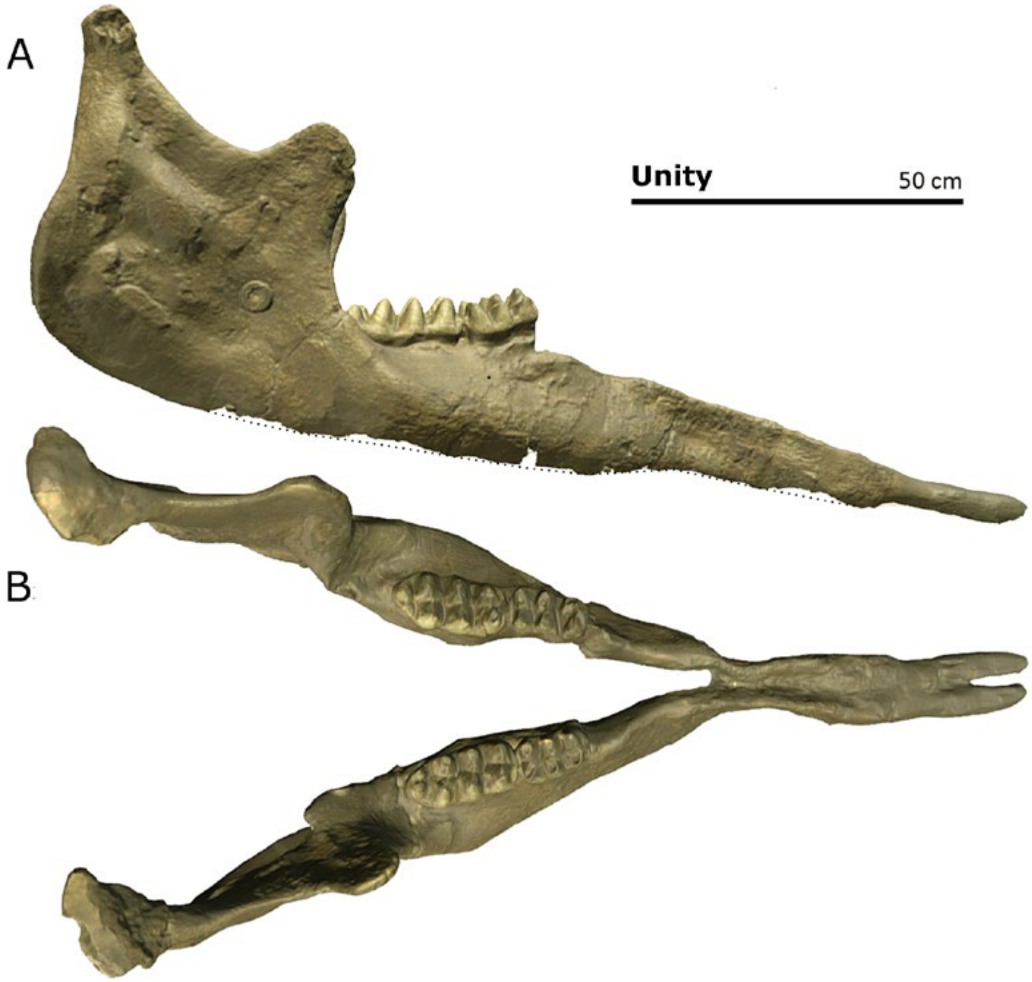


Figure 4. *Zygolophodon proavus*, mandible from Unity (OMSI 1946.02.1026) with a very long symphysis and mandibular tusks. It was found in the same locality as the cranium, but 12 years later. (A) Lateral and (B) occlusal aspects of the 3D model. Note in (A) that the lower margin of the ramus is preserved, but not included in the 3D model.

Table 2. Mandibular measurements (in cm) of the mandibles from Unity (*Zygolophodon proavus*) and Black Butte (“*Mammut furlongi*”)

	Unity OMSI-1946.02.1026t			**Black Butte** UO F 10291	**Definitions**	
	sin		dext		Tassy 2013	Göhlich 1997
Greatest length including lower tusks	-	(144)	-	-	1	
Greatest length (without tusks)	-	(122)	-	-		GL
Length (anterior end to	-	-	-	-		L1
Length (anterior end to angulus mandibularis)	117	-	114	-	4	
Length of symphysis	-	(min 40-42)	-	-	2	LS
Length from symphyseal angle to posterior end of caput mandibularis	83	-	83	52		L2
Length from symphyseal angle to medial projection of trigonum retromolare behind m3	42	-	41	31	3	
Length from anterior end of symphysis to posterior end of m3	86	-	83	-		LCp
Max. distance between processus coronoideus and angulus mandibularis	36	-	38	-	22	
Length from posterior end of m3 to posterior border of ascending ramus (ramus mandibulae)	33	-	34	-		LR1
Min length of ramus mandibulae (nearest points of anterior and posterior edges of ramus mandibulae)	28	-	(26)	-		
Length of ascending ramus (from anterior edge of proc. coronoideus to posterior end of caput mandibulae)	44	-	44	(20)		LR2
Length of tooth row (m2-m3)	26,6	-	26	-		L m2+m3
Distance of smallest width of symphysis to symphyseal angle	-	11	-	-		
	-	-	-	-		
Anterior width of symphysis	-	11	-	-	10	
Max width of symphysis	-	11	-	-	11	BS2
Min width of symphysis	-	7	-	8	12	BS
Min width of symphyseal through	-	4	-	2,7	14	BSr
Anterior width of symphyseal trough	-	6	-	-	13	
Width of mandible at symphyseal angle	-	19,5	-	16,5	9	BS1
Min distance between m1 (anterior end)	-	-	-	5,8		Am1 min
Min distance between m2 (anterior end)	-	12	-	6,6		Am2 min
Max distance between m2 (posterior end)	-	14	-	8,7		Am2 max
Min distance between m3 (anterior end)	-	14	-	10		Am3 min
Min distance between m3 (anterior end)	-	17	-	-		Am3 max
Width over both proc. coronoidei	-	48	-	38		AP
Min distance between both caput mandibulae	-	33	-	-		Amc
Max width over both caput mandibulae	-	56	-	-		AlC
Max width over both corpora mandibulae at level of anterior origin of ascending ramus	-	46	-	37	6	
Width of horizontal ramus (corpus mandibulae) at level of origin of ascending ramus	14		14	12 (dext)	7	

Table 2, continued. Mandibular measurements (in cm) of the mandibles from Unity (*Zygolophodon proavus*) and Black Butte (“*Mammut furlongi*”)

	Unity OMSI-1946.02.1026t			**Black Butte** UO F 10291	**Definitions**	
	sin		dext		Tassy 2013	Göhlich 1997
Max width of horizontal ramus (corpus mandibulae)	15		16	12 (dext)		
Width of horizontal ramus in front of dentition	8		8	6 (sin+ dext)	8	
Height anterior end of symphysis	-	8	-	-	19	
Height of symphysis at level of symphyseal angle	-	13	-	11	18	HS1
Height at symphysis at most narrow level	-	11	-	-		HS2
Height of symphysis in front of dentition	(18)	-	(14)	12	16	HCp2
Height of horizontal ramus posterior to dentition	15	-	15	-	17	HCp1
Min Height of ascending ramus	28	-	(30)	-		HRI
Height of ascending ramus to caput mandibulae	*38*	-	*(42)*	-	*20*	*HRcd*
Height of ascending ramus at proc. coronoideus	*35*	-	*(37)*	-		*HRr*

Table 3. Detailed measurements (in mm) of the molar dentition of the Unity, Black Butte, and Hermiston specimens

L – max. length, W – max. width, WI-IV – width over 1st to 4th loph(id), H – height of molar on 2nd (II) loph(id). Values in parenthesis indicate estimated measurements of slightly damaged/restored teeth.

Unity (OMSI 1946.02.1026), **Black Butte** (UO F 10291/2) **Hermiston** (UO OR 7024)

	L mm	**W mm**	**WI mm**	**WII mm**	**WIII mm**	**WIV mm**	**H mm**	**L/W ration**	**W/L index**
Unity									
M3 sup dext	142	82	79	82	78	48	II 64	1.73	57.8
M3 sup sin	149	85	80	85	80	51	II 65	1.75	57.0
M2 sup dext	107	70	66	70	68	-	-	1.52	65,4
M2 sup sin	107	73	68	73	69	-	-	1.47	68.2
M2+M3 sup sin	256								
M2+M3 sup dext	246								
m3 inf dext	158	76	73	76	74	47	-	2.07	48.1
m3 inf sin	158	80	73	79	78	48	II 60	2.0	50
m2 inf dext	105	67	56	62	66	-	-	1.56	63.8
m2 inf sin	(111)	67	58	62	67	-	-	1.66	60.3
m2+m3 inf sin	270								
m2+m3 inf dext	260								

Table 3, continued. Detailed measurements (in mm) of the molar dentition of the Unity, Black Butte, and Hermiston specimens

L – max. length, W – max. width, WI-IV – width over 1st to 4th loph(id), H – height of molar on 2nd (II) loph(id). Values in parenthesis indicate estimated measurements of slightly damaged/restored teeth.

Unity (OMSI 1946.02.1026), **Black Butte** (UO F 10291/2) **Hermiston** (UO OR 7024)

	L mm	W mm	WI mm	WII mm	WIII mm	WIV mm	H mm	L/W ration	W/L index
Black Butte									
m3 inf dext	170	78	75	(78)	-	67	-	2.18	45.9
m3 inf sin	160	78	73	78	-	-		2.5	46.4
m2 inf dext	109	67	58	64	67	-		1.62	61.5
m2 inf sin	106	66	57	62	66	-		1.61	62.3
m1inf dex	73	55	-	-	-	-		1.33	75.3
m1 inf sin	74	54	-	-	-	-		1.37	73.0
m2+m3 inf sin	(279)	-	-	-	-	--		-	-
m2+m3 inf dext	(166)					-		-	-
Hermiston									
M3 sup dext	178	98	98	96	93	64		1.82	55.0
M3 sup sin	167	96	96	92,5	88	64	(II 61)	1.74	57.5
M2 sup dext	113	84	83	83.5	77	-	-	1.35	74.4
M2 sup sin	110	80	79	79.5	76	-	-	1.37	72,3
M2+M3 sup dext	292	-	-	-	-	-	-	-	-
M2+M3 sup sin	282	-	-	-	-	-	-	-	-

The cranium has been mentioned and figured only in connection with Oregon geology or fossils, e.g., as *Mi. merriami* (Baldwin, 1964; Orr & Orr, 1999; 2009). Retallack (2004) attributed it to *Gomphotherium osborni*, (BARBOUR, 1916) referring to another find nearby. However, the mammutid nature of the Unity specimen is clear.

In 2005, the Oregon History Project (OrHi 10688) posted a note on A.W. Hancock online with a photo showing him with his "*Miomastodon*" maxilla (Fig. 3B) (Allen, 2005). This note led to our interest in the "Hancock cranium", its subsequent investigation, and description in this paper almost 80 years after its discovery.

LOCALITY AND STRATIGRAPHY OF THE UNITY MAMMUTID (Figs. 1 and 2)

The locality where the specimen was found is about 4 km NE of Unity, Baker County, OR, and 21.5 km NE from Ironside, Malheur County, OR (44.45°N 18.15W) (reconstructed from Retallack, 2004: Fig. 1 Point 8). Earlier papers mentioning the site were less precise, referring to it as "near Ironside in Malheur County" (Orr & Orr, 1999; 2009).

The mammutid specimen is from the Ironside Formation, equivalent in age to the Juntura Formation (Retallack, 2004). In Orr & Orr (1999; 2009), the locality was erroneously attributed to the underlying Mascall Formation. The faunal and floral context, however, indicate a Clarendonian age (Retallack, 2004; 2009). Dates from nearby ash deposits suggest an age range between 11.5 and 11.8 Ma, corresponding with lithologically similar ashes from the Great Basin (Perkins et al., 1998). Therefore, an age of about 11-12 Ma can be inferred for the Ironside-Juntura Formations. Retallack (2004) describes the paleo-environment of the Unity locality as a live oak woodland and savanna, based on fossil flora and soils.

DESCRIPTION OF THE UNITY SPECIMEN

The skull of the "Hancock Mastodon" consists of a mostly complete mandible and ventral portions of the cranium including the premaxilla, the maxilla and the basicranium (Fig. 3 – 6). As described below, the reconstruction of the cranium is anatomically incorrect.

Measurements of the mandible are given in Table 2, those for the dentition in Table 3.

MANDIBLE (Fig. 4)

The mandible is well-preserved, but has broken posterior to the symphyseal angle where it is partly restored. None of the foramina, usually present on the mandible, can be located – perhaps due to the restoration. Nevertheless, the following characters can be confidently described.

The mandible has a long, narrow symphysis with two lower tusks. The anterior-most end of the symphysis was restored; therefore, its exact length is unclear. However, the minimal preserved length of the symphysis is 40 cm, which is about one third longer than the length of the tooth row (m2-m3). The symphysis is not deflected relative to the horizontal ramus, so the ventral border of the mandible is almost straight. Unfortunately, the mandible has been broken just posterior to the symphyseal angle; so, we cannot be confident that the attachment between horizontal ramus and symphysis exactly reflects the original condition. The straight ventral margin of the mandible declines about 10° relative to the occlusal surface of the tooth row. The protruding symphysis is almost as long as the horizontal ramus (corpus mandibulae) and thus longirostrine. In its anterior part, it is wider than high, but is mediolaterally constricted just anterior to the symphyseal angle; at this narrowest point the symphysis is taller than wide, and both lateral surfaces are concave; this concavity is distinctly deeper on the left side than on the right side, which is probably due to post-depositional breakage. A symphyseal groove on the dorsal side of the symphysis is shallow in its anterior part but gets deeper and narrower, delimited by ridges on each side, towards the symphyseal angle.

The angle between the two horizontal rami is about 35°. The horizontal rami are inflated laterally with the tooth rows shifted towards the medial/lingual sides. The divergence of both tooth rows is only about 15°. Ventral to the m3 the medial wall of the horizontal ramus is deeply concave, leading to a narrow ventral margin of the horizontal ramus. Posterior the m3, a large trigonum retromolare projects medioposteriorly. The ascending ramus is mediolaterally narrow, but anteroposteriorly long. Its anterior and posterior margin are parallel and almost vertical in relation to the horizontal ramus. The ventral margin of the ascending ramus rises slightly from below the distal end of the m3 towards the mandibular angle, which is rounded. The processus coronoideus is blunt and rounded. The caput mandibulae (condyle) is somewhat higher than the processus coronoideus and forms a transversely expanded ellipsoid condyle. The shape of the incisura mandibulae is reconstructed on both sides. The fossa masseterica is preserved only on the right ascending ramus where it covers only the upper quarter. Its position is similar to *M. americanum*, but is shallower.

CRANIUM (Figs. 3, 5 and 6)

The following portions of the ventral cranium are preserved: the ventral os incisivum with both tusk alveoli, the maxilla with both tooth rows, the most anterior part of the left zygomatic arch, and the basicranium including the os temporale with both mandibular fossae and the ventral half of the occipital region with occipital condyles and foramen magnum. No sutures between the bones or any foramina are visible.

As is visible in the historic photos, the ventral cranium was broken between basicranium and maxilla (Fig. 3), and the two portions were reconstructed in a slightly incorrect anatomical position. In the current arrangement, mandible and maxilla cannot occlude because the basicranium was attached too ventrally to the maxillary portion. The basicranium should be inclined and shifted dorsally in relation to the maxilla, which was performed using the photo of the digital 3D model (Fig. 6C),

The facial and dorsal part of the cranium is also freehand-reconstructed (Fig. 5D). In comparison to *M. americanum* (Fig. 5A), the cranium of *Zygolophodon* has a straight profile with a high

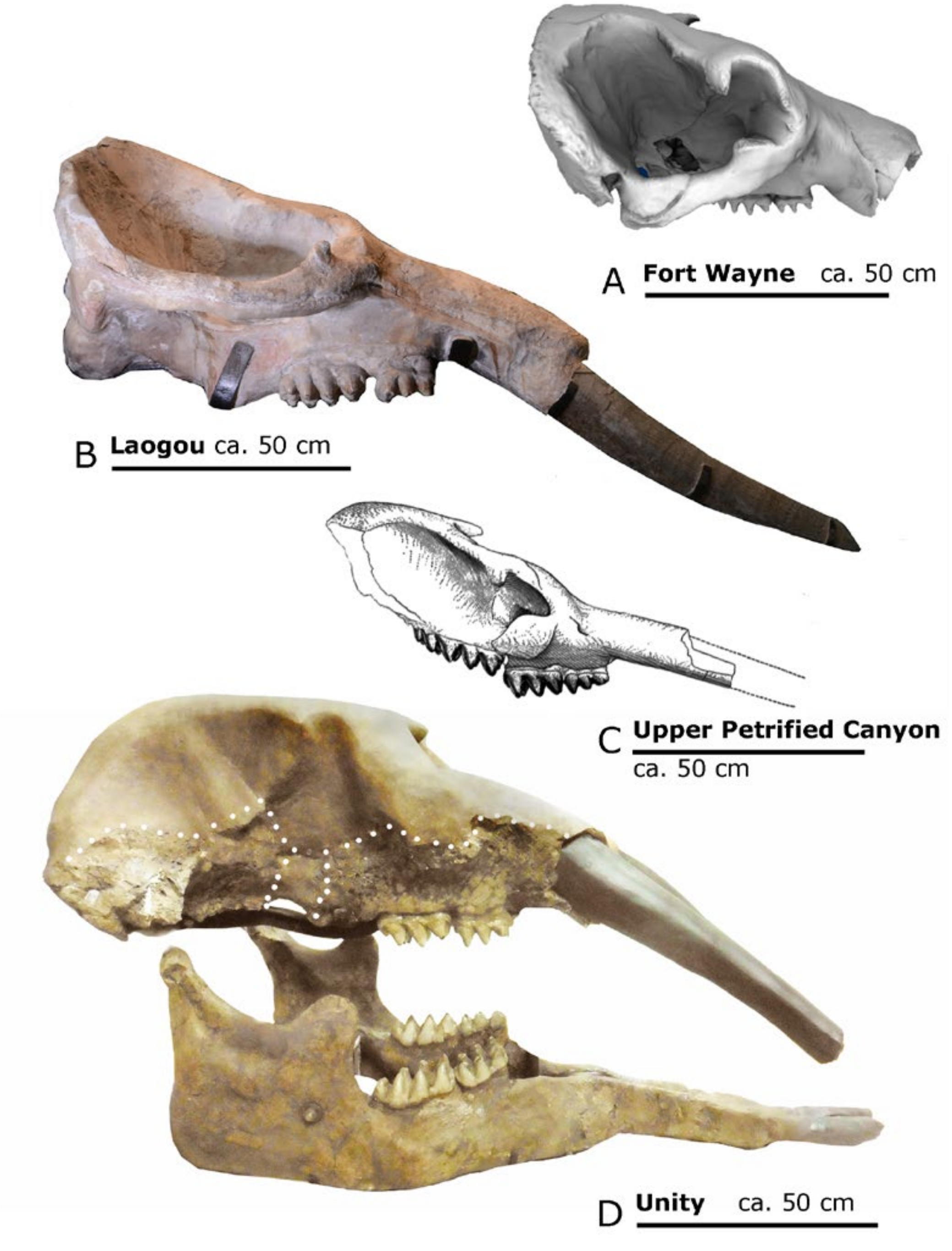


Figure 5. Crania of Mammutidae. – (A) Cranium of *Mammut americanum*, Bueshing Mastodon, Fort Wayne (Indiana), Upper Pleistocene, (Indiana State Museum and UMORF, ISM 71.3.26. - 3D model (credit: UMORF). (B) *Zygolophodon* sp., Laogou, Gansu Province, China; late Middle Miocene, approximately 13-12 Ma, (Gansu Provincial Museum, GPM ZR001141) (photo credit: Shi-Qui Wang, IVPP). (C) Partial cranium assigned as *Mammut nevadanum* from Upper Petrified Canyon (from MacDonald, 1959). (D) Photo of *Zygolophodon proavus* from Unity as it is exhibited in the Oregon Museum of Science and Industry, Portland OR (OMSI 1946.02.1026). Note that the part above the line of white dots is freehand reconstructed.

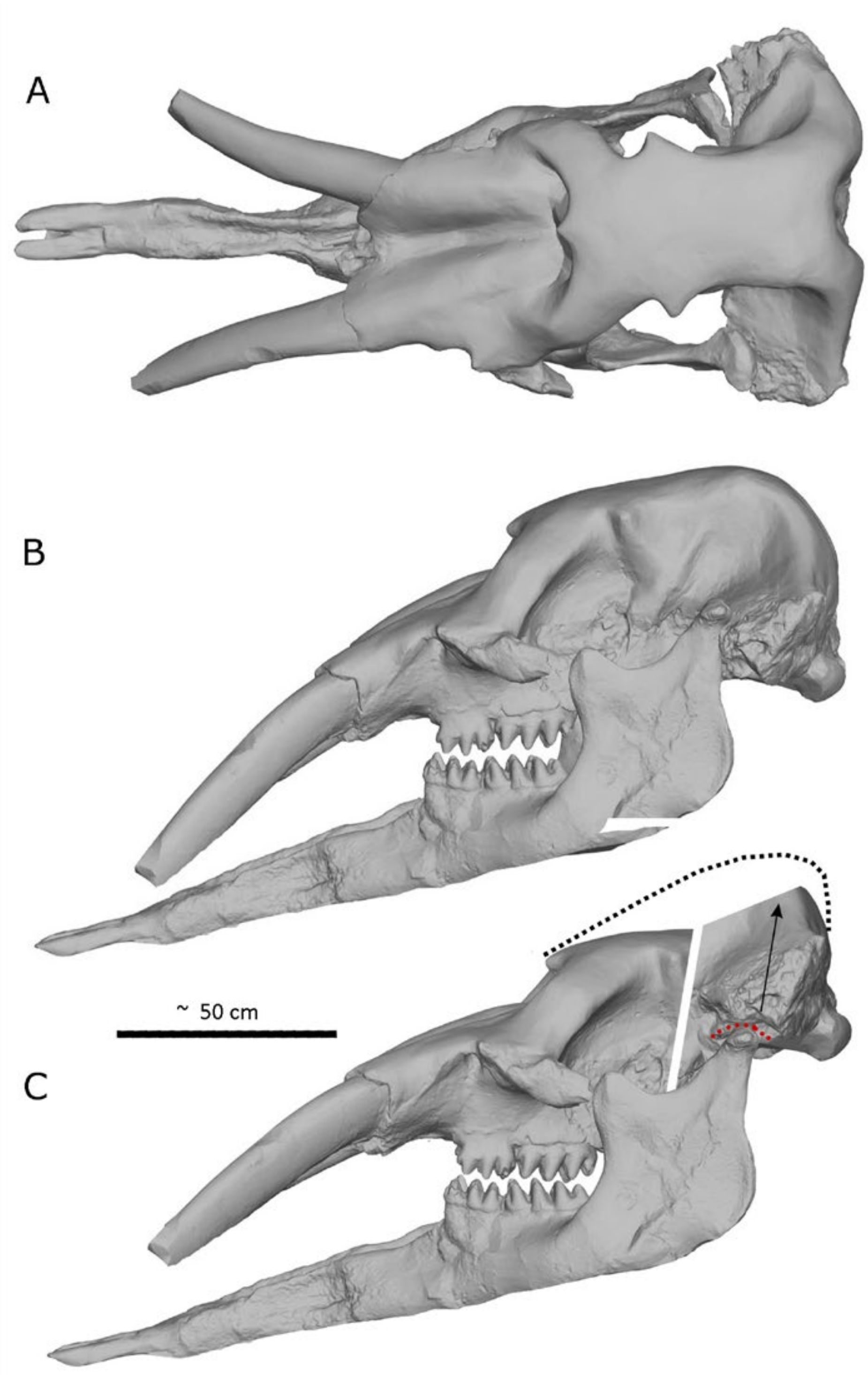


Figure 6. *Zygolophodon proavus* from Unity (OMSI). Reconstructions with 3D models. Mandible brought into a natural position. (A) Dorsal aspect showing the extent of the mandibular symphysis in relation to the upper tusks. The entire dorsal aspect of the cranium is restored as apparent in Fig. 5. (B) Lateral aspect with m2/M2 brought into occlusion. (C) Approach to correct the inaccurate reconstruction of the maxilla and the occipital region assuming a straight profile and a high occiput, as in *Zygolophodon* from Upper Petrified Canyon (NV) and Laojou (China) (Fig. 5B and C).

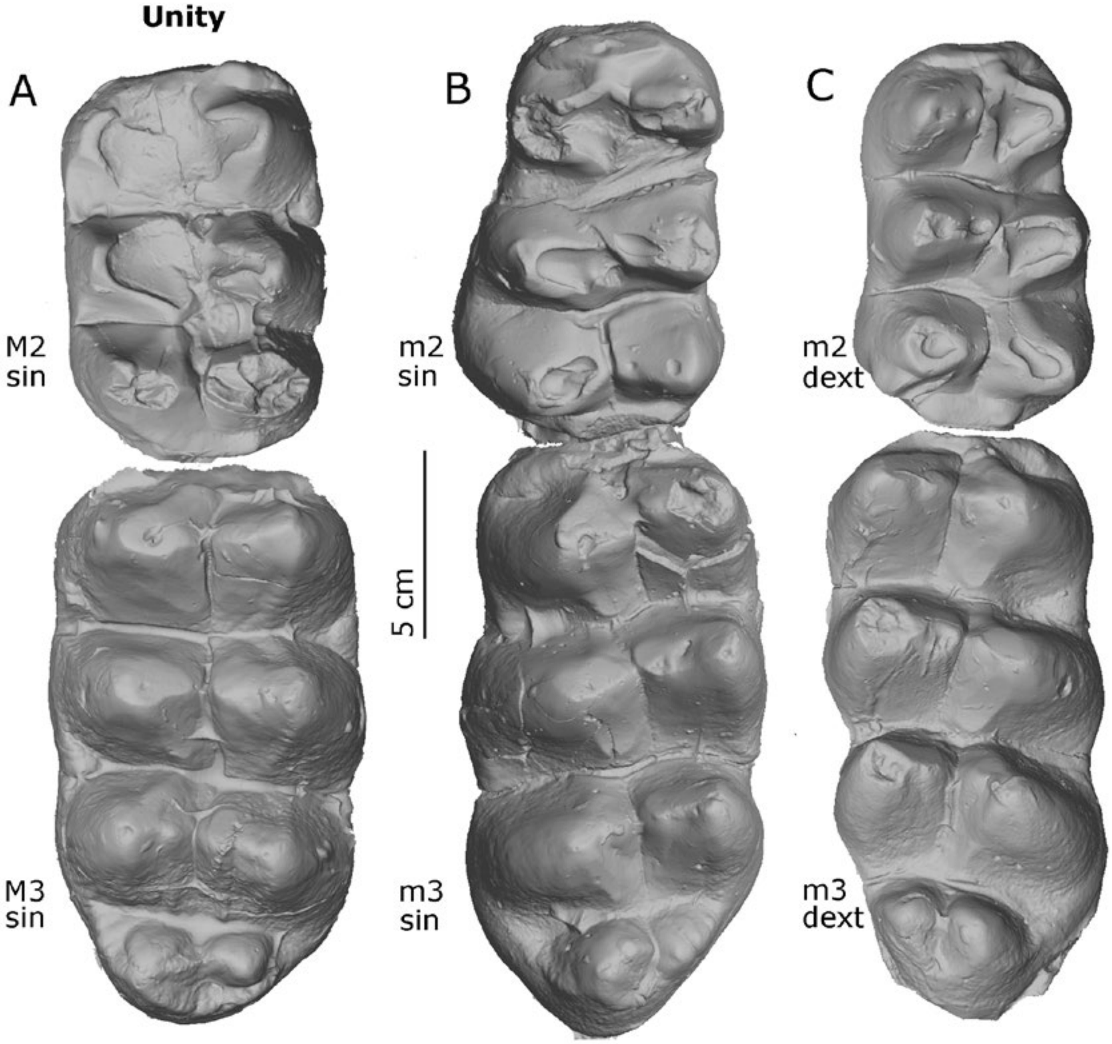


Figure 7. *Zygolophodon proavus*, Unity specimen (OMSI 1946.02.1026). (A) Left upper molars (M2 and M3) and (B) left and (C) right lower molars (m2 and m3) (3D images from casts).

occiput. The braincase is less domed. Examples of the *Zygolophodon* profile are preserved in the crania from Upper Petrified Canyon (MacDonald, 1959) (Fig. 5C) and from Laogou (CN) (Fig. 5B).

The maximal width of the skull at the occipital bone is greater than 70 cm. The foramen magnum is about 6.5 cm wide and opens caudoventrally. Ventrally on the basicranium, fossae mandibulares with the articular facets for the mandibular condyles are preserved on both sides. The maximal width of these articular facets is about 22 cm and their anteroposterior length is about 12 cm. The anterior-most part of the zygomatic arch carries a moderately swollen processus zygomaticus maxillae. The maxilla contains both parallel tooth rows with well-preserved M2 and M3. The os incisivum forming the alveoli for the upper tusks is also preserved.

DENTITION

Figs. 7 and 8 Measurements in Table 3.

TUSKS

Both the partial skull and mandible were excavated with tusks. The upper tusks, which were originally preserved in situ, are documented in historical photos from 1941 and 1953 prior to the restoration (Figs. 3A -B). The upper tusks project 60-80 cm and are curved slightly downwards. Both tusks are missing the tips. The photo from 1941 shows the presence of an enamel band along the lateroventral side of the right tusk. In the restored skull, the tusks are replaced by casts. The whereabouts of the original tusks remain unknown. Historical photos (Fig. 3A) of the skull suggest that the original tusks may have been less divergent than currently reconstructed in the restored skull on display (Figs. 3C and 5A).

The two lower tusks emerging from the elongated symphysis are mostly restored or even replaced by casts in the mandible on display. However, the original mandible excavated in 1953 was figured in the Geological Newsletter of the Geological Society of Oregon County (1953/7: 77). It shows the long symphysis and lower tusks of similar size.

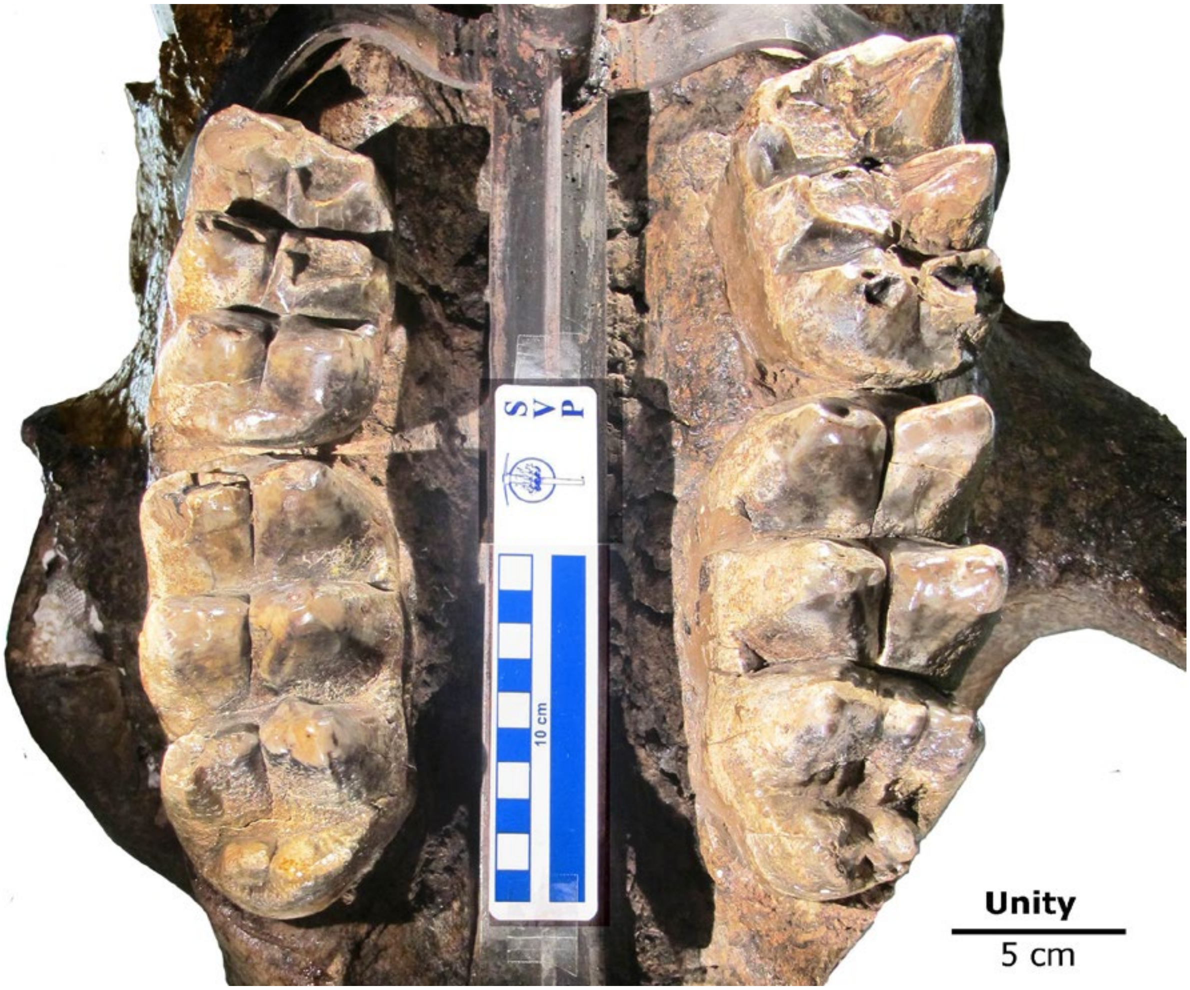


Figure 8. *Zygolophodon proavus*, Unity specimen (OMSI 1946.02.1026), maxilla with parallel oriented tooth rows (left and right M2-M3) (photo of the mounted specimen).

MOLARS

The mandible contains m2 and m3 on both sides (Figs. 7A-C). The maxilla holds the right and left M2 and M3. The tooth rows of the maxilla are almost parallel.

LOWER m2

Left and right m2 are preserved; in the left, the tip of the 1st pretrite main cusp is broken, in the right the 3rd posttrite main cusp is damaged. Furthermore, the left m2 is affected in situ by a crack between the 1st and 2nd lophid forming a narrow gap (therefore the reported measurement of the length of the left m2 is slightly longer than in the unbroken right m2).

The m2 are trilophodont and taper anteriorly. The lophids are slightly oblique and the posttrite half-lophids are anteroposteriorly compressed. The two anterior-most lophids are arranged straight in line, whereas the 3rd lophid forms a slight chevron. All lophids are worn through to the dentine, hampering reconstruction of the number of conelets per half-lophid. The wear pattern illustrates the presence of posterior crescentoids (bulge-like conules) on the 1st and 2nd pretrite half-lophids and a weak anterior crescentoid in the 1st pretrite half-lophid. All valleys are unblocked. No posttrite crescentoids or zygodont crests are visible. There is a low anterior and low crenelated posterior cingulum present. There are no traces of cementum.

LOWER m3

Left and right m3 are present in the mandible. The m3 consist of three lophids and a well-developed talonid.

The top of the 1st posttrite main cusps of the left m3 and the tips of the 2nd and 3rd posttrite main cusps of the right m3 are damaged. The crown pattern is zygodont with anteroposteriorly-compressed lophids that are arranged obliquely. The m3 exhibit initial wear, reaching the dentine only in the 1st pretrite half-lophid; the 2nd and 3rd pretrite half-lophids show steep anterior wear facets only on their tips. The pretrite half-lophids seem to be made up of a main cusp and one mesoconelet, whereas the two to three conelets in the posttrite half-lophids are less distinctive. On all three pretrite half-lophids, very weak bulge-like anterior crescentoids and vestigial, crest-like posttrite crescentoids are present. All valleys are completely unblocked and open. The development of the talonids of the left and right m3 are slightly different; in the right m3, the talonid is made up of a single, large pretrite cusp and a single, smaller posttrite cusp, separated by the median sulcus; in the left m3, the pretrite and posttrite half-lophids are each subdivided in two to three conelets. A very weak crenelated bulge is running down the labial slope of the pretrite main cusp of the talonid.

UPPER M2

Both M2 are complete, only the tips of the 3rd loph of the left M2 and the 1st posttrite main cusp of the right M2 are broken (Fig. 8). The 1st and 2nd pretrite half-lophs show extensive wear, deeper in the left M2 than in the right. Therefore, more morphological details are visible on the right M2. The M2 are trilophodont. All three transverse lophs are straight. The number of mesoconelets per loph cannot be deduced due to advanced wear stage. The wear pattern exhibits an anterior and posterior crescentoid on the 1st loph, and an anterior crescentoid on the 2nd and 3rd loph. Weak zygodont crests are developed on all three posttrite half-lophs. All lophs are slightly compressed anteroposteriorly. Besides a low anterior and posterior cingulum, residual lingual and labial cingula are present in the 1st valley. No cementum is visible.

UPPER M3

Both M3 are complete; only the top of the 1st and 3rd posttrite half-loph in the right M3 is damaged. The M3 is made up by three lophs plus a talon. All lophs are slightly compressed anteroposteriorly. All lophs are arranged in a straight line, without any chevroning. The teeth are slightly worn, but barely reach the dentine level in the 1st and 2nd loph. The wear facets on the tips of the first two lophs are steeply sloping anteriorly. Weak anterior crescentoids are present in the 1st and 3rd pretrite half-loph, vestigial posterior crescentoids are developed in the 1st and 2nd loph. All valleys are unblocked and open. All posttrite half-lophs show weak anterior and posterior zygodont crests. In unworn lophs, the pretrite half-lophs consist of a main

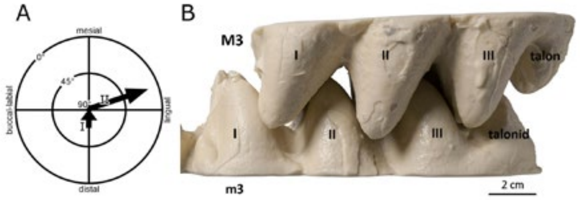


Figure 9. Mammutid occlusion pattern. (A) Mastication compass for *Zygolophodon* indicating the direction and inclination of the occluding left lower jaw during the two phases of the power stroke. Phase I leads to centric occlusion (in the center of the graph) where the subsequent phase II starts. Phase I is very steep, almost orthal, with a slight mesial component, whereas phase II is less inclined and in mesio-lingual direction. – (B) Labial aspect of the left M3 and m3 in full occlusion. The first loph of the M3 occludes posteriorly to the first lophid of the m3. At the end of phase II the M3 extends significantly more labially than the m3. Molar casts are from the Unity specimen.

cusp plus one mesoconelet, whereas the posttrite half-lophs are made up by two to three conelets. The talon consists of a large pretrite cusp and a smaller, single posttrite cusp; the latter is split into two small cones in the right M3. On the posterior slope of the pretrite main cusp of the talon a low crenelated cingulum descends in lingual direction. There is a low crenelated anterior cingulum and the remains of a lingual cingulum in the anterior two pretrite valleys, and a knob-like remnant of a labial cingulum in the first posttrite valley. No cementum is preserved.

THE MASTICATION PATTERN (Fig. 9)

In zygolophodont molars the lophids of the lower jaw intercalate with the valleys between lophs in the upper jaw (Fig. 9). The lophids run across the lophs only when the teeth are extensively worn. Molars in lighter wear illustrate the zygodont mastication pattern. In moderately worn lower molars, wear is greater on the buccal side than on the lingual. In upper molars this pattern is reversed. This pretrite-posttrite phenomenon (Vacek, 1877) was often described for bunodont and lophodont proboscideans. This mastication pattern causes unequal wear (Koenigswald, 2014; 2016). The power stroke in most mammals consists of two phases, which may differ in their functional intensity. In *Zygolophodon* the lower jaw occludes with a movement in a very steep, orthal direction. The lophids intercalate with the valleys of the upper molars and compress the plant fibers. There is no shearing comparable to deinotheres, which have very distinct cutting edges and facets (Koenigswald et al., 2013). After the lophs and lophids occlude in central occlusion, phase two begins. During this phase, movement of the lower tooth row is almost horizontal and directed in a lateral to mesio-lateral direction (Fig. 9A). Its direction is controlled by the orientation of the lophs. When the lower molars move in lingual direction, their lingual sides lose contact with the upper molars earlier than the buccal sides. Thus, in lower molars, the contact with the antagonists and is longer on their buccal or sides and the abrasion is more intense, characterizing the posttrite sides. Correspondingly, the upper molars show more abrasion on their lingual than on the buccal side. This pretrite-posttrite phenomenon is obvious in the second molars (M2/m2) of the Unity specimen (Fig 7A-C) and often visible in other molars of *Zygolophodon*. Even the deciduous premolars in *Mammut cosoensis* (Plate S11) reflect this pattern. In *M. americanum*, however, the pretrite-posttrite phenomenon is generally less obvious, indicating that in this species the orthal movement during phase one is dominant and the lateral movement of phase two less significant. Few teeth show striations in lateral direction. However, the existence of phase two can be traced in some teeth.

INDIVIDUAL AGE

The individual age of mammutid specimens can be deduced from their dentition. The eruption of specific tooth positions and subsequent wear of the cheek teeth provide data that can be compared to extant taxa if they are related and have a similar dentition.

In the Unity specimen, the m1/M1 are shed and no residual alveoli are present in the maxilla. In the mandible, the relevant areas of the dentary are remodeled. The m2/M2 are worn to dentine level in all loph/ids as well as in the 1st loph/id of the m3/M3. Compared to the age groups established

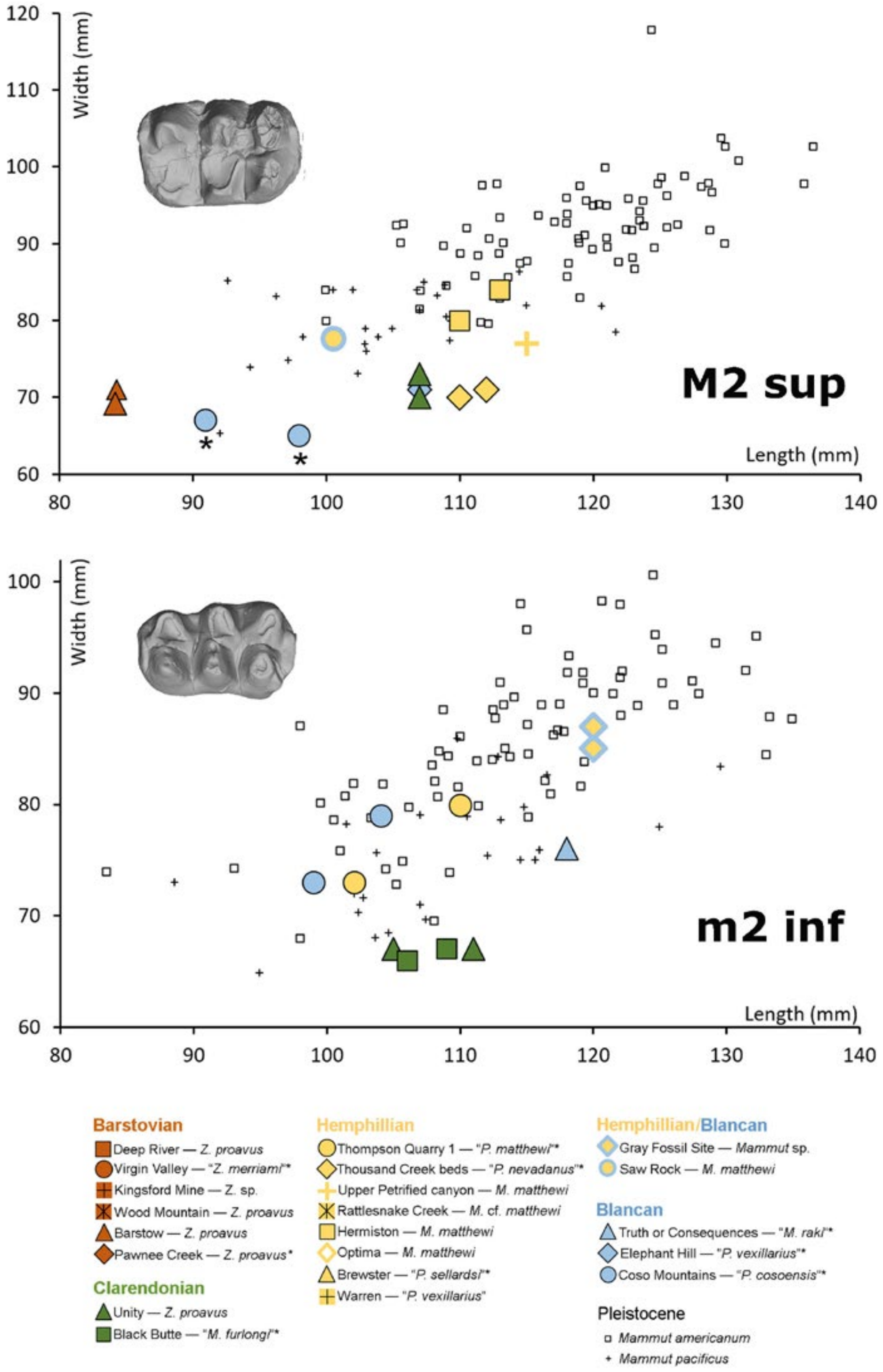


Figure 10. Length/width plot of Miocene and Pliocene M2/m2 of mammutids from North America compared to the range of variation in Pleistocene *Mammut americanum* (open squares) and *Mammut pacificum* (small crosses) (data for *M. americanum* and *M. pacificum* from Dooley Jr et al. (2019) Figure 11 Length/width plot of Miocene and Pliocene M3/m3 of mammutids from North America compared to the range of variation in Pleistocene *Mammut americanum* (open squares) and *Mammut pacificum* (small crosses) (data for *M. americanum* and *M. pacificum* from Dooley Jr et al. (2019).

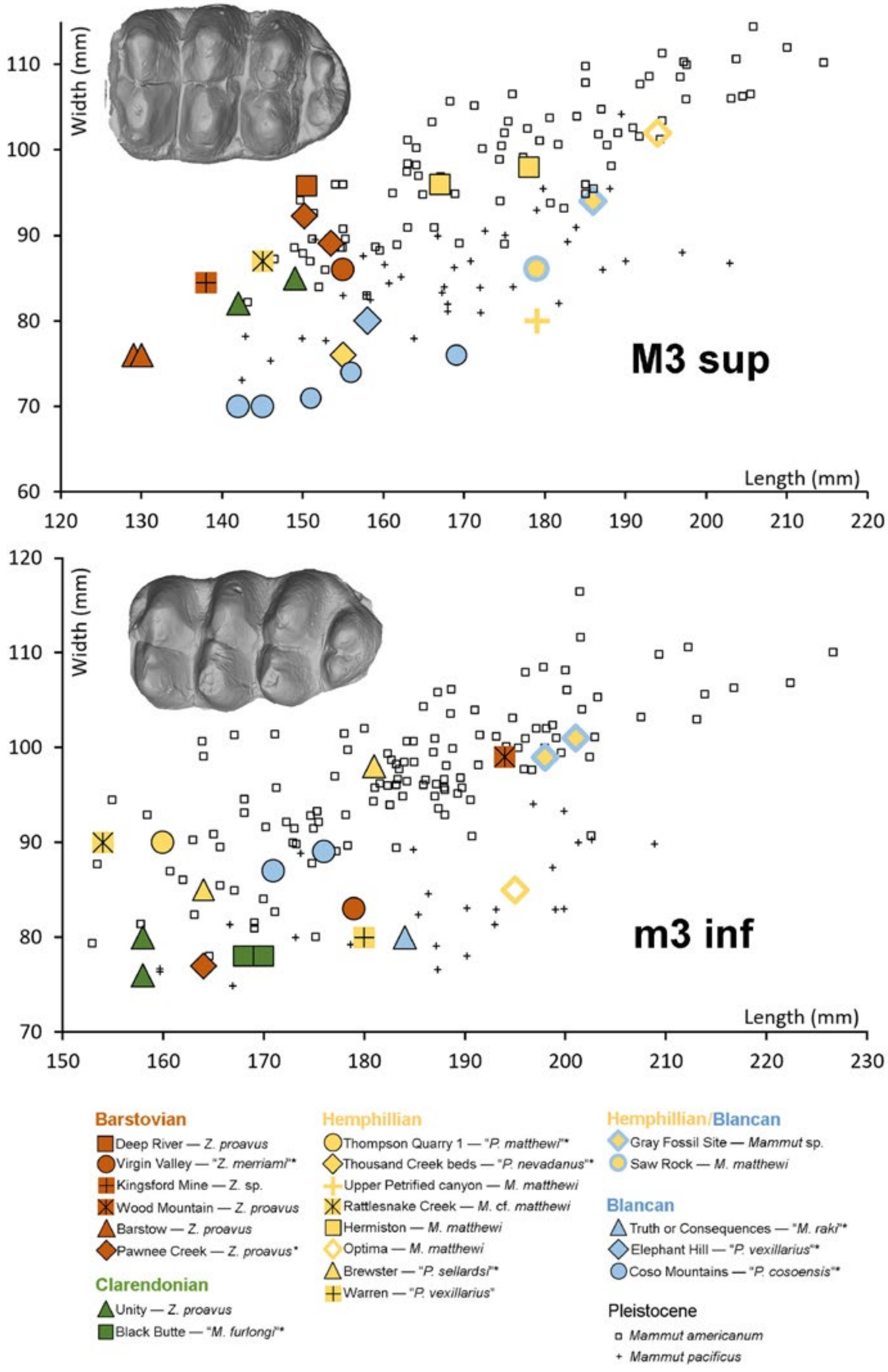


Figure 11. Length/width plot of Miocene and Pliocene M3/m3 of mammutids from North America compared to the range of variation in Pleistocene *Mammut americanum* (open squares) and *Mammut pacificum* (small crosses) (data for *M. americanum* and *M. pacificum* from Dooley Jr et al. (2019).

for *M. americanum* by Saunders (1977: tab.16), the Unity specimen corresponds to the age group "young adult" to "mature". Assuming a similar tooth replacement for *Zygophodon* like in *Gomphotherium angustidens* (CUVIER, 1817), the Unity specimen corresponds to age class XIX, as defined by Tassy (2013). A comparable stage of wear occurs 26-32 AEY (African Elephant years), when compared to the age classes of *Loxodonta africana* (BLUMENBACH, 1797) as established by Laws (1966). We note that AEY is a relatively accurate sequence on the basis of life history, however, it is not necessarily equivalent to solar years, and should be considered an approximation, especially when AEY are applied to fossil taxa.

SYSTEMATIC IDENTIFICATION

In the pruned taxonomy of Miocene mammutids only *Z. proavus* and "*M. furlongi*" occur during the Clarendonian of North America. The Unity specimen was preliminarily identified by G.G. Simpson as *Mi. merriami*, although Simpson made this recognition having only seen the maxilla and the tusks. *Mi. merriami* was synonymized with *Z. proavus*. All characters observed in the cranium and the mandible confirm the first assignment of the Unity specimen to *Z. proavus*. It is distinguished from more advanced *Mammut* by its long symphysis with mandibular tusks, and the downward curving upper tusks exhibiting a lateroventral enamel band.

The long symphysis with mandibular tusks is a plesiomorphic character within Mammutids. Unfortunately, in most Miocene mandibles the symphysis is broken which hampers comparisons and analyses. The Wood Mountain specimen (SK-CDN) from the Barstovian is almost complete and has a moderately long symphysis (i.e., symphyseal length is slightly longer than tooth row (m2+m3), but shorter than the horizontal ramus); however, its relative symphyseal length is shorter than in Unity specimen. This indicates some variability in the symphyseal length within Miocene Mammutidae. The short symphysis of "*M. furlongi*" from Black Butte (OR), contemporary with Unity, does not necessarily indicate a different species, but may be a sex-linked morphological difference, as discussed below.

The molars of the Unity specimen show a typical zygodont pattern with anteroposteriorly compressed loph/ids and very weak central conules. The lower and upper molars are relatively small compared to other Neogene mammutids from North America (Figs. 10 and 11), but fall within the range of *Z. proavus*. The size of the molars (m3 and M3) in the Unity specimen are close to those of the type specimen of *Z. proavus* from Pawnee Creek, and closest to the coeval "*M. furlongi*" from Black Butte, although the m3 of this mandible has one lophid more than the Unity specimen.

The lower m3 of the Clarendonian Unity specimen has only three lophids and a talonid. This differs from all m3s from Barstovian sites (Virgin Valley, Wood Mountain, and Pawnee Creek) and from Black Butte which are all identified as *Z. proavus* (see Lofgren & Anand, 2011). The lack of a fourth lophid in the Unity specimen is regarded as an individual variation and does not justify establishment of a new species.

The assignment of the Unity specimen to *Z. proavus* sets a time marker for the latest occurrence of this species at about 11 Ma during the Clarendonian instead of the late Barstovian at 13.6 Ma, extending the duration of *Z. proavus* more than 2.5 Ma.

"*MAMMUT FURLONGI*" SHOTWELL & RUSSELL, 1963

The Black Butte mandible

Locality: Black Butte, Malheur Co. Oregon (43°46'N 118°06'W)

Stratigraphy: Clarendonian (Retallack, 2004)

Specimen: subadult mandible (UO F 10291/2) with left and right m1-m2 and erupting m3, short symphysis and no trace of lower tusks

Type locality of "*Mammut (Pliomastodon) furlongi*"

Published figures: Shotwell & Russell, 1963: figs. 68-69

In this paper: Figs. 12 and 13

Because the taxon "*M. furlongi*" was not mentioned in the reviews of fossil proboscideans, e.g. Shoshani & Tassy (1996), the species is little known and deserves a more detailed description. We refer to the specific mandible as "*M. furlongi*" because the independence of the species as well as

Figure 12. “*Mammut furlongi*” type from Black Butte (OR), Clarendonian. Mandible with m1 to m3 (UO F 10291). The m3 is not fully erupted. (A) Occlusal and (B) lateral aspect.

its association with the genus *Mammut* is uncertain.

An additional fragmentary left M3 (UO F 6802) (Plate 1C) was designated as paratype of “*M. furlongi*” (Shotwell & Russell, 1963). It comes from a separate, nearby locality (UO 2343), but its mammutid affiliation is questionable due to the presence of strong pretrite conules. It is likely that this specimen is a gomphotheriid; in the UO inventory catalog this tooth is listed as “*Platybelodon*” BORRISAK, 1928.

LOCALITY AND STRATIGRAPHY

The Black Butte locality (43.6°N 118.2W) is close to the town of Juntura (Malheur Co., OR), about 70 km south of Unity (OR). The Black Butte fauna yielded the mandible of "*M. furlongi*" either in the localities UO2448 or UO2337. Stratigraphically, both are close to a basalt (at 152m in the profile) that was dated at 11.6 Ma (Orcutt & Hopkins 2011; Retallack 2004; Retallack personal communication, July 2020). The sediments belong to the Juntura formation, chronologically equivalent to the Ironside Formation. Thus, the Black Butte and Unity specimens are from the same region and of the same age.

REDESCRIPTION OF THE MANDIBLE AND ITS MOLARS

Preserved in this subadult mandible (UO F 10921) are left and right m1-m2 and erupting m3 with typical zygodont morphology. Measurements for the mandible and dentition are given in Table 2 and Table 3, respectively.

The tip of the tapering symphysis is broken off, but the fracture surface shows no traces of mandibular tusks or their alveoli. It is likely that this mandible has a short symphysis. The symphyseal trough is deep and gutter-like. The reconstructed shape of the mandible as figured in Shotwell & Russell (1963) may cause the incorrect impression of the ramus ascendens. Its ventro-posterior part is missing on both sides and therefore the shape of the mandibular angle is not known (Fig. 12). On the right ascending ramus remnants of the coronoid process and the condylar process are preserved, which are of similar height. The ascending ramus is anteroposteriorly narrow. The medial walls of both rami are largely broken. A large foramen mentale pierces the lateral horizontal ramus just below the contact of m1 and m2. An additional small foramen opens on both sides of the preserved symphysis.

Tooth replacement in this specimen reached a subadult stage. The m1 was still functional. Its first lophid is situated slightly anterior to the symphyseal angle. Only the two anterior lophids of the erupting m3 reach the level of occlusion.

The m1 shows heavy wear to the dentine level on the posttrite side. The m2 are in light wear. The diagonally arranged lophids of both (trilophodont) intermediate molars are clearly zygodont with only very weak pretrite crescentoids, and are anteroposteriorly compressed (Fig. 13B). The oblique arrangement of the lophids is compensated by the curvature of the (subadult) mandible. When the mandible shifts in mesial direction during the second phase of the power stroke, the lophids slide along the lophs of the antagonists.

Both m3 are incompletely erupted; however, due to breakage of the bone, the left m3 is completely visible and exhibits four lophids plus a talonid (Fig. 13C). Pretrite conules are much reduced, all valleys are unblocked. The pretrite half-lophids are made up by two to three conelets, the posttrite half lophids by three to four conelets. Also, the m3 exhibit a clear zygodont pattern.

DISCUSSION AND COMPARISON

Shotwell & Russell (1963) assigned "*M. furlongi*", *M. matthewi*, and all Pliocene mammutids to *Pliomastodon*, which they regarded as a subgenus of *Mammut*. The Black Butte mandible they described as "*Mammut (P.) furlongi*", differing from *M. matthewi* in the conelets present on the lophids. Symphyseal characters are not explicit in the diagnosis. Because the Black Butte mandible is from the Juntura formation, a chronological equivalent of the Ironside formation, it is important to compare it to the coeval Unity specimen. The measurements of both dentitions are similar (Figs. 10 and 11). The length of the m3 is slightly longer than that of the Unity specimen (see Table 3). It has four lophids plus a distinct talonid as most m3 of the Miocene, whereas the Unity specimen has only 3 lophids with a talonid, which is regarded as individual variability. A more significant difference is the short symphysis and the lack of mandibular tusks in the Black Butte mandible. The symphyseal trough in the Black Butte mandible is deeper and more gutter-like relative to the Unity mandible. Further, the anteroposterior length of the ascending ramus in the Black Butte mandible is shorter than in the Unity mandible.

Thus, Black Butte and Unity provided two different types of mandibles that might represent different taxa. The brevirostrine and tuskless state of the Black Butte mandible is similar to the genus *Mammut.* However, the shape of the upper tusks and a possible presence of an enamel band remains unknown. Thus, assignment to the genus *Mammut* cannot be confirmed. If the Black Butte mandible represents the genus *Mammut*, it would be the earliest occurrence of this genus in the late Clarendonian at about 10 Ma.

The possibility that the Black Butte mandible with its brevorostrine symphysis without tusks represents a lineage parallel to *M. matthewi* and continued to the late Pleistocene *M. pacificum* was assumed by Dooley et al. (2019). However,

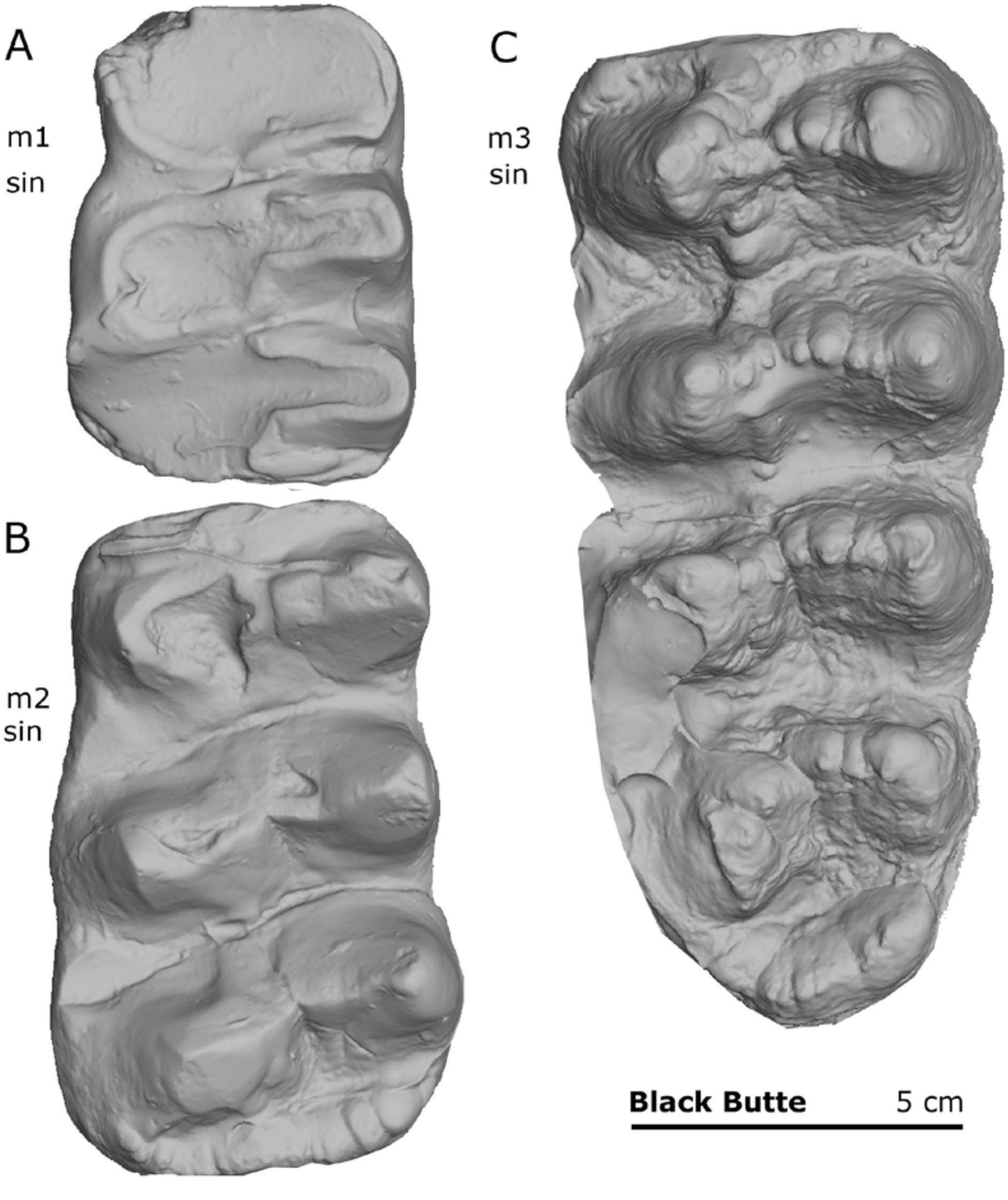


Figure 13. Left molars of type specimen of "*Mammut furlongi*" from Black Butte (UO F 10291) Clarendonian, (A) m1, (B) m2, and (C) m3. (3D images from casts).

a separate evolutionary line of brevirostrine mammutids in North America is not the only available explanation. Similar diversity in symphyseal morphology also occurs at several sites in Eurasia. Therefore, we discuss other possibilities below: individual variability or a sex-linked morphological differences.

MAMMUT MATTHEWI (OSBORN, 1921)

Hermiston

Locality: Westend Blowout, 12 miles SW of Hermiston, Morrow Co., Oregon (45.7°N 119.5°W)

Stratigraphy: Dalles formation, late Hemphillian (Shotwell, 1958: 276)

Materials: Maxilla with M2 and M3 on both sides, and basicranium (UO F 7024). The large tusk and femur reported in field notes during excavation are not available; their whereabouts are unknown.

In this paper: Figs. 14, 15, and 16.

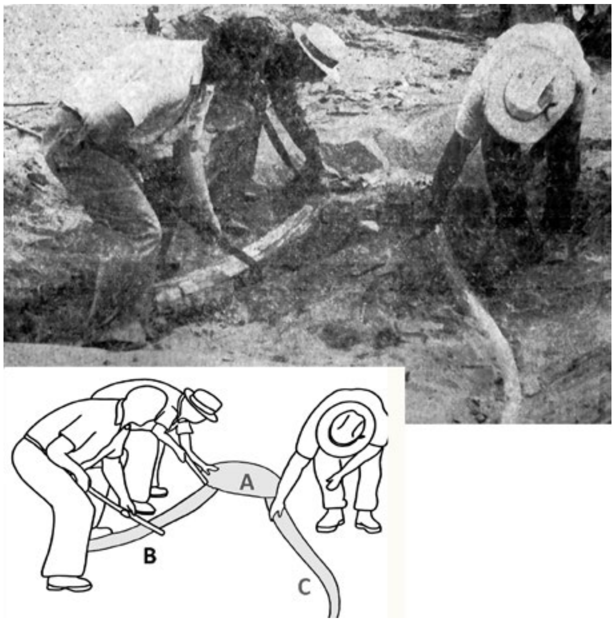


Figure 14. Newspaper photo and line drawing of the excavation of the fragmentary skull of the Hermiston mastodon, July 7th 1954 (*East Oregonian*). Visible on the photo are both tusks in situ; the dorsal skull roof was already eroded but the ventrally facing basicranium and maxilla, were imbedded in situ in the sediment. URL: https://www.eastoregonian.com/community/vault/shifting-sands-reveal-giant-mastodon-near-hermiston/article_cc388858-0268-55c9-a2ae-81d69d176bce.html. Image used with permission of the *East Oregonian*.

LOCALITY AND STRATIGRAPHY

The Westend Blowout (45.7°N 119.5°W), (locality number of University of Oregon: UO 2349 = Ordnance locality in Martin, 2008), 17.7 km (12 miles) SW of Hermiston, Morrow Co., OR, is listed here as Hermiston. According to field notes and a contemporary newspaper article, bones were found by a farmer, Frank Swaggart, in July 1954 and then excavated for the UO by J.A. Shotwell and H. Alvey. An excavation photo (Fig. 14) from the local newspaper "*East Oregonian*" from July 7th 1954, shows the specimen with both tusks in situ. The skull was exposed from its dorsal side, but its roof was already eroded. Half of the right tusk and an almost complete left tusk were found. In the photo, the left tusk seems to be more slender, but it is partially covered with sediment. In the excavation records one plaster jacket of a tusk of at least 2 m (most probably the left tusk) is mentioned, but is not present in the current collection. The upper tusks were thick and curved - flaring laterally and then slightly curving medially towards the tips. Such curvature is not known in *Zygolophodon*. It is unknown if an enamel band was present.

The sediments belong to the Dalles formation, which represents the late Hemphillian. Martin (2008: 187) analyzed the rodent fauna and correlated it with the late Hemphillian (Hh3), below the extinction datum of the mustelid Plesiogulo ZDANSKY,1924 at 5.6 Ma. Shotwell (1958) described the environment as a woodland.

DESCRIPTION OF THE HERMISTON MAXILLA

BASICRANIUM AND UPPER TUSKS

At the time of excavation, the cranium was found dorsal side up, with tooth rows embedded in the local sediments. The roof of the skull was heavily weathered and only the ventral side of the cranium is preserved, from the anterior part of the palatine to the occipital condyles (Fig. 15). Both condyles are well preserved but slightly distorted relative to the rest of the cranium. The transverse

Figure 15. *Mammut matthewi* from Hermiston, locality Westend Blowout (OR), Late Hemphillian (UO Or 7024). Photo of the maxilla still preserved in plaster jacket. Right tusk-size and orientation digitally reconstructed from the alveolus.

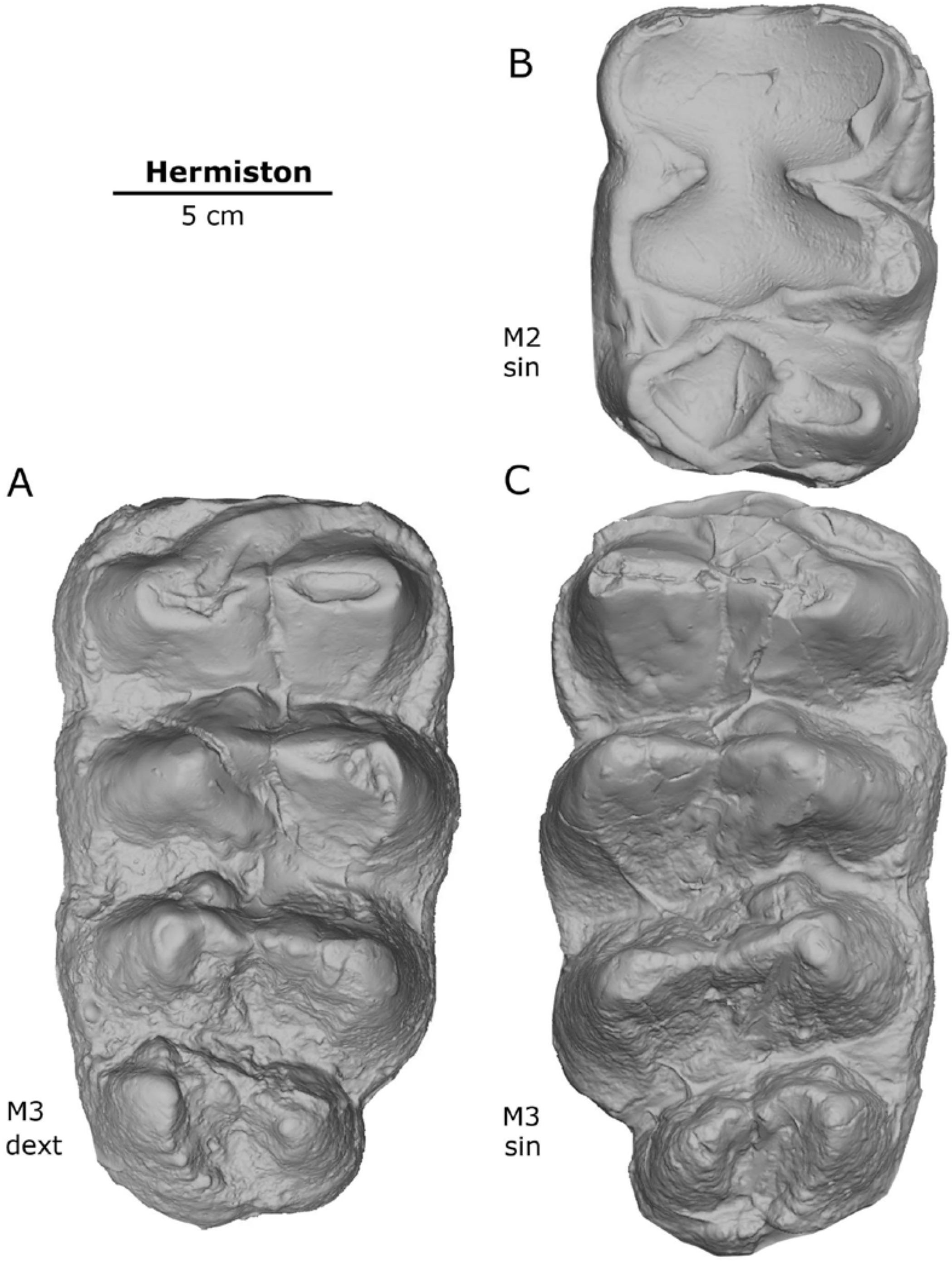


Figure 16. *Mammut matthewi* from Hermiston (OR), Late Hemphillian (UO Or 7024). 3D images from casts of upper molars (A) right M3, (B) left M2 and (C) left M3.

width of both condyles is 230 mm and their anteroposterior length is 120 mm. The enclosed oramen magnum is 63 mm wide. Most bones of the basicranium are broken. A pair of large choanae, with a width of 105 mm, opens just behind the M3. The anterior rim of the choanae is thick and robust and carries a pair of cone-like spinae nasales caudales. The M3 are slightly divergent anteriorly, the M2 are almost parallel.

Only one pair of foramina palatinum majores is present, situated between the 3rd lophs of the M3s and forming slit-like sulci of about 6 cm length. In the anterior part of the palatinum, the interalveolar crest is curvate and the minimal distance between the crests is 145 mm. The shape of the remnants of the anterior right palatine indicates a large alveolus and thus a large tusk. The size and bend of the right alveolus suggests a tusk about 20 cm in diameter at its base. According to field notes by J. A. Shotwell (July 22, 1954) on file at the UO, a tusk was also found with the cranium and excavation photos show a slightly curved tusk, in situ (Fig. 15). The plaster jacket of the left tusk had a length of at least 2.1 m. Thus, the tusk from Hermiston differs from the straighter and shorter tusk in *Zygolophodon*.

UPPER MOLARS (Fig.16, measurements in Table 3)

Left and right M2 sup are heavily worn on all three lophs, the first two lophs are congruent. The right M2 is slightly more worn than the left one. The 3rd pretrite half-loph shows a reduced trefoil pattern.

Left and right M3 sup are slightly worn and consist of four lophs. The 4th loph is smaller in comparison to the anterior ones. Only the 1st loph is worn though the enamel to the dentine. 1st and 2nd pretrite half-lophs exhibit anterior and posterior crescentoids; on the 3rd loph there is a single anterior pretrite conule; a tiny anterior conule is present in the 4th pretrite loph. Posttrite zygodont-crests are present on the posterior slopes of the anterior three lophs. All lophs are relatively high and anteroposteriorly compressed, especially the posttrite half-lophids resulting in wide posttrite valleys. Although the 1st and 2nd valleys are slightly blocked, the 3rd valley is open. There is a weak lingual cingulum and a low posterior cingulum on the M3. The maxillary tooth rows are slightly divergent anteriorly. No traces of cementum are visible.

The wear stages of M2 and M3 are very different; while the M2 are extensively worn, only the 1st loph of the M3 is in wear. Such a strong discrepancy in the wear stages between M2 and M3 is not observed in the Unity specimen described above or the Coso Mountain specimen, described below. In the latter two, the first three lophs of the M3 are in early wear, while the M2 is moderately worn down.

SYSTEMATIC IDENTIFICATION

The partial skull from Hermiston is assigned to *M. matthewi*. The preserved molars (M2 and M3) are quite large for Hemphillian mammutids (see Figs. 10 and 11), but fall within the size range of specimens referred to *M. matthewi* (from Thousand Creek Beds (NV), Elephant Hill (CA), Saw Rock (KS), Upper Petrified Canyon (NV), Optima (OK) (Hibbard 1944; Savage 1941; MacDonald 1959). The type specimens of *M. matthewi* (isolated molars from Thompson Quarry 1, Nebraska, figured in Osborn 1936, figs 101 and 102) are all incomplete and do not allow quantitative comparisons.

The preserved molars do not exhibit unambiguous dental characters, which would clearly distinguish this specimen from specimens referred to *Z. proavus*. However, compared to the upper M3 of the specimens from Unity and Barstow, the posttrite half-lophs of the M3 of the Hermiston maxilla are more anteroposteriorly compressed. Furthermore, the large size of the upper tusks, visible in the large diameter of the partially preserved alveolus, and their direction of curvature, documented in the historic excavation photo, prevents assignment to *Zygolophodon*. Our specific identification of the Hermiston specimen to *M. matthewi* is primarily based on its stratigraphic age, because most remains of *M. matthewi* range from the late Hemphillian to early Blancan. For the general morphological knowledge of the species *M. matthewi*, the Hermiston specimen contributes the almost parallel orientation of the maxillary tooth rows and the presence of large tusks.

COMPARISON TO OTHER BARSTOVIAN, HEMPHILLIAN, AND BLANCAN MAMMUTIDS

For a detailed discussion and comparison of the Unity skull, the Black Butte mandible, and the

Table 4. Distribution of characters in from Miocene and Pliocene mammutids of North American

1 – Symphysis: **0** not preserved, **1** longer than length m2+m3, **2** same length as m2+m3, **3** shorter than m2+m3
2 - Lower incisors: **0** not preserved, **1** long, **2** short, **3** definitely not present
3 – Enamel band in I sup: **0** not preserved, **1** present, **2** absent
4 – Shape of the upper tusk: **0** unknown, **1** straight, **2** slightly down-curved, **3** up-curved
5 – Number of lophids in m3: **0** not preserved, **3+** three with talonid, **4+** four with talonid, **5+** five with talonid
6 – Number of lophs in M3: **0** not preserved, **3+** three with talon, **4+** four with talon

Characters	**1**	**2**	**3**	**4**	**5**	**6**
Locality and stratigraphy	Symphysis	I inf	I sup-enamel band	I sup-shape	m3 inf lophids	M3 sup lophs
Barstovian						
Deep River	0	0	0	0	0	3+
Virgin Valley	0	0	1	0	4+	3+
Kingsford Mine	0	0	0	0	0	3+
Pawnee Creek	2	2	1	1	4+	3+
Wood Mountain	1-2	2	0		4	3+
Barstow	0	0	0	0	0	3+
Clarendonian						
Black Butte	3	3			4+	
Unity	1	1	1	1	3	4+
Hemphillian						
Thousand Creeks Beds	0	0	2	1-2	0	4+
Rattlesnake Creek	0	0	0	0	4	0
Warren 112 115	0	0	0	0	4+	0
Brewster	3	2	0	0	4	0
Hermiston	0	0	0	1-2	0	3+
Gray Fossil Site	2	2	2	0	4+	0
Elephant Hill	2	1	2	2	4+	4+
Blancan						
Truth or Consequences	3	2	0	0	5	0
Coso Mountains	3	3	2	2	4+	4+

Hermiston maxilla, we consider several mammutid remains studied first-hand and/or described in the literature. The number of sites with comparable material is limited. Only those sites that produced meaningful and morphologically relevant mammutid material are included. The characters used for comparison are detailed in the chapter methods and summarized in Table 4.

The sites are discussed in order of stratigraphic position (Fig. 3) and their geographic location is shown in Fig. 2. The affiliation with historic species names, although now mostly synonymized, are noted for clarity. Several occurrences were initially described as new species despite poor representation of diagnostic skeletal elements among isolated individual animals. One author (Hibbard 1944) expressed the problem, stating: "Since the skull and lower jaw of *Pliomastodon adamsi* are unknown, its relationship to the other forms is not known." Table 1 lists species that have been established for North American Miocene and Pliocene localities, along with their affiliations to various genera and their synonyms.

BARSTOVIAN

Deep River Formation (MN)

Locality: Deep River Formation, Meagher Co., Montana (approximately 46°N 111°W)

Stratigraphy: Early Barstovian

Material: isolated right M3 (AMNH 8137)

Type locality of *Tetrabelodon brevidens* COPE, 1889

Published figures: Cope, 1889: fig. 5; Osborn, 1936: figs. 456-457; Madden, 1980: text-fig. 3

Referred herein to: *Zygolophodon proavus*

In this paper: Plate 1B

The M3 sup (AMNH 8137) was described and figured by Cope (1889: fig. 5) as *Tetrabelodon brevidens*. OSBORN,1936 referred this tooth to the genus *Rhynchotherium* FALCONER, 1868. It was recognized as a mammutid tooth by Schlesinger (1917: 159) and Madden (1980). Madden (1980) referred this specimen to the invalid name *Zygolophodon "tapiroides"* CUVIER, 1824 later it was included in *Z. proavus* (Lambert & Shoshani 1998).

The original figure of Cope (1889) shows a relatively low crowned molar with a zygodont pattern, having three lophs and a talon. Measurements given by Cope (1889), Madden (1980) and Lofgren & Anand (2011) vary, but all indicate that the tooth is somewhat bigger and relatively wider than the type specimen of *Z. proavus* from Pawnee Creek. However, measurements are still within the large range of variability for this species (Figs. 14 and 15).

The tooth is similar in size to the one from Unity, but slightly wider. Following the drawn figures in Cope (1889) and Osborn (1936) the crown of the M3 seems to correspond best to a mammutid; the valleys are wide and rather unblocked and the pretrite central conules are reduced in size. However, the crown morphology of the same tooth (AMNH 8137) looks quite different in the photo figured in Madden (1980) and Plate 1B. Based on the photo, the valleys of the M3 from Deep River (MT) are rather narrow and the central conules on the first and second lophs seem stronger (compared to those of Mammutids) and the first and second valley blocked. All in all, the photo gives a clearly more bunodont impression of the tooth. Therefore, an affiliation with gomphotheres cannot be ruled out. In our opinion, only the large width of the crown suggests a possible affiliation to mammutids.

Virgin Valley (NV)

Locality: Virgin Valley, McGee, Humboldt Co., Nevada (41.5°N 118°W)

Stratigraphy: lowest beds of Virgin Valley locality 1065, Early Barstovian (15.18-15.84 Ma, Tedford et al., 2004)

Material: Incomplete m2 and m3 [DMNS EPV 92 (original number Col 92)]; Cast AMNH 14471)

Type locality of *Miomastodon merriami* OSBORN, 1921

Published figures: Osborn, 1921: figs. 1 and 2; 1936: figs. 98B, 99, 653B; Tobien, 1975: fig. 2; Wang et al., 2020: fig 4

Referred herein to: *Zygolophodon proavus*

In this paper: Plate 2

Osborn (1921 and 1936) lists and figures left and right m3, and a M2 and M3 as well as a partial upper tusk. Except for the right m3 (Plate 2B), most teeth are incompletely preserved and partly restored. The m3 have four lophids and a strong talonid. Osborn counts four to five lophids. The M3 has three lophs and a strong talon. For the upper tusk, Osborn (1936) mentions a broad enamel band (Plate 2C). The m3 (Plate 2B) was chosen as the type of *M. merriami*. All these teeth may represent a single individual - although this was not clear in the description.

The length of the m3 (179 mm) given by Osborn (1936: 159) is clearly longer than those from Unity. A figured incomplete M3 seems to represent the same individual. Osborn (1936: 159) estimated its length as 154 mm. If one takes the M3/m3 ratio as a basis, the M3 is comparatively short. Its length may be reconstructed incorrectly or the m3 and M3 do, in fact, not stem from the same individual. Merriam (1911: 272) figured some mammutid tooth fragments from High Rock Canyon (NV) (UCMP 21227) which is related to the Virgin Valley fauna. These fragments, however, do not contribute comparative morphological data.

North Coalinga (CA)

Locality: North Coalinga Fauna, California Coast Range, Fresno Co., California, see Bode, 1935: Fig. 5a/c/d (36,4°N 120.3W)

Stratigraphy: Early Barstovian, ~15.7 Ma, Tedford et al., 2004

Materials: right dp3 (CIT1628), right dP3 (CIT1630)

Referred herein to: *Mammutidae indet.*

Published figures: Bode, 1935: fig. 5

Bode (1935) pictured four deciduous premolars of *Miomastodon* sp. from the *Merychippus* Zone in the North Coalinga district, California. Other specimens were present, but unfigured. Two of the figured premolars (Bode, 1935: fig. 5a, 5b) compare favorably in size and morphology to upper and lower 3rd deciduous premolars of *M. americanum* (Green & Hulbert, 2005). A third (Bode, 1935: fig. 5c) is more likely a gomphotheriid dp3, and the fourth (Bode, 1935: fig. 5d) is from an unknown bunodont proboscidean.

This is one of the stratigraphically earliest sites of mammutids in North America, and one of very few sites where deciduous molars of mammutids are preserved.

Kingsford Mine (FL)

Locality: Kingsford mine, Polk County, Bone Valley, Florida (28°N 82°W)

Stratigraphy: Early Late Barstovian, Bradley Fauna

Materials: right M3 (UF 1168099)

Published figures: Hulbert, 2001: fig.15.9

Referred herein to: cf. *Zygolophodon proavus*

In this paper: Plate 1A

Hulbert (2001) figured a worn upper M3 from the Bradley Fauna as *Zygolophodon* sp. Webb & Crissinger (1983) assigned this fauna to the early late Barstovian. Green (2002) argues for a Middle Miocene age, and uses the species name *Z. tapiroides*. The worn M3 has three lophs and a small talon. Measurements from a cast (Hulbert 2001: fig. 15.9; Hulbert personal communication, June 2020) are in the range of Barstovian *Z. proavus*, between Barstow and Pawnee Creek (Table 6) specimens.

The deeply worn crown allows no detailed description of crown morphology. The M3 from Kingsford Mine is rather wide and shows a strong lingual cingulum, suggesting a mammutid affiliation. However, a bunodont taxon cannot be excluded on the basis of the poorly preserved wear pattern. Therefore, we regard the systematic identification as *Zygolophodon* as unsecure. The heavily worn molar represents an old individual.

Wood Mountain (SK CDN)

Locality: *Zygolophodon* Quarry between Rockglen and Quantock, Saskatchewan, Canada (approximately 49.15°N 106°W)

Stratigraphy: Barstovian, Wood Mountain Formation

Material: almost complete mandible with m3 and fragmentary m2, moderately long symphysis with lower tusks (RSM1665.1) described as *Z. proavus*. An isolated, fragmentary right M3 (RSM 9999) is not accepted as mammutid.

Published figures: Madden & Storer, 1985: figs.1-2

Referred herein to: *Zygolophodon proavus*

In this paper: Plate 3

The mandible with large tusks was identified as *Z. proavus* by Madden & Storer (1985). The specimen is, however, somewhat unique due to its large tooth size. The length of the m3 (194 mm) is one of the largest known of all known Miocene mammutids from North America (Fig. 16). It is similar in length to another large-sized m3 from northwest Nebraska (Hemphillian, AMNH 19248a, Osborn, 1936: 159, fig. 101). Dimensions were given by Madden & Storer (1985). The m3 from Wood Mountain is about 20-25% longer than the m3 from Pawnee Creek, the type of *Z. proavus*, and the m3s from Unity. Relative to the combined length of the m2 + m3, the Wood Mountain mandible has a shorter symphysis and shorter lower tusks than the Unity mandible. However, the relative diameter of the lower tusks is very similar.

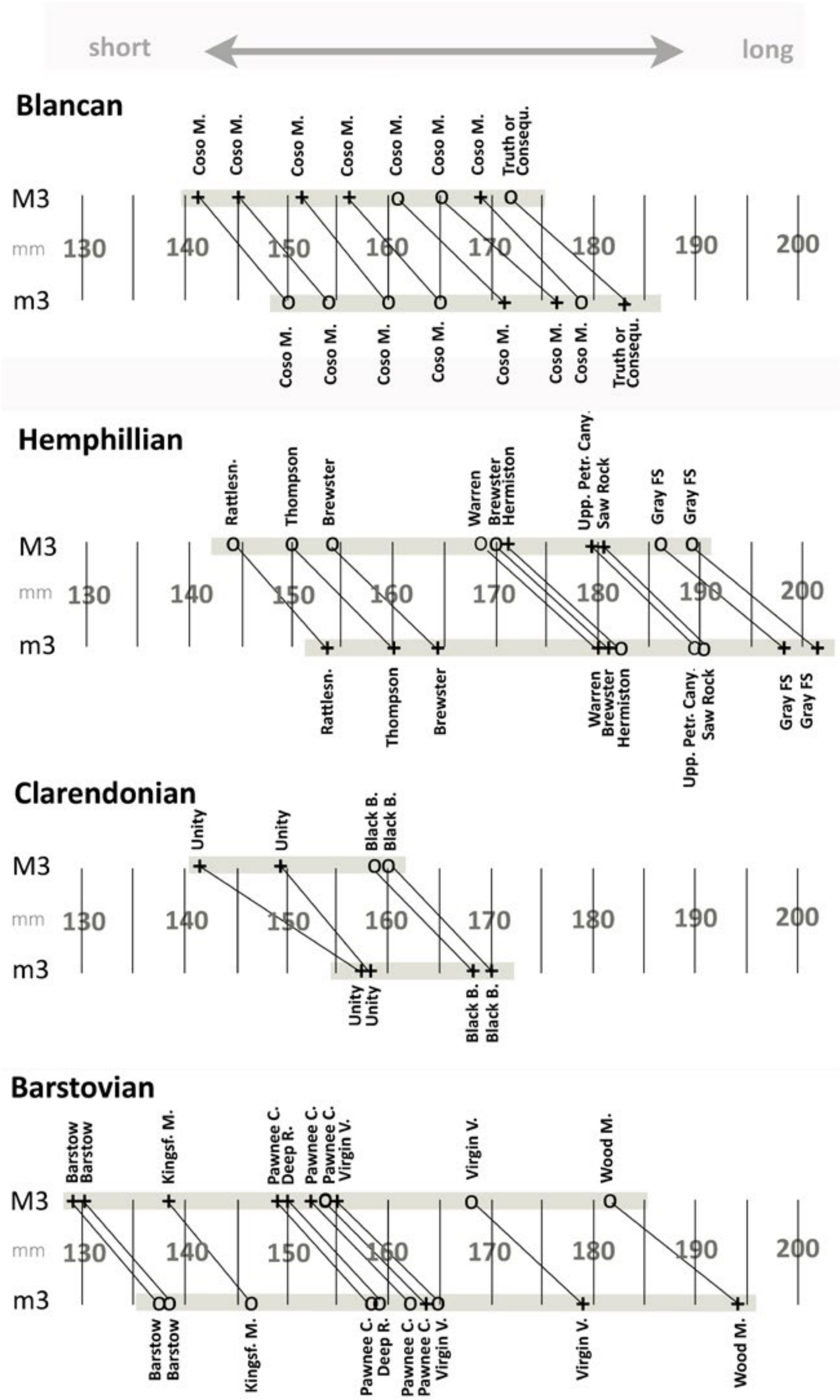


Figure 17. North American Mio-Pliocene mammutids, comparison of the relative length of the m3/M3 from various localities. Generally, only upper or lower molars are preserved. Therefore, the M3/m3 ratio as preserved in the individuals from Unity and the Gray Fossil Site are used to predict an approximate length of missing antagonists (m3=M3 x 1.06 respectively M3 =m3 x 0.939). The gray bars indicate variability in length of m3 and M3 found in our sample. No general increase in length can be observed between the Barstovian and Blancan. (+ measured values, o reconstructed values).

The Wood Mountain mandible and the Barstow maxilla are regarded as conspecific and from similar stratigraphic positions (Lofgren & Anand, 2011). Their M3/m3 ratio, however, is very different. The Wood Mountain specimen (m3 length: 194 mm) is clearly larger than the predicted length of the m3 for the Barstow specimen (about 135 mm) (Fig.17). The size difference does not necessarily indicate different taxa since this degree of variability can also be found in molars of *M. americanum* (Dooley et al., 2019).

Barstow (CA)

Locality: Barstow Mud hills a few miles north of Barstow, California (35°N 117°W)

Stratigraphy: Barstovian, Barstow Formation (Lofgren & Anand, 2011)

Material: Basicranium with partial maxilla with left and right M2-M3 (RAM 908) described as *Z. proavus* by Lofgren & Anand (2011)

Published figures: Lofgren & Anand, 2011: figs. 3 and 4

We agree with the identification as: *Zygolophodon proavus*

In this paper: Plate 4

Lofgren & Anand (2011) described the specimen and gave detailed information about the locality and its stratigraphy. Both tooth rows preserved in the maxilla are almost parallel to each other. The trilophodont M2 are heavily damaged and deeply worn; the M3 consist of three lophs and a strong talon. The molars exhibit a zygodont pattern. The M2 and M3 of the Barstow specimen are the smallest of all compared mammutid teeth from North America (Figs. 10 and 11).

As mentioned above, the predicted length of the lower m3 of the Barstow maxilla is 135 mm, and thus extremely short compared to other mammutids. Lofgren and Anand (2011) compared the Barstow maxilla to the Wood Mountain mandible (m3 length of 194 mm) and assigned them both to *Z. proavus*. This size difference may indicate that the maxilla from Barstow and the Wood Mountain mandible represents a sex-linked morphological difference or a different species. We hesitate, however, creating new species on the basis of size only, because the type specimen from Pawnee Creek is intermediate between these two extremes. The reconstructed length of m3 from Barstow is 10% smaller than the type specimen of *Z. proavus* from Pawnee Creek, which again is about 10% smaller than the m3 from Wood Mountain.

Pawnee Creek (CO)

Locality: HQ Quarry, west of Pawnee Buttes in Weld Co., Colorado (40.5°'N 103.3°W)

Stratigraphy: Early Barstovian, 14 – 14.5 Ma. Tedford 2004; Prothero & Dold, 2008

Specimen: incomplete mandible (missing ascending ramus) with m3 and fragmentary m2, incomplete symphysis with portion of lower tusk, associated M2 and M3 and upper tusks with enamel band (FAM 23337, 23345)

Type series of *Miomastodon proavus* COPE, 1873

Published figures: Frick, 1933: figs. 16, 24, 28; Osborn, 1936: figs. 100, 326

Referred herein to: *Zygolophodon proavus*

Cope (1873) described and figured a poorly preserved dP4 (AMNH 8523) as the type of a new mammutid species *proavus*. Frick (1933) enriched the information by adding an incomplete mandible with m2-m3 and lower tusks and an upper tusk referred to the same individual (FAM 23345). From the same locality, but with a different number (FAM 23337) an upper M2 and M3 and an upper tusk were documented. Frick (1933) assigned this material to the Cope's species *proavus*. Osborn (1936) included the species into *Mi. merriami* using the original figures.

According to these figures (Frick, 1933: fig. 28 and Osborn, 1936, fig. 100), the symphysis of the mandible with two lower tusks, is at least of the same length as m2+m3 and not ventrally inclined. The upper tusks are almost straight or slightly curved ventrally and exhibit a broad lateral enamel band. The molars of the Pawnee Creek mandible are somewhat more worn than in the Unity specimen, but the wear pattern of the trefoils in the former indicate somewhat stronger anterior pretrite central conules in the M3 and somewhat stronger posterior ones in the m3 than in the Unity specimen. The M3 from Pawnee Creek (FAM 2337) and Unity are of similar size and have three and a half lophs. In addition, the m3 of Pawnee Creek and Unity share similar dimensions, but the posterior most lophid is more strongly developed in the Pawnee Creek specimen. The m3 of Pawnee Creek has four lophids plus a small talonid, whereas the m3s from Unity have only three lophs with a strong talonid. In comparison to the Unity specimen, the somewhat shorter symphysis and the fourth lophid in the m3 may indicate a more advanced character stage, however, this may also represent individual

CLARENDONIAN

Unity (OR)

Locality: Unity, Baker Co., Oregon (44.45°N 118.15°W)

Stratigraphy: Clarendonian, Ironside Formation.

Materials: Maxilla with M2-M3 and upper tusks and basicranium with associated longirostrine mandible with m2-m3 and lower tusks; “Hancock’s Mastodon” (OMSI 1946.02.1026)

Referred herein to: *Zygolophodon proavus*

Detailed description and discussion above in this paper, Plate 5

Black Butte (OR)

Locality: Black Butte, Malheur Co., Oregon (43.6N 118.2°W)

Stratigraphy: Clarendonian, Juntura Formation

Materials: Mandible of a subadult with left and right m1-m3 (m3 not completely erupted yet) (UO F 10291 and 10292), symphysis broken, but without any traces of alveoli for lower tusks

Type of “*M. furlongi*” SHOTWELL & RUSSELL, 1963 (fig. 68). The taxonomic affinity of this specimen is uncertain, therefore, we use the original name “*M. furlongi*”. Detailed description and discussion above in this paper.

HEMPHILLIAN

Thompson Quarry 1 (NE)

Locality: Thompson Quarry 1, Aphelops Draw, Sioux Co., Nebraska (42.4N 103.8°W) (= Snake Creek). This locality is distinct from ‘Aphelops Quarry’, although both are within Aphelops Draw.

Stratigraphy: Hemphillian, Snake Creek Formation, Johnson Member B level (*Procamelus-Hipparion* Zone) (Skinner et al., 1977)

Material: right m3 (AMNH 18237)

Type locality of *Pliomastodon matthewi* OSBORN, 1921

Published figures: Osborn, 1921: fig. 1A; Osborn, 1936: fig. 102; Tobien, 1975: Fig. 23

Referred herein to: *Mammut matthewi*

Osborn (1921) selected an incomplete last molar AMNH 18237 as holotype, which he regarded to be a right upper M3. The tooth has four lophs and a small talon. Osborn characterized his new species “by the rapid narrowing of the posterior half of the crown”. MacDonald (1959) and Tobien (1975) determined the tooth as a lower right m3 instead of an upper M3. We agree with this identification due to the oblique arrangement of the lophids, typical of the lower m3. The paratypes are incomplete and even less informative. Osborn (1926) based his new genus *Pliomastodon* on the species matthewi. Shoshani & Tassy (1996) listed *Pliomastodon* under *Mammut. M. matthewi* is regarded as the dominant Pliocene mammutid, but diagnostic characters are poorly preserved in the type specimen, the fragmentary m3. Material from the type locality provides no additional information about the mandible or the upper tusk.

Thousand Creek Beds (NV)

Locality: Thousand creek Beds, 4 mi NW of Hot Spring, Humboldt Co., Nevada (41.1°N 117°W)

Stratigraphy: Early Hemphillian, Hh1/Hh2 (8.0-7.1 Ma Prothero et al., 2008)

Material: maxilla with left and right M2-M3 (M3 not fully erupted) and right upper tusk (LACM CIT 63-1922)

Type locality of *Pliomastodon* nevadanus STOCK, 1936

Published figures: Stock 1936: figs. 1-3

Referred herein to: *Mammut nevadanum*

In this paper: Plate 6

The maxilla described as *P. nevadanum* was synonymized with *M. matthewi* (Shoshani & Tassy, 1996). This maxilla includes M2 and M3 on both sides. Tooth rows are slightly divergent, anteriorly. The M3 has four lophs and a loph-like talon. It is in an early stage of eruption; thus the individual was a young adult. The upper tusk is almost straight and does not have an enamel band. However, the lateral surface of the anterior end of the upper tusk is unusually rough which might indicate the possibility that there was a remnant of an enamel band (observed by UG and WvK). But this observation is uncertain given the preservation of extant material. Compared to the Hermiston specimen, the M2 from Thousand Creek Beds is more slender. More precisely, it is of similar length but clearly narrower. In addition, the M3 is distinctly narrower and somewhat shorter than in the Hermiston specimen, despite the fact that the Thousand Creek Beds M3 is made up by one more loph than the larger Hermiston M3. We regard *M. matthewi* from Thousand Creek Beds as the earliest occurrence of the genus *Mammut*.

Upper Petrified Canyon (NV)

Locality: Upper Petrified Canyon (= Smith Valley), East of Smith Valley, Lyon Co, Nevada, Loc V4841 (38.75°N 119.2°W)

Stratigraphy: late early Hemphillian (8.5-6.5 Ma) (Kelly and Secord, 2009)

Material: Cranium with right M1-M3 (M3 not erupted), part of left tusk (UCMP 38645)

Published figure: MacDonald, 1959: fig. 4

Referred herein as: *Mammut matthewi*

In this paper: Fig. 6C

MacDonald (1959) stressed the similarity of the cranium to *P. nevadanum* from Thousand Creek. The tusks have no enamel. The M3 has 4 lophs and a talon.

Rattlesnake Creek (OR)

Locality: Rattlesnake Creek, near John Day Fossil Beds National Monument on route 26, Wheeler Co., Oregon (44.5°N 119.6°W)

Stratigraphy: Hemphillian (7.2-7.05 Ma) Retallack, 2004; Prothero et al., 2006)

Material: very incomplete right horizontal ramus with m2, m3 (JODA 1321); left maxilla fragment with M3 and first loph of M2 (JODA 1322)

Referred herein to: *Mammut matthewi*

In this paper: Plate 7

The Rattlesnake Formation, dated paleomagnetically by Prothero et al. (2006), yielded a fragmentary left mandible with m2 and m3 as well as a fragmentary maxilla with M3, which provide comparative measurements. Both lower molars (m2 and m3) exhibit a strong lingual cingulum on the first posttrite lophid, which is very unusual. Lingual and/or labial cingula are not typical for lower molars.

Hermiston (OR)

Locality: Westend Blowout west of Hermiston, Morrow Co., Oregon (45.7°N 119.5°W)

Stratigraphy: Dallas formation, late Hemphillian (Shotwell, 1958: 276)

Material: Maxilla with both M2 and M3 and basicranium (UO F 7024)

We refer the maxilla to *M. matthewi*. Detailed description and discussion above in this paper (Figs. 15 and 16)

Optima (OK)

Locality: Optima, Texas Co., Oklahoma (36.75°N 101.15°W)

Stratigraphy: Late Hemphillian Hh3 ~5.5 Ma (Tedford et al. 1987; Gordon & Czaplewski, 2000)

Published figures: none

Material: “short jawed” mandible with m3

Referred herein as: *Mammut matthewi*

Savage (1941) described the fauna from Optima OK and refers an incomplete right and left ramus, upper and lower cheek-teeth, deciduous and permanent upper and lower tusks to *Pliomastodon*. A right m3 compares favorably with *P. matthewi* Osborn (1936) from Snake Creek (= Thompson Quarry 1) in having a rapidly narrowing posterior half of the crown including the third and fourth crests (Savage,1941).

Brewster, Palmetto Fauna (FL)

Locality: Brewster (Palmetto), Bone Valley 30 km south of Mulberry, Florida (27.7°N 82°W)

Stratigraphy: Latest Hemphillian (Hh 4) – Palmetto fauna about 5-4.5 Ma (Hulbert, 2015)

Material: left and right horizontal ramus with m2-m3, symphysis and ascending ramus missing (UF/

FGS/V3822) (Webb et al., 2008)

Type locality of *Pliomastodon* sellardsi SIMPSON, 1930

Published figures: Simpson, 1930: figs. 22+23; Osborn, 1936: figs. 104, 105; Hulbert, 2001: fig. 15.8

Referred herein to: *Mammut matthewi*

In this paper: Plate 8

Simpson (1930) described a mandible from the Bone Valley in central Florida as *P. sellardsi*. The m3 in this specimen is about 15% smaller than the type *P. matthewi.* The symphysis is incomplete, but preserved alveoli indicate the presence of two lower tusks. The m3 exhibit four lophids and a small talonid; the pretrite crescentoids are largely reduced and the valleys are open.

Compared to the Hermiston maxilla, the upper molars of the Brewster specimen are likely shorter. The predicted length of a potential M3 of the Brewster specimen is estimated to be 153 mm in contrast to 167 and 178 mm in the Hermiston M3. The species was synonymized with *M. matthewi* by Shoshani & Tassy, 1996; Hulbert, 2015.

Warren (CA)

Locality: Warren, Horned Toad Hills, Localities UCMP 318115 and 318112 along northwestern margin of the Mohave Desert, California (35.01°N 118.2°W)

Stratigraphy: Late Hemphillian, Horned Toad Fm., Lawler Tuff dated to 4.83 +0.04 Ma (May et al., 2011)

Materials: associated left m2 and left and right m3 (UCMP 318112); fragmentary right mandible with partial m3 (UCMP 318113); fragmentary left mandible with m3 (UCMP 318115); partial left m2 UCMP (320613); magnum (UCMP 318614)

Published figures: May et al. 2011: figs. 54, 55

Referred herein to: *Mammut matthewi*

Member 2 of the Horned Toad Formation has yielded 24 taxa of fossil mammals referred to the Warren Local Fauna. Two m3 are attributed to *P. vexillarium* by May et al. (2011), but no measurements are provided. A right m3 has four unworn and crest-like lophids and a well-separated talonid. Its length is about 178 mm, estimated from a photo with scale. A left m3 is heavily worn and has a small talonid.

HEMPHILLIAN – BLANCAN

Gray Fossil Site (TN)

Locality: Gray Fossil Site, Washington Co., Tennessee (36.4°N 118.3°W)

Stratigraphy: Uppermost Hemphillian 4.5-4.9 Ma (Samuels et al., 2018)

Material: Skeleton of a mammutid with mandible in preparation.

Referred herein to: *Mammut* sp.

In this paper: Plate 9

The Gray Fossil Site is located in the Valley and Ridge region of northeastern Tennessee. Fossil bearing deposits consist of laminated clay beds filling the basin of a 1.8 hectare sinkhole complex in limestones of the Ordovician-aged Knox Group. Biochronological studies of 9 mammalian taxa indicate an age of 4.5 to 4.9 Ma (Samuels et al., 2018). At this time, the site would have been a sinkhole pond. During sedimentation, a large, diverse collection of plants and animals were encapsulated within the basin fill. To date, over 200 plant and vertebrate taxa have been excavated from the site, including 14 species that are new to science (Samuels et al., 2018; Widga et al., 2017b).

Proboscidean materials have been known from the site since 2000 when road crews discovered tusk ivory and foot elements. A large, relatively complete mammutid skeleton was found in 2015. Although this specimen is still in the process of being prepared, it is notable in several respects. First, it is a complete skeleton — missing only the left patella. Molar size and morphology is very similar to other species within *Mammut*. However, the mandibular symphysis is more elongated (length of symphysis is about equal to the length of m2+m3) and exhibits large mandibular tusks. The skull and tusks are still undergoing preparation. In their current state, the upper tusks are relatively straight. This specimen will be subject to a full description once preparation is completed.

Saw Rock (KS)

Locality: Saw Rock near Liberal, Seward Co. Kansas (37.2°N 100.9°W)

Stratigraphy: Late Hemphillian/Early Blancan, 5.0-4.8 ma (Martin, 2021)

Table 5. Compilation of tooth measurements of the second lower and upper molars (m2 and M2) from North America with L/W ratios and W/L indices

m2

Locality	Tooth position	Specimen number	Length	Width	L/W ratio	W/L Index	Source
Barstovian							
Wood Mountain	m2 inf	SMNH P 165	-	84	-	-	Madden & Storer 1985
Clarendonian							
Unity	m2 dext	OMSI	105	67	1.57	63.8	this study
Unity	m2 sin	OMSI	(111)	67	(1.66)	(60.3)	this study
Black Butte	m2 sin	UO F 1091	106	66	1.61	62.3	this study
Black Butte	m2 dext	UO F 1092	109	67	1.62	61.4	this study
Hemphillian							
Rattlesnake Creek	m2	JODA 1321	102	73	1.39	71.6	this study
Brewster	m2	UF FSV-3822	110	80	1.37	72.7	Simpson 1930
Blancan							
Truth and Consequences	m2	FAM 23335	118	76	1.55	64.4	Morgan & Lucas 1999
Coso Mountains	m2 sin	LACM (CIT) 284-1720	104	79	1.32	75.9	this study
Coso Mountains	m2 dext	LACM (CIT) 284-1720	99	73	1.36	73.7	this study

M2

Locality	Tooth position	Specimen number	Length	Width	L/W ratio	W/L Index	Source
Barstovian							
Barstow	M2 sin	RAM 908	84.3	70.8	1.19	83.9	Lofgren & Anand 2011
Barstow	M2 dext	RAM 908	84.2	69.1	1.22	82.9	Lofgren & Anand 2011
Pawnee Creek	M2 sin	FAM 23337	109.4	-	-	-	Lofgren & Anand 2011
Pawnee Creek	M2 dext	FAM 23337	105.3	-	-	-	Lofgren & Anand 2011
Clarendonian							
Unity	M2 dext	OMSI	109	67	1.62	61.5	this study
Unity	M2 sin	OMSI	106	66	1.61	62.3	this study
Black Butte	M2 sin	UO F 10291/2	106	66	1,60	62.3	this study
Black Butte	M2 dext	UO F 10291/2	109	67	1,62	72.7	this study
Hemphillian							
Thousand Creek Beds	M2 dext	CIT 63/1922	112	71	1.57	63.7	this study
Thousand Creek Beds	M2 sin	CIT 63/1922	110	70	1.58	63.3	this study
Upper Petrified Canyon	M2	UCMP 38645	115	77.5	1.48	67.4	MacDonald 1959
Hermiston	M2 sin	UO OR 7024	110	84	1.35	76.8	this study
Hermiston	M2 dext	UO OR 7024	113	80	1.37	70.8	this study
Blancan							
Coso-Mountains	M2 sin	CIT 284/1720	98	65	1.51	66.3	this study

Table 6. Compilation of tooth measurements of the last lower and upper lower molars (m3 and M3) from North America with L/W ratio and W/L indices.

m3

Locality	Tooth position	Specimen number	Length in mm	Width in mm	L/W ratio	W/L Index	Source
Barstovian							
Virgin Valley	m3 sin	EPV.92 (AMNH 14.471)	179	83	2.16	46.4	measured from photo Colorado Mus.
Wood Mountain	m3 sin	SMNH P 165	194	99	1.96	51.0	Madden & Storer, 1985
Pawnee Creek	m3 sin	FAM 23345	164	77	2.13	47	Frick 1933, Osborn 1936: 156
Clarendonian							
Unity	m3 sin	OMSI 1946	158	80	1.97	50.6	this study
Unity	m3 dext	OMSI 1946	158	76	2.07	48.1	this study
Black Butte	m3 sin	UO F 10291/2	170	78	2.18	45.9	this study
Black Butte	m3 dext	UO F 10291/2	168	78	2.15	46.4	this study
Hemphillian							
Thompson Quarry 1	m3 dext		c.160	90	c.1.78	c.56.3	Tobien, 1975
Rattlesnake Creek	m3 dext	JODA 1321	154	90	1.71	58.4	this study
Optima	m3		195	85	2.29	43.6.	Savage, 1941
Brewster	m3	UF FSV-3822	164	95	1.72	58.0	Simpson, 1930
Brewster	m3	UF FSV-5376	181	98	1.85?	54.1?	Osborn 1936
Warren	m3	UCMP 319112	c.180	c.80	-	-	May et al., 2011
Gray Fossil Site	m3 dext	ETMNH 305	198	99	2	50	this study
Gray Fossil Site	m3 sin	ETMNH 305	201	101	1.99	50.2	this study
Blancan							
Truth or Consequences	m3 dext	FAM 23335	184	80	2.30	43.5	Morgan & Lucas, 1999
Coso-Mountains	m3 sin	LACM (CIT) 63-1922	176	89	2.05	48.8	this study
Coso-Mountains	m3 dext	LACM (CIT) 63-1922	171	87	1.97	50.9	this study

M3

Locality	Tooth position	Specimen number	Length in mm	Width in mm	L/W ratio	W/L Index	Source
Barstovian							
Deep River	M3 dext	AMNH 8137	150.2	95.8	1.56	64	Lofgren & Anand, 2011
Virgin Valley	M3	DMNS EVP 92	155	86	1.80	55.4	measured from photo Colorado Mus.
Kingsford Mine	M3 dext	UF 116809	138	85	1.62	61.6	measured from fig.
Barstow	M3 sin	RAM 908	129	76	1.69	58.9	this study
Barstow	M3 dext	RAM 908	130	76.0	1.71	58.5	this study
Pawnee Creek	M3 sin	FAM 23337	153.5	89.1	1.72	58.2	Lofgren & Anand, 2011
Pawnee Creek	M3 dex	FAM 23337	150.2	92.3	1.63	61.5	Lofgren & Anand, 2011

Table 6, continued. Compilation of tooth measurements of the last lower and upper lower molars (m3 and M3) from North America with L/W ratio and W/L indices.

M3

Locality	Tooth position	Specimen number	Length in mm	Width in mm	L/W ratio	W/L Index	Source
Clarendonian							
Unity	M3 sin	OMSI 1946	149	85	1.75	57.0	this study
Unity	M3 dext	OMSI 1946	142	82	1.73	57.7	this study
Hemphillian							
Thousand Creek Beds	M3 dext	LACM (CIT) 63/1922	155	77	2.01	49.7	this study
Upper Petrified Canyon	M3	UCMP 38645	179	80	2.23	44,7	MacDonald, 1959
Rattlesnake	M3	JODA 1322	145	87	1.67	60.0	this study
Optima	M3		194	102	1.9	52.5	Savage, 1941
Hermiston	M3 sin	UO OR 7024	167	96	1.74	57.4	this study
Hermiston	M3 dext	UO OR 7024	178	98	1.81	55.1	this study
Gray Fossil Site	M3 dext	ETMNH 305	190	100	-	-	this study
Blancan							
Saw Rock	M3	KU 6788	179	86	2.08	48	Hibbard, 1944
Coso-Mountains	M3 dext	LACM (CIT) 284/1720	145	70	2.07	48.3	this study
Coso-Mountains	M3 sin	LACM (CIT) 284/1720	142	70	2.03	49.3	this study
Coso-Mountains	M3 sin	LACM (CIT) 284/2015	151	71	2.12	47	this study
Coso-Mountains	M3 dext	LACM (CIT) 284/2015	(156)	(74)	2.11	47.4	this study
Coso-Mountains	M3 sin	LACM (CIT) 284/855	169	76	2.22	45	this study

Specimen: fragmentary maxilla with M2 and M3 dext (KUVP 6788) and an upper tusk

Type locality of: *Pliomastodon adamsi* HIBBARD, 1944

Published figure: Hibbard, 1944, pl.2

Referred herein as: *Mammut matthewi*

Hibbard (1944) describes a maxillary fragment with a weathered M2 and a M3 present on both sides. The M3 contains 4 lophs and a talon. It is slightly longer than those of *M. nevadanum* and *M. cosoensis*. Fragments indicate a long tusk having a rounded cross-section and no enamel band. This morphology agrees favorably with *Mammut*. Cranial and mandibular characters are unknown. Hibbard based the new species on the size only, without any discussion of significant morphological variability.

BLANCAN

Truth or Consequences (NM)

Locality: Truth or Consequences (=Hot Springs), Elephant Butte Reservoir Sierra Co., New Mexico (33.1°N 107.5°W)

Stratigraphy: Early Blancan, Palomas formation (Tedford, 1981)

Materials: partial mandible with m2 and m3 (FAM 23335)

Type locality of *Mastodon raki* FRICK, 1933

Published figures: Frick, 1933: figs. 25A, 29A; Osborn, 1936: fig. 122; Lucas & Morgan, 1999: fig.1

Referred herein as: *Mammut raki*

The mandible has a very short symphysis, which is shorter than the length of the m3 (184 mm). There are alveoli for two mandibular tusks. The unworn m3 consists of five lophids (or four with a large talonid). Although the m3 is erupted, the alveoli of the m1 are still visible indicating a late retention of the most anterior molar. The species *M. raki* was synonymized with *M. americanum* by Shoshani & Tassy (1996) but regarded as a valid taxon by Lucas & Morgan (1999). The m3 differs, however, from *M. americanum* in its slenderness (Fig. 10).

Compared to the Black Butte mandible, the m3 of both taxa are slender but that of *M. raki* is somewhat longer; the m2 of *M. raki* however, is somewhat longer and less slender (Fig. 11; Table 5). In size, the molars of *M. raki* overlap with the range of *M. pacificum*. But Dooley et al. (2019) stresses that *M. raki* is not synonymous with the late Pleistocene *M. pacificum*, because of the presence of mandibular tusks in *M. raki*.

Elephant Hill (CA)

Locality: Elephant Hill (or North Dome, Kettleman Hills, V911085) about 5 km southwest of Coalinga, Fresno Co., California (36°N 120.3°N)

Stratigraphy: Blancan, San Joachim Formation (3.0 - 4.1 Ma)

Specimen: Partial cranium with crowns of M2-M3 largely missing, short portion of upper tusk, left and right horizontal rami with m2-m3 (UCMP 28301) and a heavily damaged, femur

Type locality of *Pliomastodon vexillarius* MATTHEW, 1930

Referred herein to: *Mammut vexillarius*

Published figures: Matthew ,1930: figs. 1, 2 and plates; Osborn, 1936: figs. 106 -108

A reconstruction of the cranium shows strong dorsally-curved tusks and anteriorly divergent tooth rows in the maxilla (Matthew, 1930). The symphysis of the mandible is incomplete, but was probably relatively short and without mandibular tusks (Osborn, 1936: 162). While Matthew (1930: 338) described the tusks as enamel-less, Osborn (1936: 162) mentions a thin strip of a lateral enamel band at the base of the tusk. All molars in the skull and mandible are poorly preserved. The M3 has four lophs with a substantial talon, similar to the M3 from Thousand Creek Beds (*M. nevadanum*), whereas the type M3 of *M. matthewi* from Thompson Quarry 1 has only three lophs. Measurements given for the M3 are 158 mm in length and 80 mm in width (Osborn 1936), somewhat smaller than those from Hermiston.

While Saunders (1996: 273) accepted *M. vexillarium* as a separate species besides *M. matthewi*, it occurs in Shoshani & Tassy (1996, Appendix) as a synonym of *M. matthewi*.

Coso Mountains (CA)

Locality: Coso Mountains, Inyo Co., California (approximately 36°N 118°W)

Stratigraphy : Blancan, about 3 Ma (Bacon et al., 1982)

Materials: anterior portion of cranium with left and right M2-M3 and incomplete upper tusks (LACM CIT 284/1719), holotype of *Pliomastodon cosoensis* (Schultz 1937). The mandible with left and right m2-m3 (LACM CIT 284/1720, paratype) probably not of same individual as the holotype; additional material from same locality: maxilla with left and right dP3-M1 (LACM CIT 284/2036); left and right M3 (LACM CIT 284/2015), left M3 (LACM CIT 284/855)

Type locality of *Pliomastodon cosoensis* SCHULTZ, 1937

Published figures: Schultz, 1937: pl. 5-7

Referred herein to: *Mammut cosoensis*

In this paper: Plates 10 to 12

The cranial fragment contains the maxilla and two upper tusks with slight dorsal curvature but without an enamel band (Schultz, 1937). An additional mandible, not belonging to the cranium, was described as having a short symphysis without any traces of tusks. However, the symphyseal portion of the mandible and most of the ascending rami are largely restored (observed by WK, UG); therefore, nothing can be said about these features. The m3 has four lophids and a distinct talonid, the M3 also has four lophs and a talon. Dimensions of the M2 and several M3 (listed above) are smaller than those of the Hermiston maxilla. The various M3 from this locality are also characterized by their slenderness (Figs. 10 and 11). The juvenile maxilla (Plate 12) contains part of the deciduous dentition. The dP2 and dP3 are significantly smaller than those from North Coalinga. Shoshani & Tassy (1996) regard this species as valid, but includes it in the genus *Mammut*.

EURASIAN MAMMUTID SITES USED FOR COMPARISONS

Some Miocene and Pliocene sites in Eurasia are considered here for comparison. Either they provided important cranial details, as in Laogou (CN), or they produced tuskless mammutid mandibles with a short symphysis, comparable to "*M. furlongi*". They will be discussed in the chapter below.

Yanghecun (CN)

Locality: Yanghecum, Xihe-Linxian Basin, Gansu Prov., (China) (approximately 35°N 192°E)

Stratigraphy: Middle Miocene 11-12 Ma

Material: type of *Sinomammut tobieni.* Incomplete mandible with a relatively short, tuskless symphysis (GIOTC 0984-9-178) and fully worn m2 and moderately worn m3, ascending rami missing.

Published figures: Mothé et al., 2016a: fig. 1, 2, 3d; Wang et al., 2014: fig. 1, 4, 5

In this paper: Fig. 18A

Laogou (CN)

Laogou, Linxian Basin, Gansu Prov. (China). (35.45°N 103.42°E)

Stratigraphy: Late Middle Miocene

Material: Complete cranium with M2 and M3 of both sides, tusks with an enamel band and molars, assigned to "*Miomastodon*" (=*Zygolophodon*) gobiensis OSBORN & GRANGER; 1932 (GPM ZR001141), (Li et al., 2020)

In this paper: Fig. 18B

Mikulov (CZ)

Locality: Mikulov "Czujan's sand pit" (Czech Republic) (48.8°N 16.3°E)

Stratigraphy: Middle Miocene, latest Badenian, latest MN6

Material: Several fragmentary mandibles and postcranial elements of *Z. turicensis* (MZN Ot 7527 and 7528), two out of three available mandibles are brevirostrine and tuskless.

Published figures: Březina 2014: pl.4-6

In this paper: Fig. 18E and F

Wolkersdorf (AT)

Locality: Wolkersdorf, Vienna Basin (Austria) (48.42°N 16.52°E)

Stratigraphy: Late Miocene, MN11 (Harzhauser et al., 2004)

Material: Mandible with m1-m3 and a short, tuskless symphysis (NHMW 1981/0086/0001, unpublished)

In this paper: Fig: 17C

Vialette (FR)

Locality : Vialette near Le Puy-en-Velay, Haute Loire (France) (45.1°N 3.9°E)

Stratigraphy: Pliocene, MN16 (Lacombat et al., 2008)

Material: Complete subadult mandible with m1-m2 and unerupted germ of m3 with very short symphysis and without tusks or alveoli (ML 2017 2662)

It is worth mentioning, another fragmentary mandible (both hemi-mandibles, ML V232) from the same site, clearly show large alveoli for lower tusks). Both specimens were assigned to the same species, *"M." borsoni* HAYS, 1834 by Lortet & Chantre (1878)

No published figures of ML 2017 2662

In this paper: Fig. 18B

Fauverney (FR)

Locality: Mas-De-Marmot (Côte d'Or) (France) (47.25°N 5.15°E)

Stratigraphy: Mio-Pliocene (uncertain position)

Material: Both hemi-mandibles (cast, ML 2027-2663+4) with m2 and m3, symphysis broken, no traces of i2 or alveoli

Published figure: Lortet & Chantre, 1878, pl. XII: fig. 3, named *M. borsoni*.

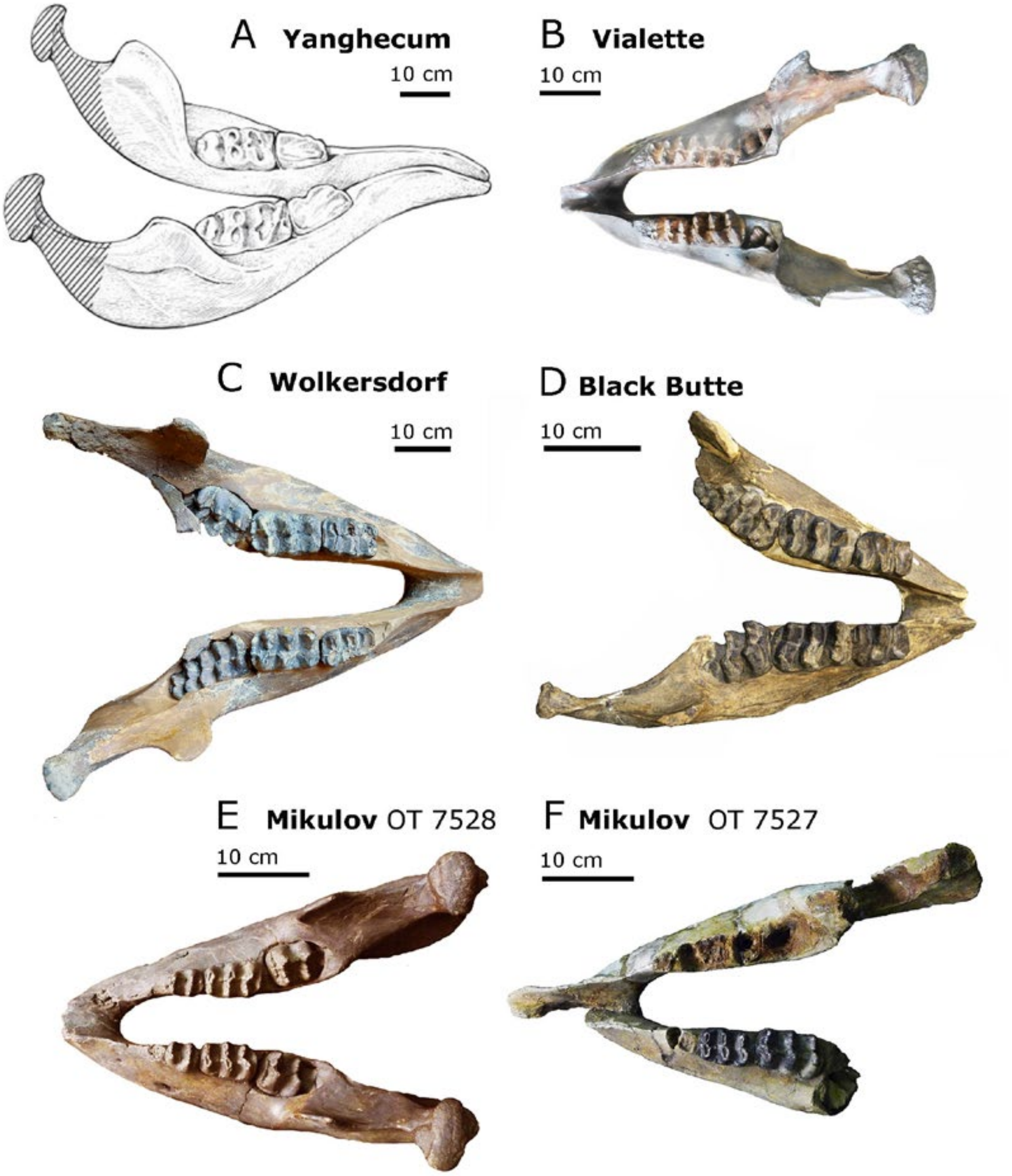


Figure 18. Selected Miocene and Pliocene mammutid mandibles with a delicate, shortened symphysis and lacking mandibular tusks from North America and Eurasia. - (A) *Sinomammut tobieni,* reconstructed mandible with m2 and m3 (GIOTC 0982-9-17) from Yanghecum (China), Middle Miocene (from Mothé et al. 2016: Fig. 1). - (B) *Zygolophodon borsoni*, mandible with m1, m2 and m3 in crypt (ML20172662) from Vialette, Haute Loire, France, Pliocene. - (C) *Zygolophodon turicensis*, mandible with m1 and m2; m3 in crypt (NHMW1981/86/1) from Wolkersdorf (Austria) Middle Miocene MN 9-11. - (D) "*Mammut furlongi*", mandible with m1, m2, and m3 partially in crypt (UO F 10291/2 see Fig. 10) from Black Butte, Oregon, Clarendonian. – (E and F) *Zygolophodon turicensis*, mandibles from Mikulov (Czech Republic), Middle Miocene MN 8-9, E: MZM Ot 7528 with p4, m1, and m2. F: MZM Ot 7527 with left m1 and m2, (E-F photo credit: J. Bředzina, MZM).

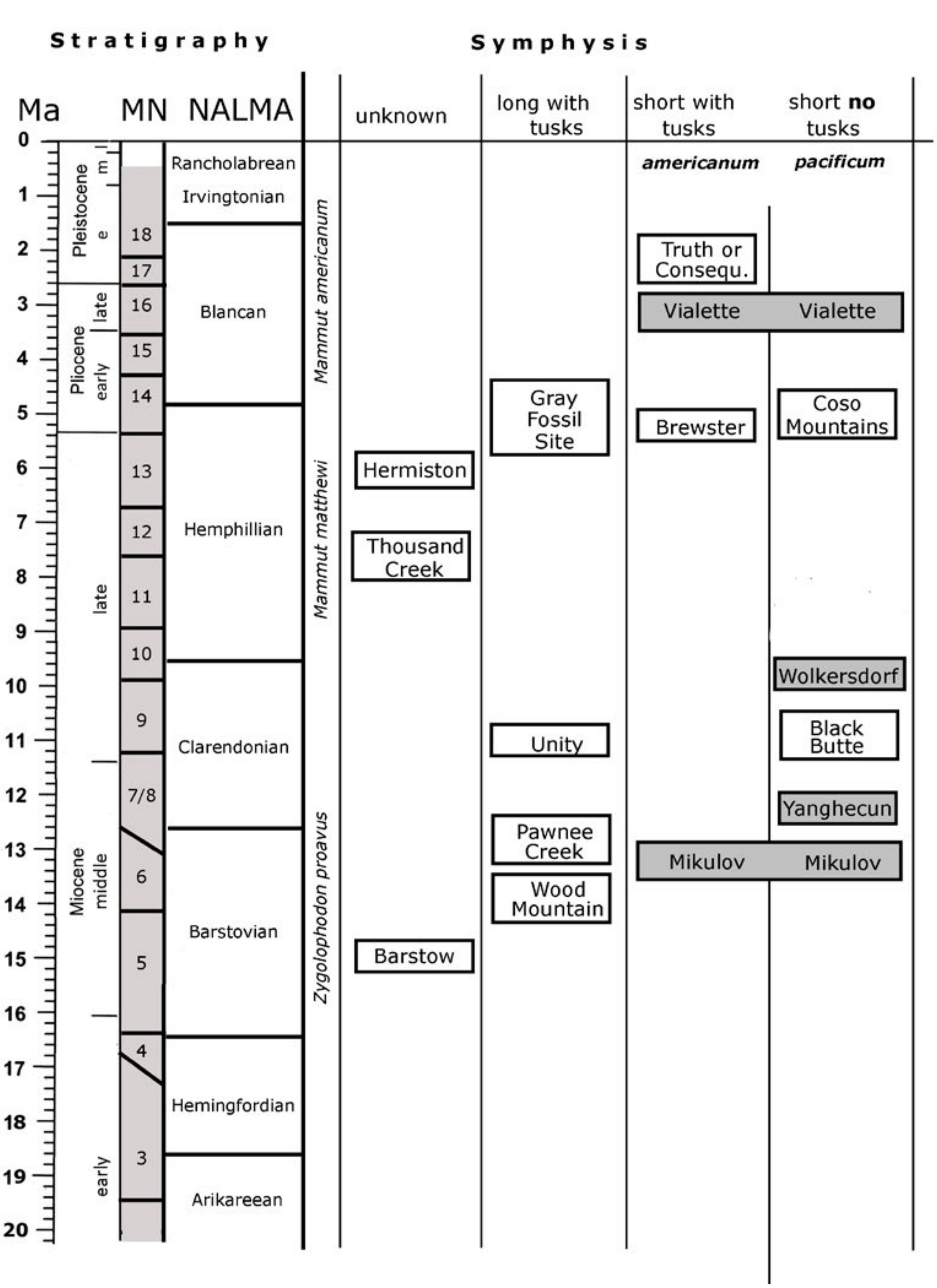


Figure 19. Formation of the symphysis in mammutid mandibles, arranged according to approximate stratigraphic position. - Despite a small sample size, there is a large amount of variation in the symphysis of Miocene and Pliocene mammutids. The primitive condition of a long symphysis with mandibular tusks is present in *Zygolophodon proavus* and occurs until the uppermost Hemphillian (Gray Fossil Site). Most of the younger mammutids have a shortened symphysis with or without mandibular tusks. However, there are some exceptions in the Miocene with a delicate, shortened symphysis lacking mandibular tusks, as occur in North America, Black Butte (OR), and in Eurasia (gray boxes), Yanghecun (China), Mikulov (Czech Republic), Wolkersdorf (Austria), and Vialette (France). These specimens are interpreted as representing individual variability or female animals according to the proposal suggesting sex-linked, morphological differences.

DISCUSSION

EVOLUTIONARY TRENDS IN MAMMUTID DENTITION

In general, the zygodont molars of mammutids are morphologically conservative throughout their evolution in both Eurasia and North America. In contrast to other proboscideans, the last molars of mammutids only occasionally added loph(id)s. Limited changes in dental morphology have been observed in specimens from the Middle Miocene to the Late Pleistocene. Those progressive molar characters were summarized by Tobien (1996: 81f) and comprise the following points: a reinforcement of the lophodont molar character through an antero-posterior compression of the loph/ids and an attenuation of the individualization of the conelets; a diminution and reduction of the crescentoids; an enhancement of the obliqueness in the lophids, especially of the lower m3; a certain reduction of the lingual/labial cingula in the m3/M3; a slight increase of the number of transverse ridges in the m3/M3; and a tendency of increase in size of the m3/M3.

All of these changes in molar characters reflect general tendencies. However, in our experience the taxonomic value of individual characters is often unclear. Therefore, it is difficult to place these characters within a general evolutionary stage.

Tusks show more obvious evolutionary changes from *Zygolophodon* to *Mammut*. In the upper tusks, the changing direction of curvature (ventrally-curved, straight, or dorsally-curved) and the loss of the enamel band are reliable characters (Tobien, 1996: 82). However, even these features are sometimes variable within an evolutionary lineage. Furthermore, the production of the lateral enamel band is age-dependent and is no longer apparent in senile individuals (see below).

Evolutionary changes also affect the lower tusks, manifesting in the reduction or loss of the lower incisors, which may be connected to the length reduction of the mandibular symphysis.

Except for *M. americanum*, relatively complete crania of mammutids are extremely rare; complete mandibles are also rare, but slightly better represented. In the evolutionary progression from *Zygolophodon* to *Mammut* there is a general tendency towards the shortening of the facial portion and the anterior parts of the mandibular symphysis.

MOLAR SIZE

The number of measurable M3, m3, M2 or m2 of North American Miocene and Pliocene mammutids is limited (Table 2 and 3, Figs. 10 and 11). Furthermore, size comparisons are hindered by the limited number of individuals that provide upper and lower dentition; in most cases only lower or upper molars are available for individuals or even taxa. To compensate for this lack of information and to enable approximate molar-length comparisons we applied the approach of estimating the length of missing elements to enable broader comparisons (see methods and Fig. 17). When measurements of upper and lower last molars are combined, taxon-specific variability becomes more evident, e.g., in *Z. proavus*. All Barstovian specimens are identified as *Z. proavus*; M/m3 length varies widely, by about 30% (Fig. 17), but this is not unusual for mammutid teeth as proven by larger datasets of *M. americanum*. Dooley et al. (2019: tab. 4) provided a survey of the variability of the dimension of M3 and m3 in *M. americanum* and *M. pacificum*. The individual length of the m3 of *M. americanum* varies between 136 and 226 mm and that of the M3 between 143 and 214 mm (Dooley et al., 2019: tabs. 4, 5). Thus, the range of variation is about 30-40 % of the median length in Pleistocene *Mammut*. Some degree of this size variation may be sex-linked, with females having smaller molars than males, as in extant and fossil proboscideans (e.g. *Gomphotherium angustidens,* Tassy, 2014). However, small sample sizes and the temporal and geographic scale of this study means that it is not possible to confidently estimate the sex of North American Mio-Pliocene mammutids using this method. Furthermore, the magnitude of this variability suggests caution is necessary when basing fine taxonomic distinctions among Neogene mammutids on molar length alone. Our observed and interpolated data of M/m3 length (Fig. 17) do not indicate a linear evolutionary size increase in molar length during the Neogene. Length/width ratio (Tables 3, 5 and 6) is potentially more informative than the comparisons of the tooth length.

Some taxa are characterized as having narrower molars than others. This ratio can be quantified by calculating “length/width” (Dooley et al., 2019) or an index “width x 100/length” (May et al., 2011).

The results are reciprocal. For easier comparison, we calculated both values in Tables 5 and 6.

The lower molars (m2, m3, Figs. 10 and 11) of the Barstovian and Clarendonian specimens (*Z. proavus* and "*M. furlongi*") are not only among the smallest specimens, but are characterized by generally narrower molars (L/W ratio: m3 1.96-2.18, Table 6)(with the exception of the m3 from Wood Mountain) than most of the Hemphillian and Blancan mammutids (L/W-ratio: m3 1.71-2.30), although this relationship is not statistically significant (Wilcoxon rank sum test: N=18;W=48.5; p=0,204). On the other hand, the upper M3 (Fig. 11, Table 6) of the Barstovian and Clarendonian specimens are also among the smallest specimens and relatively wider than most Hemphillian and Blancan mammutids (L/W-ratio: 1.56-1.80). This difference is statistically significant (N=22; W=8; p=0,001). Compared to Pleistocene mammutid taxa, the Barstovian and Clarendonian specimens generally overlap with the *M. pacificum*-range and are narrower than *M. americanum* in the m3, m2, and M2, but this is not the case with the M3 (Fig. 11), where Barstovian and Clarendonian molars overlap with small *M. americanum*, but are wider than *M. pacificum*. It is also noteworthy, that the M3 of Blancan specimens are relatively narrow (Fig. 11, L/W ratio: 2.03-2.22). In this respect, they overlap with the size range of *M. pacificum*, but are narrower than all Barstovian and Clarendonian M3 and also narrower than *M. americanum* (Fig. 11). This may be due to a biogeographic bias in Hemphillian and Blancan upper molars. Molars of *M. vexillarius, M. cosoensis,* and *M. nevadanum* from of the West Coast and the Great Basin are the narrowest in our sample (Figs. 10 and 11).

NUMBER OF LOPH(ID)S IN M3 AND M3

An evolutionary trend to enlarge the numbers of loph(id)s in the last molars is apparent in gomphotheres and Elephantidae, but evidence for a similar shift in Mammutidae is very limited (Table 4). Additional loph(id)s are created by enlarging the talon(id)s. Their size, however, varies greatly and hinders clear counting of loph(id)s.

In the m3, most Miocene-Pliocene mammutids have four lophids plus a talonid of variable size. The m3s from Unity are exceptional in having only three lophids with a talonid. The Blancan m3 from Truth or Consequences has five lophids like some other m3s of *M. americanum*, e.g. the Nine Mile Bottom Mastodon from South Carolina (Inabinett, 2020).

The M3 from Barstovian sites in our sample generally have three lophs plus a talon, like the Unity specimen from the Clarendonian. The M3s from the Hemphillian and Blancan sites in our sample have four lophs with or without an additional talon; the presence of four lophs is also a common character state in *M. americanum*.

Thus, the lower and upper last molars show a slight increase of the number of loph(ids) during their evolution in America. This vague trend is not stratigraphically linear, and is complicated by individual variability. Therefore, it is not suitable for defining differences between mammutid species.

MOLAR HEIGHT

Tobien (1996: 82) highlighted, that there is no tendency of "subhypsodonty" between *Zygolophodon* and *Mammut* molars. Saunders (1996: 271), however, mentions that cheek teeth are brachydont in *Miomastodon*, somewhat higher in *Pliomastodon*, and subhypsodont in *Mammut* from North America. This seems not to be the case in the Eurasian lineage of mammutids; it was already observed by Depéret (1887: 132) and later highlighted by Tassy (2002) that the last molars (especially the lower m3) of the Eurasian taxon *"M." borsoni* differs from *M. americanum* by relatively lower lophids. Differences in loph/id height are, however, difficult to screen, because most mammutid molars are already worn and do not reflect the original height. Our investigated sample of Neogene mammutid molars did not allow for meaningful comparisons of molar height (in unworn condition), because most of the considered specimens were affected by attrition.

UPPER TUSKS AND ENAMEL BAND

Upper tusks of *Z. proavus* are preserved from Barstovian localities Pawnee Creek and Virgin Valley (Osborn, 1936: figs. 99, 100). As they are incomplete, they can only be described as slightly down-curved to straight and exhibiting a lateral enamel band. Among the two upper tusks of *Z. proavus* from Pawnee Creek, one is relatively straight and the other shows slight

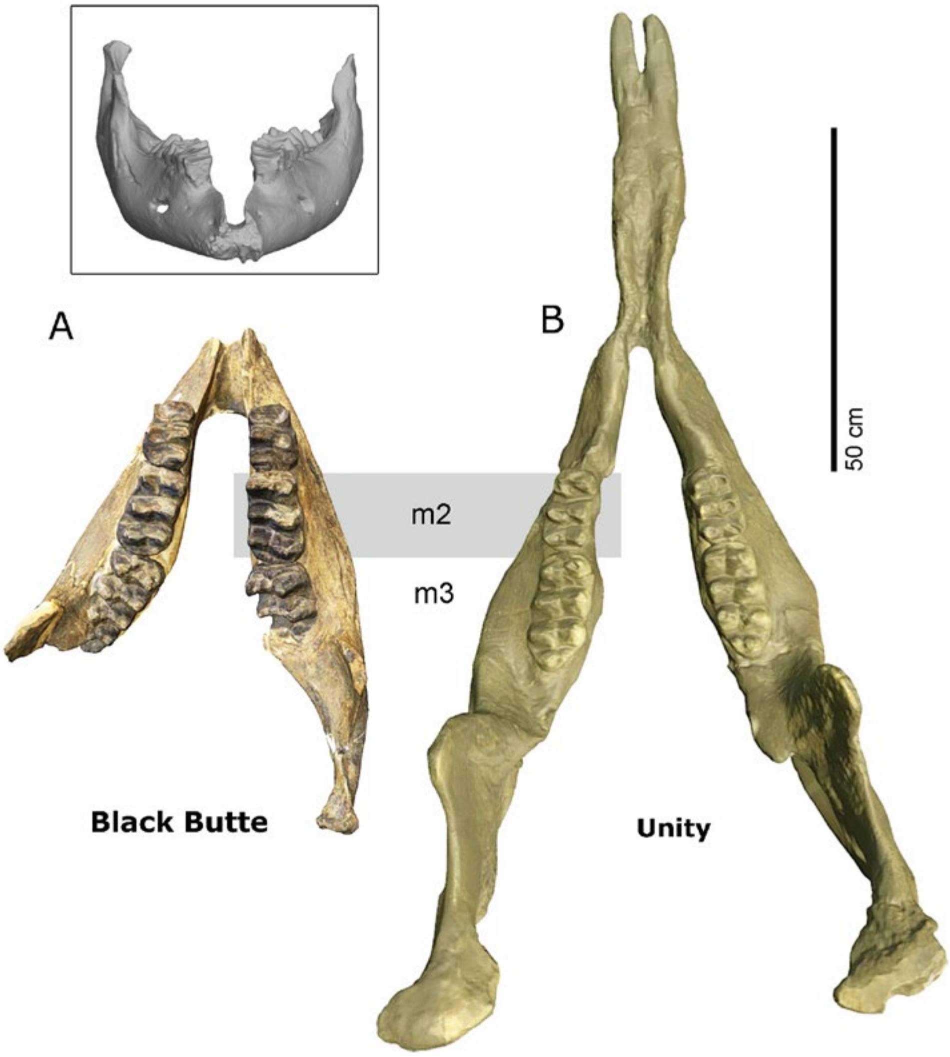


Figure 20. Comparison of two mandibles from the Ironside/Juntura formation (Clarendonian) in Oregon. (A) Mandible from Black Butte ("*Mammut furlongi*") in anterior and occlusal aspect showing the delicate, tuskless symphysis. (B) Mandible from Unity (*Zygolophodon proavus*). The two mandibles vary distinctly in their symphyseal region and the extent of the ascending ramus, exhibit similar molar dimensions, but are of different ontogenetic age. (3D models).

ventral curvature. Their cross-section varies from oval to sub-rounded. We did not consider the medioventral attrition on the tusk produced by friction with the trunk. No tusks are preserved in the Barstow maxilla. The only known tusks from the Clarendonian that are clearly identifiable as *Zygolophodon* are those from the Unity specimen. Unfortunately, they are only preserved as casts in the reconstructed skull. However, historic photos of the un-reconstructed skull (Fig. 3A) clearly show slightly divergent, ventrally-curved upper tusks with a ventro-lateral enamel band.

In contrast to *Zygolophodon*, the upper tusks of *Mammut* are, in general, more massive, straight to strongly curved dorsally, and do not have an enamel band. The cranium from Thousand Creek Beds, described initially as *P. nevadanus*, but later synonymized with *M. matthewi*, has a straight and slightly medially curved right tusk without an enamel band (Plate 6). It dates to the early Hemphillian (Prothero & Dold, 2008) and represents the earliest tusk lacking an enamel band. According to our observations no enamel band is preserved, however, it cannot be excluded that an enamel band was formed at an early age stage and later obliterated by wear. Age-related termination of the lateral enamel band is known for several proboscidean taxa, especially *G. angustidens* (Tassy 2014). MacDonald (1959) also notes the absence of an enamel band in *M. nevadanum* from Upper Petrified canyon.

The tusks of the upper Hemphillian specimen from Hermiston are known to have been long and slightly up-curved. Because this tusk is lost, no information about the enamel band is available. The upper tusk of the Gray Fossil Site mammutid, from the uppermost Hemphillian is relatively straight and does not show an enamel band.

Blancan crania with tusks are known from the Coso Mountains and from Elephant Hill. The upper tusk of *M. cosoensis* (Plate 10) is up-curved and shows no traces of a lateral enamel band. The tusks of the Blancan cranium from Elephant Hill, described as *M. vexillarium* (Matthew, 1930) show gentle dorsal curvature and are large in diameter, as is typical for Pleistocene Mammut. However, unexpectedly, a “narrow strip of thin enamel” was observed by Matthew (1930: 336) laterally on the base of the tusks, but not beyond the alveolus. This indicates that there is variability in the presence of the enamel band. The enamel band is a relic of the ancestral stage in *Zygolophodon*. No tusks with traces of the lateral enamel band are known from any later mammutids (*M. americanum*, *M. pacificum*).

When discussing the curvature or thickness of the upper tusks, individual variation, individual age and sex-linked morphology must also be considered. Sex-linked morphology in upper tusks is well-established for *M. americanum* (Smith & Fisher, 2011). Thick upper tusks and the lack of an enamel band is also typical of *“Mammut” borsoni* from Eurasia. The enlargement of the upper tusks, potentially as defensive or display organs, and the reduction of tusk enamel is shared by other proboscideans and results from parallel evolution.

Mothé et al. (2016b) recently hypothesized that the reduction of the enamel band corresponds with climatic oscillations. Since enamel diffuses heat more efficiently than dentine, they suggest the loss of tusk enamel was an adaptation to cooler climate. Testing this hypothesis will require quantitative evaluation of thermoregulation in extant proboscideans and paleontologically-driven hypothesis testing in other fossil taxa with and without enamel surfaces in their tusks.

M. PROAVUS AND “*M. FURLONGI*”, TWO SEPARATE SPECIES OR DIFFERENT SEXES?

The Unity and Black Butte sites are only 70-80 km apart and represent similar stratigraphic positions (Retallack, 2004). However, the mandibles of these specimens are very distinct. The mandible from Unity is longirostrine with long, slender tusks, whereas the Black Butte specimen is tuskless and brevirostrine (Fig. 20). Despite these differences, the size of the m2 in each mandible is very similar, indicating a similar body size.

In Mammutidae, there is a general trend to reduce the length of the symphysis and the lower tusks. But these two characters are not strictly linked, as documented in some tusked, brevirostrine mandibles of *M. americanum*. Accordingly, the Black Butte specimen may represent a more derived evolutionary stage than the Unity specimen, but this is not the only possibility. These two types of mandibles also co-occur in various North American and Eurasian localities (Fig. 19).

We see four possible explanations for such different character states in the mandible occurring together:

- Individual traumatic or inherited pathology
- Separate synchronous species exhibiting different character states
- Morphological variability within a population
- Sex-linked differences in the morphology of the symphysis and the presence of mandibular tusks.

An interpretation of the reduced and tuskless symphysis as an individual pathology cannot be simply rejected, but tuskless mandibles do not exhibit other characteristics of pathological growth such as evidence of past trauma, sickness, or strong asymmetries. As such, it is more likely that the absence of mandibular tusks is a genetically derived morphological character.

The second approach postulates separate taxa for brevirostrine and tuskless mandibles in contrast to those that are longirostrine and tusked. Following this logic, Shotwell & Russell (1963) named the Black Butte mandible "*M. furlongi*". Dooley et al. (2019) also stressed the similarity of the Miocene "*M. furlongi*" to the Pleistocene *M. pacificum* and postulated an independent evolutionary lineage of mammutids with tuskless mandibles. However, these two types of mandibles co-occur in North American and Eurasian localities during the Mio-Pliocene (see above). Therefore, it is unlikely that tuskless mandibles share a single evolutionary origin because of convergent reduction of lower tusks and symphyseal length, as occurred in multiple lineages of gomphotheres. Synchronous species of Mammutidae may have occurred, although they are difficult to identify. Establishing new taxa because of these morphological differences may be technically correct, but it does not explain mechanisms of parallelism in various geographic and stratigraphic positions (Fig. 18).

The third possibility is that brevirostrine mandibles could also be explained as morphological variants that occur rarely in a biological population. Considering the general trend towards symphyseal shortening in various proboscidean lineages, a short and gracile symphysis could be explained as a heterochronic evolutionary change. Ontogenetic formation of the symphysis might have stopped at an incomplete stage. Thus, short and tuskless symphyses might anticipate a more derived evolutionary stage that would be at no evolutionary disadvantage. The heterochronic modification of the common genetic background might explain the parallel occurrence of the phenomenon. The direction of the ontogenetic evolution of the mandible may be deduced from *G. angustidens* where the length of the symphysis increases with age (Tassy, 2013: 425). However, details of mandibular ontogeny in mammutids are currently unclear.

The final approach, that tusklessness in mammutid mandibles is a sexually dimorphic character, was proposed by Březina (2014; Březina & Ivanov, 2015) describing the Mikulov (CZ) material, where tusked and tuskless mandibles co-occur. These authors adopted the model for *G. angustidens* established by Tassy (2014) who assumed individuals who lacked mandibular tusks were female. However, we have very little information about individual variability and the strict association of tusklessness and symphysial length.

In extant proboscideans, the size of the upper incisors is determined by sex and age of the individual. The enormous tusks of male *L. africana* led to trophy hunting of old bulls. In *Elephas maximus* LINNAEUS,1758, females lack upper tusks in some populations (Sukumar, 2006). Thus, there is a strong link between sex and tusk size in extant proboscideans. *M. americanum* often lacks mandibular tusks, but they occur in both sexes (Laub, 1999; Fisher et al., 2014; Cherney et al., 2017). There are regional differences in the frequency of their occurrence (Fisher et al., 2014). Ultimately, an independent gauge of the sex of an individual is required. Comparison of pelvic morphology between individuals with and without mandibular tusks would be an ideal test for this hypothesis. Unfortunately, this is not possible for Miocene mammutids due to poor preservation of sexually diagnostic skeletal elements.

In conclusion, a sex-determined presence or absence of lower tusks in *Zygolophodon* and Miocene mammutids could explain the synchronous occurrence of both types of mandibles in North America and Eurasia. However, such a conclusion may be premature due to small sample sizes and the lack of associated sexually diagnostic skeletal elements. Furthermore, the degree of population-level morphological variability is virtually unknown. Nevertheless, it is worthwhile to bring this idea into the discussion, hoping that more and better material brings clarity. For the time being we keep *M. proavus* and "*M. furlongi*" as separate species while highlighting possible solutions to the dilemma presented by mandibular tusks.

CONCLUSION

FAUNAL EXCHANGE BETWEEN NORTH AMERICA AND EURASIA

Zygolophodon invaded North America during the lower Miocene. Many American paleontologists (e.g. Osborn, 1936; Saunders & Tassy, 1989) have postulated an endemic and continuous evolutionary transition from *Zygolophodon* to *Mammut* in North America whereas European workers (Schlesinger, 1917; 1922; Fejfar, 1961; Kubiak, 1972; Tobien, 1977; 1986; 1996) have discussed the genus *Mammut* as an immigrant from Eurasia replacing *Zygolophodon* during the late Miocene or Pliocene. Our results strengthen the model of an endemic evolution of Mammutidae in North America because the characteristics of *Mammut* appear gradually in the stratigraphic record. To date, there is no evidence that *Mammut* immigrated from North America to Eurasia.

If *Mammut* evolved endemically in North America, this has nomenclatural consequences. Blumenbach (1799) established the genus name *Mammut* for the North American *Mammut americanum*. Because a dual origin of *Mammut* in different continents is not acceptable, the name *Mammut* should be used with great care for Eurasian mammutids unless an immigration is proven. Consequently, Koenigswald et al. (2022) used the genus name with quotation marks when discussing *"Mammut" borsoni* from the Late Miocene and Pliocene in Europe.

THE GENUS *MAMMUT*

During the Blancan, various species of the genus *Mammut* are described. They all have a shortened symphysis, with or without mandibular tusks, e.g. Brewster (FL) and Truth or Consequences (NM). The Coso Mountains (CA) produced a cranium with curved upper tusks. The unassociated mandible has a short symphysis and lacks mandibular tusks. In addition to possible sex-linked differences in mandible morphology, a general reduction of the symphysis is demonstrated in *M. americanum* and *M. pacificum* during the Plio-Pleistocene. This occurs in tandem with an increase in the size of upper tusks.

Mammutid remains from the Miocene and Pliocene are rare and often too incomplete to investigate detailed changes in morphological characters through time. Furthermore, it is possible that synchronous species may be taxonomically combined due to the scarcity of differentiating characters and highly conserved morphology.

CHRONOLOGICAL TRENDS IN MAMMUTID EVOLUTION

Clarifying the Mio-Pliocene history of the North American Mammutidae is difficult because of the conservative morphology of mammutid molars and the limited number of informative specimens. Only the combination of different character states in the cranium, the mandible, upper and lower tusks is informative. Therefore, rare finds that provide several of these characters are important.

The cranium and mandible excavated at Unity (OR) represents the status for *Z. proavus* during the Clarendonian. The mandible is longirostine with well-developed mandibular tusks. The upper tusks are straight with an enamel band on their lateral side. This appearance corresponds to Barstovian material from Pawnee Creek (CO). The maxilla from Barstow (CA) is distinctly smaller and the mandible from Wood Mountain (SK CDN) is bigger. Both of these important specimens, however, are incomplete and lack further anatomical information. The mandible from Black Butte (OR), described as "*M. furlongi*", is from the same region and coeval with the Unity specimen. It is distinct however, from the Unity specimen, in having a short, gracile symphysis without mandibular tusks (Fig.19). Similar tuskless mandibles with short symphyses occur in various sites and stratigraphic levels in Eurasia, but they cannot be incorporated into a reasonable phylogenetic model on the basis of tusk presence or symphyseal length alone. Based on comparisons with other fossil and extant proboscideans, we propose these characters are sex-linked differences in morphology, not different taxa. Intra-specific diversity and the fragmentary nature of Mio-Pliocene mammutid specimens obscures the possible coexistence of different mammutid species in North America during the Barstovian and Clarendonian.

Various specimens representing Hemphillian mammutids are usually summarized as *M. matthewi*, although the type specimen is an incomplete M3 and not morphologically informative. The late Hemphillian Gray Fossil Site (TN) provides preliminary information on an almost complete skeleton. The mandible is characterized by a long symphysis and strong mandibular tusks, similar to *Zygolophodon*, but the upper tusks are long and lack an enamel band, resembling *Mammut*. The mammutid cranium found at Upper Petrified Canyon (CA) and Thousand Creek Beds (NV) described as *M. nevadanum*, have slender upper tusks without enamel, but provide no information about their mandibles. We can conclude that the maxilla from Hermiston (OR) had thick upper tusks, but the mandible was not found. Thus, it remains unclear whether they share the same significant combination of underived and derived characters, present at the Gray Fossil Site. At this time, this combination indicates the continuous evolution from *Zygolophodon* to *Mammut* in North America, contradicting a Eurasian origin of the genus *Mammut* and a second immigration to North America.

During the Blancan, various species of the genus *Mammut* are described. They all have a shortened symphysis, with or without mandibular tusks, e.g. Brewster (FL) and Truth or Consequences (NM). Coso Mountains (CA) produced a cranium with curved upper tusks. The unassociated mandible has a short symphysis and lacks mandibular tusks. A general reduction of the symphysis is present in *M. americanum* and *M. pacificum* during the Plio-Pleistocene together with an increase in the size of upper tusks.

Mammutid remains from the Miocene and Pliocene are rare and often too incomplete to investigate detailed changes in morphological characters through time. Furthermore, it is possible that synchronous species may be taxonomically combined due to the scarcity of differentiating characters and highly conserved morphology.

We observed two evolutionary trends in the mammutid symphysis: The first trend is the well-known reduction of the mandibular symphysis and the mandibular incisors. In Eurasia between the Middle Miocene *Z. turicensis* and the Pliocene *“M.” borsoni*, the symphysis becomes shorter but often includes mandibular tusks. In North America, the same trend is observed between the Middle Miocene *Z. proavus* and Plio-Pleistocene *Mammut.* In *M. americanum* the symphysis is shortened and mandibular tusks are often missing. In *M. pacificum*, however the mandibular tusks are always absent.

The second trend also reflects the shortening of the symphysis and the reduction of the mandibular tusks but is unrelated to evolutionary changes within Mammutidae. At times, these characters occur synchronously in North American and Eurasian mammutids. This phenomenon is especially conspicuous in the Clarendonian of Oregon, where we have reported the contemporary occurrence of longirostrine and brevirostrine forms. In *Z. turicensis* from Miocene European sites like Mikulov (CZ, Middle Miocene) and Wolkersdorf (AT, Late Miocene), and in Asian sites like Yanghecun (China, Middle Miocene) the co-occurrence of both mandible types is less obvious, because mandibles generally have a shortened symphysis due to evolutionary trends. A tuskless *Z. borsoni* mandible was found in Vialette (FR). Another tuskless mandible comes from the Coso Mountains (CA). We suggest that the reduced symphysis and loss of mandibular tusks may occur in females prior to males as a sex-linked morphological difference.

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PLATES

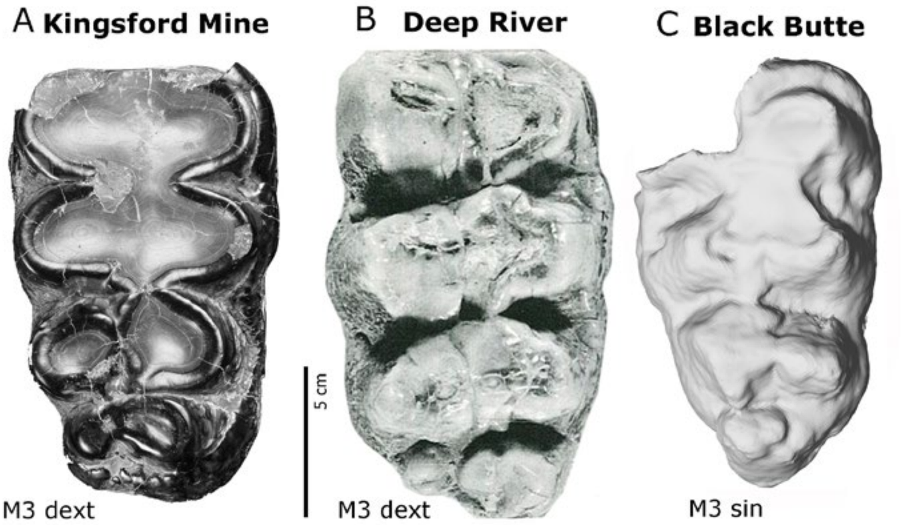

Plate 1. (A) *Zygolophodon* sp. M3, Kingsford Mine, Florida (UF 116809 (B) M3 from Deep River, Montana, discussed as *Zygolophodon* (Madden, 1980), but here regarded as a gomphotheriid. (C) M3 from Black Butte (UO F 6802), Oregon, it was referred to "*Mammut furlongi*" by Shotwell & Russell (1963), but is not accepted as a mammutid in this study. (Photo credits: A - Florida Museum; B - J. of Paleontology; C - 3D model from cast).

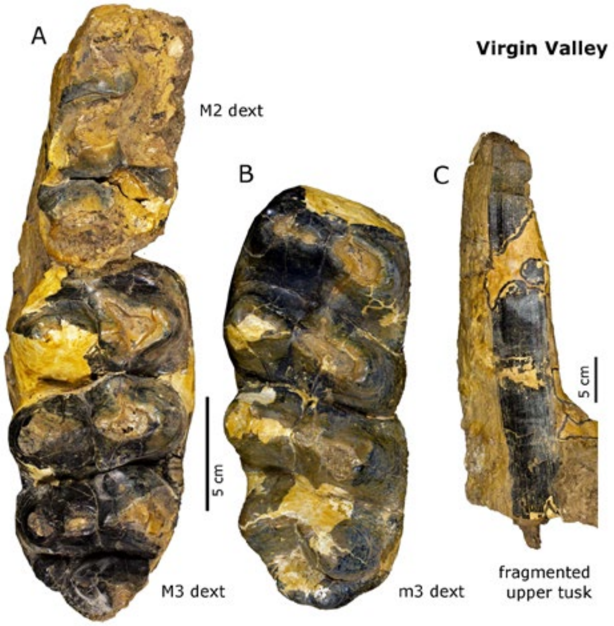

Plate 2. *Zygolophodon proavus* (type material of *Miomastodon merriami*), Virgin Valley, Nevada. (A) M2 and M3 of the right maxilla. (B) Left m3. (C) fragment of upper tusk with enamel band. (DMNSEVP 92) (Photo credit: Denver Museum of Nature and Science).

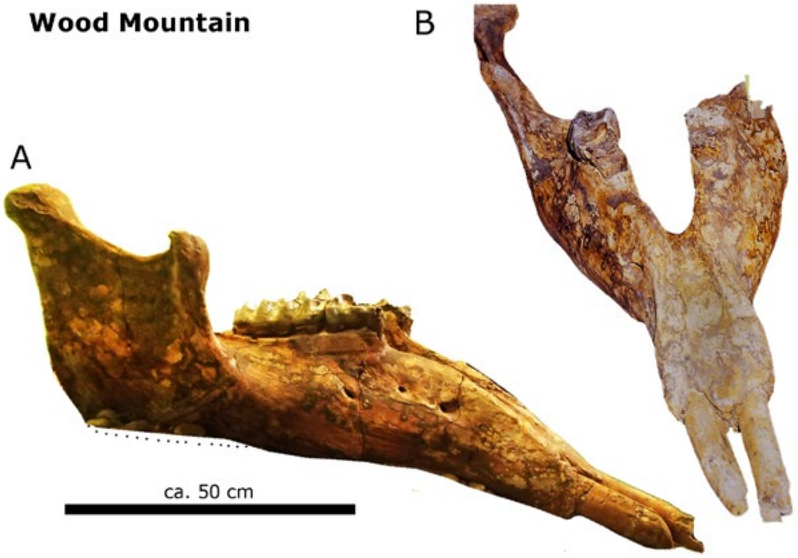

Plate 3. (A) *Zygolophodon proavus*, Wood Mountain (RSM P1165.1), Saskatchewan, Canada. (A) Lateral aspect of the mandible (B) Anterior aspect showing the long symphysis with the symphyseal trough (from Storer, 1989 and RSM).

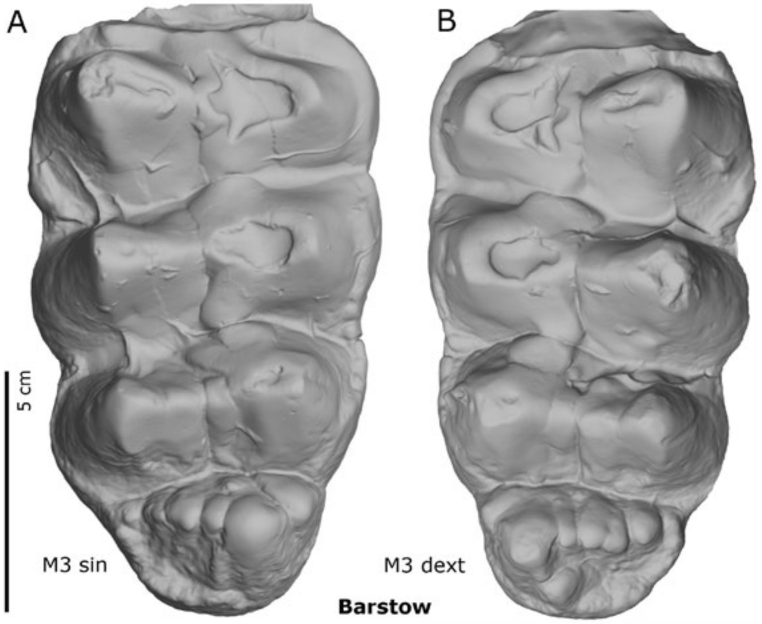

Plate 4. *Zygolophodon proavus*, Barstow, Barstovian, California. 3D-scans of left and right M3 (RAM 908); (3D models from casts).

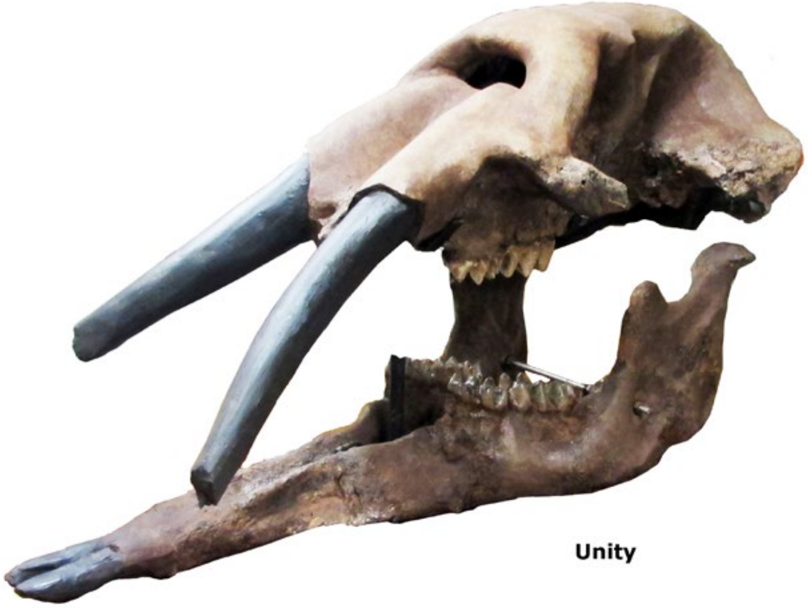

Plate 5. *Zygolophodon proavus* from Unity (Oregon) Clarendonian, Oregon Museum of Science and Industry (OMSI 1946.02.1026), Portland OR. It is the only individual from a Miocene mammutid (so far), where the mandible is preserved together with the cranium. The upper part of the cranium is restored.

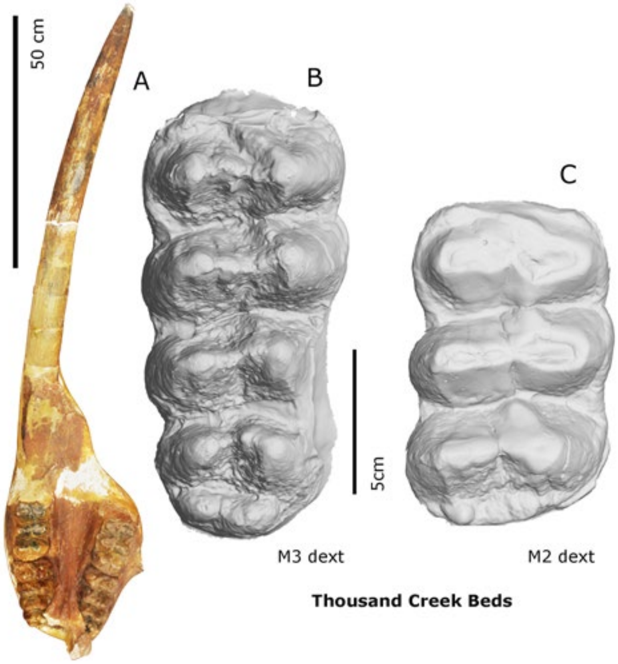

Plate 6. *Mammut matthewi (*type specimen of *M. nevadanum)* (LACM CIT 63-1922), Thousand Creek Beds (Humboldt Co, Nevada), early Hemphillian. (A) Partial cranium (photo credit: LACM), (B) Right M3 and (C) right M2. (B and C are 3D models from casts).

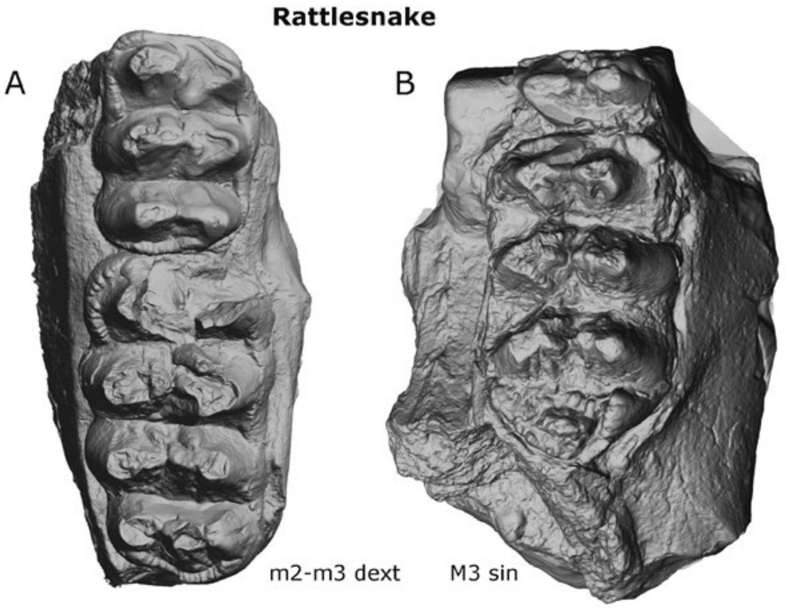

Plate 7. Mammutid molars from Hemphillian fauna of Rattlesnake, Oregon. (A) Fragmented mandible with left m2 and m3 (JODA 1321). (B) Left M3 (JODA 1322). (3D models from casts).

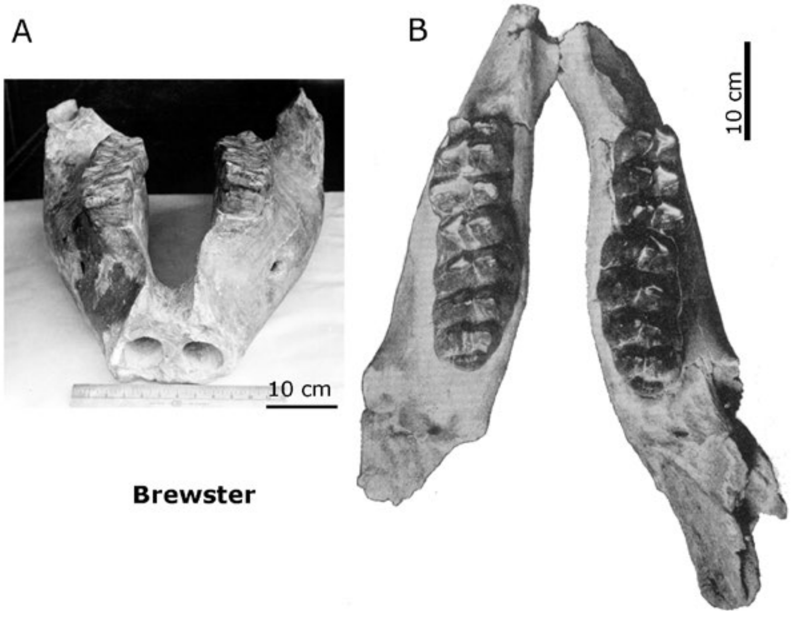

Plate 8. Mammutid mandible from the late Hemphillian Palmetto fauna from Brewster (Florida) described as *Pliomastidon sellardsi* by Simpson 1930 and later synonymized as *Mammut matthewi* (Hulbert, 2015). Only the right ramus is currently extant (UF/FGS/3822). (A) Photo of the partially reconstructed symphysis with alveoli for mandibular tusks. (B) Mandible with short symphysis in occlusal aspect; (photo credits: Florida Memory Project).

Plate 9. Mammutid mandible with a long symphysis from Gray Fossil Site (Tennessee) during preparation; (photo credit: GFS).

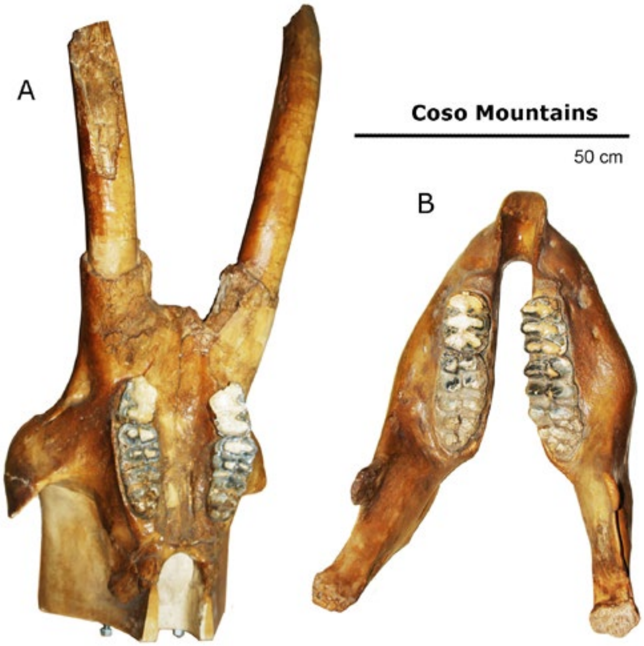

Plate 10. *Mammut cosoensis*, from the Blancan Coso Mountain (California), type specimens of *Pliomastodon cosoensis.* (A) Cranium with strong dorsally curving tusks (LACM (CIT) 284-1719) and (B) mandible with short symphysis (LACM CIT 284-1720). A and B are not from the same individual. The symphysis in B is partly restored; (photo credit: LACM).

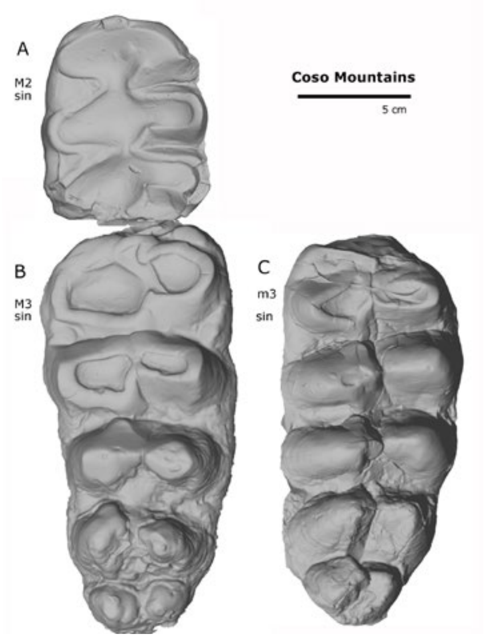

Plate 11. *Mammut cosoensis* from the Blancan Coso Mountains (California), upper molars (A & B) and lower m3 (C) from the type specimen (see Plate 10); (3D models from casts).

Plate 12. *Mammut cosoensis* from the Blancan Coso Mountains (California). Isolated maxilla with deciduous dentition: dP2, dP3, and dP4. (LACM CIT 284/2036); (photo credit LACM).

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