

# First reported Mio-Pliocene *Mammut matthewi* from Louisiana

Connor D. White



# PAN-AMERICAN PALEONTOLOGY

---

## Board of Editors

Frederick S. Rogers, Franklin Pierce University, Rindge, NH •

### Editor for Invertebrates

Blaine W. Schubert, East Tennessee State University, Johnson City, TN • **Editor for Vertebrates**

James I. Mead, The Mammoth Site, Hot Springs, SD • **Editor-at-Large**

Sam Rexing, Eagle Hill Institute, Steuben, ME • **Production Editor**

Joerg-Henner Lotze, Eagle Hill Institute, Steuben, ME • **Publisher**

## Associate Editors

Richard C. Hulbert Jr., Florida Museum of Natural History (ret), Gainesville, FL

Christopher N. Jass, Royal Alberta Museum, Edmonton, AB, Canada

H. Gregory McDonald, Fort Collins, CO

Joshua X. Samuels, Eastern Tennessee State University, Johnson City, TN

Jeremy B. Stout, Nature Center at Steele Creek Park, Bristol, TN

♦ *Pan-American Paleontology* is a peer-reviewed journal that publishes articles focusing on the paleontology of the Americas (ISSN 3066-117X [online]). Manuscripts based on studies outside of this region that provide information on aspects of paleontology within this region may be considered at the Editor's discretion.

♦ Manuscript subject matter - The journal welcomes manuscripts based on paleontological discoveries of terrestrial, freshwater, and marine organisms and their communities. Manuscript subjects may include paleozoology, paleobotany, micropaleontology, systematics/taxonomy and specimen-based research, paleoecology (including trace fossils), paleoenvironments, paleobiogeography, and paleoclimate.

♦ It offers article-by-article online publication for prompt distribution to a global audience.

♦ It offers authors the option of publishing large files such as data tables, and audio and video clips as online supplemental files.

♦ Special issues - *Pan-American Paleontology* welcomes proposals for special issues that are based on conference proceedings or on a series of invitational articles. Special issue editors can rely on the publisher's years of experiences in efficiently handling most details relating to the publication of special issues.

♦ Indexing - *Pan-American Paleontology* is a young journal whose indexing at this time is by way of author entries in Google Scholar and Researchgate. Its indexing coverage is expected to become comparable to that of the Institute's first 3 journals (*Northeastern Naturalist*, *Southeastern Naturalist*, and *Journal of the North Atlantic*). These 3 journals are included in full-text in BioOne.org and JSTOR.org and are indexed in Web of Science (clarivate.com) and EBSCO.com.

♦ The journal's staff is pleased to discuss ideas for manuscripts and to assist during all stages of manuscript preparation. The journal has a page charge to help defray a portion of the costs of publishing manuscripts. Instructions for Authors are available online on the journal's website (<http://www.eaglehill.us/papa>).

♦ It is co-published with the *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, *Urban Naturalist*, *Eastern Biologist*, and *Journal of the North Atlantic*.

♦ It is available online in full-text version on the journal's website (<http://www.eaglehill.us/papa>). Arrangements for inclusion in other databases are being pursued.

---

**Cover Photograph:** All fossil material assigned to Thompson Creek mastodon, *Mammut matthewi*, from Pascagoula Formation, Thompson Creek site, West Feliciana Parish, Louisiana. Specimens include upper tusks, partial cranium, and isolated upper right M2 (LSUMG-V-17901), as well as a partial anterior thoracic vertebra (LSUMG-V-17937). Model towards the bottom right of the page is a reconstruction of the orientation of the two isolated tusks of the Thompson Creek mastodon (LSUMG-V-17901) by paleoartist Nic Bushell. Photographs © Connor D. White and Mason Kirkland.

---

**Pan-American Paleontology** (ISSN # 3066-117X) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone 207-546-2821 Ext. 4, FAX 207-546-3042. E-mail: [office@eaglehill.us](mailto:office@eaglehill.us). Webpage: <http://www.eaglehill.us/epal>. Copyright © 2026, all rights reserved. Published on an article by article basis. **Special issue proposals are welcome.** *Pan-American Paleontology* is an open access journal. **Authors:** Submission guidelines are available at <http://www.eaglehill.us/epal>. **Co-published journals:** The *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, and *Urban Naturalist*, each with a separate Board of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

## First reported Mio-Pliocene *Mammut matthewi* from Louisiana

Connor D. White<sup>1, 2, \*</sup>

**Abstract** - A partial cranium with M2-M3 and associated tusks of a mammutid were collected from the Thompson Creek site in West Feliciana Parish, Louisiana. This site is considered to be part of the Pas-cagoula Formation, and mammalian biochronology supports an age of Hemphillian 4 (latest Miocene to earliest Pliocene) for the fauna. Dental morphology supports an identification of *Mammut matthewi*, and wear of the M2 and M3 indicates that the specimen is a mature individual. Two complete upper tusks were recovered. These tusks are significant due to their unusually small girth proportional to their length, compared to Pleistocene *Mammut* and are mostly straight with a slight curvature in two planes. The Thompson Creek specimen represents the first pre-Pleistocene mastodon found in Louisiana and the only known record of *M. matthewi* from the Gulf Coastal Plain west of peninsular Florida.

### Introduction

Fossils of Neogene mammutids are rare in North America. In a recent review of North American Mio-Pliocene mammutids (von Koenigswald et al. 2023), only 23 localities across North America were considered. Most of these localities contained specimens that were incomplete and limited to isolated molars, partial mandibles, and upper tusks, with only three complete maxillae (Cope 1873, 1889; Frick 1933; Hibbard 1944; Matthew 1930; Osborn 1921, 1926; Osborn 1936; Schultz 1937; Shotwell and Russell 1963; Simpson 1930; Stock 1936; von Koenigswald et al. 2023). The identification of North American proboscidean taxa, especially Miocene and Pliocene material, relies primarily on dental characters (Cope 1873, 1889; Frick 1933; Hibbard 1944; Hodgson et al. 2008; Dooley et al. 2019; King and Saunders 1984; Matthew 1930; Osborn 1921, 1926; Osborn 1936; Saunders 1977; Schultz 1937; Shotwell and Russell 1963; Simpson 1930; Stock 1936; von Koenigswald et al. 2023). Few studies focus on explicitly outlining differences in postcranial proboscidean anatomy and morphology, as postcranial proboscidean material is generally considered to be less diagnostic than dental elements (Hodgson et al. 2008; Olsen 1972). Dooley et al. (2019), is one of the few studies that included postcranial characters, stating that specimens of *Mammut pacificus* could be differentiated from *Mammut americanum* by having six sacral vertebrae and femurs with a greater mid-shaft diameter proportional to the length. Isolated teeth tend to be better preserved and more frequently recovered than postcrania, but morphologically conservative molars and the fragmentary nature of Miocene and Pliocene *Mammut* specimens makes taxonomic identification and differentiation difficult (von Koenigswald et al. 2023). Most named North American Miocene and Pliocene mammutid species are no longer considered to be valid, with many taxa synonymized due to poorly preserved type specimens and unreliable morphological characters (Lambert and Shoshani 1998; Shoshani and Tassy 1996).

<sup>1</sup>Louisiana State University Museum of Natural Science, Louisiana State University and Agricultural and Mechanical College, Baton Rouge, Louisiana, USA. <sup>2</sup>Department of Geosciences, Baylor University, Waco, Texas, USA. \*Corresponding author: Connor\_white3@baylor.edu.

Manuscript Editor: Blaine Schubert, East Tennessee State University.

New research and discoveries are causing researchers to re-evaluate what we know of the genus *Mammut*. Until recently, it was accepted that all Pleistocene *Mammut* fossils were the American mastodon, *Mammut americanum* (Dooley et al. 2019, Fisher 2018, Kurtén and Anderson 1980, Saunders 1996). However, a new species of Pleistocene *Mammut*, *M. pacificus*, was described by Dooley et al. (2019). *Mammut pacificus*, the Pacific mastodon, primarily differs from *M. americanum* by having narrower teeth with greater length to width ratios, as well as other differences in their skeletal characters (Dooley et al. 2019). Follow up studies have extended the range of *M. pacificus* to Montana and Oregon, USA; Alberta, Canada; and Hidalgo and Jalisco, Mexico (Dooley et al. 2025a, McDonald et al. 2020). The recovery of 35 complete mitochondrial genomes from specimens of *M. americanum* across North America, has revealed six distinct mitochondrial clades of Pleistocene mastodons (Karpinski et al. 2020). The recovery of mitochondrial DNA from two mastodons in American Falls, Idaho, assigns them to Clade Y, and raises important questions to the level of interaction between *M. pacificus* and *M. americanum* (Karpinski et al. 2023). Researchers have proposed that Clade M, which diverged from the other mitochondrial clades approximately 3.03 Ma (Karpinski et al. 2020), represents *M. pacificus* (Dooley et al. 2025a). If correct, this indicates that *M. pacificus* diverged from *M. americanum* within the Pliocene (Dooley et al. 2025a).

These studies highlight the need for further revision of all North American Mammutidae. Unfortunately, the lack of adequate Miocene and Pliocene specimens continues to frustrate research on Neogene mammutids (von Koenigswald et al. 2023). Many of these specimens have been synonymized with existing taxa, chiefly *Mammut matthewi*, due to a lack of diagnostic characters (Shoshani and Tassy 1996). There is ongoing debate whether these taxa may have been excessively lumped together, and if the validity of some should be reconsidered (Dooley et al. 2019, Inabinett 2020, von Koenigswald et al. 2023). For clarity, this paper will refer to Mio-Pliocene mammutid specimens by their pre-synonymized species name and commonly used locality name following von Koenigswald et al. (2023). It should also be noted that von Koenigswald et al. (2023) raised a nomenclature point about the taxonomic names of various mammutid taxa. Specifically, the authors note that the scientific names of *Mammut nevadanus*, *M. vexillarius*, and *M. pacificus* do not end in the correct Latin suffix. Thus, they changed these names to *M. nevadanum*, *M. vexillarium*, and *M. pacificum* in their publication (von Koenigswald et al. 2023). For the purposes of the current paper, the earlier names for these species will be used for consistency and continuity with the broader literature. However, it is realized that future taxonomic work may fully synonymize these earlier names.

Descriptions of new material of Neogene mammutids are important for gaining insight into early North American mammutids. There are three cataloged Neogene proboscidean specimens recovered from Louisiana. These specimens are currently housed in the Louisiana State University Museum of Natural Science (LSUMNS) Vertebrate Paleontology Collection in Baton Rouge, Louisiana. LSUMG-V-3635 is a fragment of a cheek tooth assigned to *Gomphotherium* sp. reported from the Fort Johnson (formerly Fort Polk) fossil site in Vernon Parish, Louisiana (Schiebout 1997). However, due to its fragmentary nature and the lack of diagnostic characters, it has recently been referred to as *Proboscidea incertae sedis* (Dooley et al. 2025b). LSUMG-V-17901 is cataloged as “Mastodon” and was recovered from a Hemphillian faunal assemblage from the Pascagoula Formation in West Feliciana Parish, Louisiana (Schiebout et al. 2006). The specimen consisted of a partial cranium with both upper left and right M3s in the cranium, an associated and incomplete upper right M2, and two associated complete upper tusks. The specimen was still being prepared when the fossil

site and the recovered materials were first reported in Schiebout et al. (2006), thus no formal description of the material was completed. In a later study, LSUMG-V-17901 was briefly described and assigned to *Mammut* cf. *M. matthewi* (Yann 2010). LSUMG-V-17937 was cataloged as “Mastodon?” and consists of three vertebrate centrum fragments and a partial neural spine. It was recovered from the same riverbank at the Thompson Creek site as LSUMG-V-17901. Although it was not associated in previous studies (Yann 2010), the current paper considers LSUMG-V-17901 and LSUMG-V-17937 to represent a single individual as both specimens were found in the same general location and there are no overlapping elements. This study formally describes LSUMG-V-17901 and LSUMG-V-17937 as the Thompson Creek mastodon, the first reported Mio-Pliocene mastodon from Louisiana and incorporates these results into the context of North American Mio-Pliocene mammutids.

### Geologic and Biotic Setting

In June 2005 amateur naturalist Kerry Dicharry reported the discovery of a mastodon palate with teeth protruding out of a creek bed in the Tunica Hills region to Judith Schiebout of Louisiana State University (LSU; Schiebout et al. 2006). Field surveys conducted by a team of researchers from LSU revealed two large tusks that were associated with a palate, as well as numerous other fossil specimens from other taxa (Schiebout et al. 2006). The fossil specimens were discovered in the Thompson Creek riverbed at the Thompson Creek site (Fig. 1). Thompson Creek forms the border between West Feliciana Parish and East Feliciana Parish, with the Thompson Creek site located on the north bank of Thompson Creek within West Feliciana Parish (McCulloh 2016, Schiebout et al. 2006, Yann 2010). The

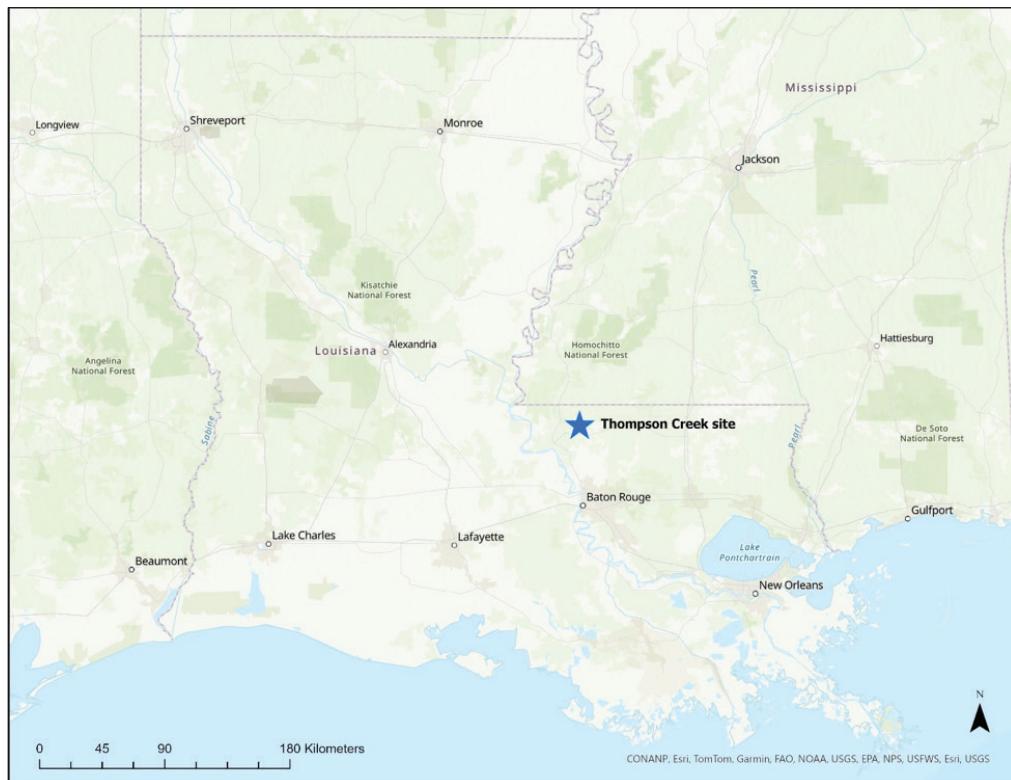


Figure 1. Map of Louisiana with location of Thompson Creek site.

Thompson Creek site is identified as LSUMG-VL-1057 in the Louisiana State University Museum of Natural Science (LSUMNS) Vertebrate Paleontology Collection database. The locality was initially referred to as the “Tunica Hills site” in Schiebout et al. (2006), and as the “TunicaHills/Kerry site” in Yann (2010). In order to more accurately reflect the location of the site and differentiate it from other localities in the Tunica Hills region, this paper refers to LSUMG-VL-1057 as the “Thompson Creek site.”

The LSU team excavated a diverse assemblage of vertebrate specimens from the Thompson Creek site (Schiebout et al. 2006), and over one hundred specimens are currently cataloged. During recovery the specimens were initially thought to be Pleistocene in age, as numerous isolated Pleistocene fossils have been recovered as float in creeks that have weathered out of loess deposits in the region (Chandler 1998, Domning 1969, Schiebout et al. 2006, Yann 2010). However, the specimens were later reported to be Miocene in age, since they were recovered from Miocene-aged clays, and the faunal assemblage was consistent with a Hemphillian North American Land Mammal Age (NALMA; Schiebout et al. 2006).

The Thompson Creek fauna was excavated from blue-green clay that was referred to the Pascagoula Formation (Schiebout et al. 2006). The Pascagoula Formation is considered Miocene in age, based on its stratigraphic position. However, a major concern was whether the specimens recovered from the Pascagoula Formation were actually *in situ*, or if the recovered materials were Pleistocene fossils that were reworked into the Miocene clays. To determine if the specimens recovered from the Pascagoula Formation were in context, Yann (2010) conducted a rare earth element (REE) analysis on specimens and nodules recovered from the Pascagoula Formation and various Pleistocene sites in the Tunica Hills region. The REE analysis revealed two distinct signatures for the Pascagoula specimens and Pleistocene specimens, which indicated that the Thompson Creek site specimens do represent *in situ* Pascagoula Formation material (Yann 2010).

The vertebrate fauna excavated from the Thompson Creek site is consistent with the latest Hemphillian (Hh4) NALMA (Schiebout et al. 2006). Remains from *Mammut* sp., *Pleiolama/Alforjas* sp., *Hexameryx simpsoni*, an unidentified juvenile cervid, *Neohipparrison eurystyle*, *Nannippus* sp., *Cormohipparrison emsliei*, *Astrohippus* sp., cf. *Hipparrison*, and *Teleoceras* sp. have been reported from the site (Schiebout et al. 2006, Yann 2010). Microfossils include remains from *Compemys*, *Abelmoschomys*(?), frog, salamander, snake, turtle, gar, fish, and a crocodilian tooth (Schiebout et al. 2006). The presence of *Pleiolama/Alforjas*, *Hexameryx simpsoni*, *Neohipparrison eurystyle*, *Nannippus* sp., *Cormohipparrison* sp., *Teleoceras* sp., and an unidentified cervid are characteristic of Hemphillian 4 (Schiebout et al. 2006, Tedford et al. 2004). Most of these genera were extinct by the end of the Hemphillian, although both *Nannippus* and *Cormohipparrison* have been found in the later Early Pliocene Blanca NALMA (Bell et al. 2004, Tedford et al. 2004). The presence of a cervid is also significant, as cervids did not immigrate into North America until the latest Miocene around 5 Ma (Gilbert et al. 2006, Webb 2000). This identification should be considered tentative, however, as the cervid specimen has not been studied in detail. The fauna of the Thompson Creek site supports an age of Hemphillian 4, which dates from 5.9 to 4.6 Ma and places the Pascagoula Formation at the Thompson Creek site within the latest Miocene to earliest Pliocene (Tedford et al. 2004).

No pollen, phytoliths, or other plant material was reported from the Thompson Creek site, so it is unknown exactly what flora would have been present at Thompson Creek during Hemphillian 4. The presence of both browsers and grazers indicates a forested environment with open grasslands, likely a savanna. The presence of fish, turtle, and alligator remains indicates wetlands or other permanent bodies of water, with the depositional environment

of the Pascagoula Formation's blue-green, clayey silt interpreted as an estuary (Schiebout et al. 2006). Therefore, it is likely that the Thompson Creek site was an estuary where the estuarine rivers created aquatic ecosystems, forested riparian zones, and drier upland grasslands. The site likely contained various trees, shrubs, aquatic plants, and grasses.

The Thompson Creek site is significant as it represents the first report of vertebrate fossils from the Pascagoula Formation in Louisiana (Schiebout et al. 2006). The site was first reported as one of two major Miocene terrestrial fossil sites in the entire state (Schiebout et al. 2006), although the site is now considered to be latest Miocene to earliest Pliocene. Unfortunately, most of the specimens recovered from the Thompson Creek site have not been studied in detail. The original report on the site only listed recovered specimens without formally describing them (Schiebout et al. 2006), while a later study did describe and identify some of the larger macrofossils (Yann 2010). This study seeks to formally describe the Mio-Pliocene mammutid recovered from the Thompson Creek site.

## Materials and Methods

### Measurements and Terminology

Tusks were measured using the schema of Smith (2010). The straight-line distance from tip to base of the tusk was measured to the nearest millimeter. The full length of the tusk along the outer curve was measured with a 30-meter fabric tape measure to the nearest millimeter. This scale was taped to the tusk at every 10 cm using blue painter's tape; the diameter of the tusk was measured using a pair of digital calipers at 10 cm intervals to the nearest millimeter.

Following Gillette and Madsen (1993), the width of the palate from the lingual side of one M3 to the lingual side of the opposite M3 was measured from the anterior-most and posterior-most side of the M3s using digital calipers and a tape measure. The angle of convergence for the tooth row was estimated using a photograph of the palate in ImageJ.

Dental terminology follows Saunders (1977), with additional terminology from Tassy (1996) (Fig. 2). Measurements of the total antero-posterior length of the M3 and the width of each loph follows Dooley et al. (2019). The total length of the M3 was measured to the nearest centimeter with a 30-meter tape measure, as the available digital calipers were too small to measure the full length. Digital calipers were used to measure the width of each loph to the nearest hundredths of a millimeter. On the 1<sup>st</sup> and 2<sup>nd</sup> loph of each molar, part of the enamel was missing, so the thickness of the missing enamel was estimated based on the thickness of the enamel on the 3<sup>rd</sup> and 4<sup>th</sup> lophs.

A heavily worn right M2 was associated with the palate and fits into the remnants of the right M2 alveolus on the palate. The M2 was missing the pretrite cusp of the protoloph when it was recovered, and the missing section was reconstructed with plaster when the specimen was prepared. Total length and width measurements were still available from the intact margins of the M2. The total length and width of the M2 was measured with digital calipers. Length/width ratios were calculated by dividing total length of each tooth with its maximum width (Dooley et al. 2019, von Koenigswald et al. 2023).

### 3D Models

Photos of the palate and tusks were captured on an iPhone 6S by the author. The 3D photogrammetric models were rendered in Agisoft Metashape 1.8.4 and are available on MorphoSource. The 3D models of the partial cranium, left tusk, and right tusk can be viewed at Showcase Biological Specimen // MorphoSource under the species *Mammut matthewi*.

To determine the correct orientation and side of the two isolated tusks, the 3D photogrammetric models of the tusks were attached to a 3D scan of the Cohoes mastodon skull in four possible orientations. The Cohoes mastodon is housed in New York State Museum Vertebrate Paleontology collection with catalog number NYSM VP101. The skull was scanned by Bernard Means of the Virtual Curation Lab at Virginia Commonwealth University. The 3D model of the skull is available on the Virtual Curation Lab's Sketchfab (<https://sketchfab.com/3d-models/cohoes-mastodon-skull-vcu-3d-3632-21cf1d2d26d4ca9963f9-ad2a6cebab9>) and licensed under a Creative Commons CC BY-NC-ND 4.0. The model of the Cohoes mastodon skull is used with permission from the New York State Museum.

### Institutional Abbreviations

AMNH FM (American Museum of Natural History Fossil Mammal Collection, New York, New York); AMNH F:AM (Frick Collection at the AMNH); DMNH EPV (Denver Museum of Nature and Science, Denver, Colorado); ETMNH (East Tennessee State University Museum of Natural History collection, Gray, Tennessee); JODA (John Day Fossil Beds National Monument, Oregon); KUVP (University of Kansas Vertebrate Paleontology, Lawrence, Kansas); LACM (CIT) (Los Angeles County Museum of Natural History, Los Angeles, California, currently housed in California Institute of Technology, Pasadena, California collection); LSUMG-V (Louisiana State University Museum of Natural Science Vertebrate Paleontology Collection, Baton Rouge, Louisiana); LSUMNS (Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana); NYSM VP (New York State Museum Vertebrate Paleontology collection, Albany, New York); OMSI (Oregon Museum of Science and Industry, Portland, Oregon); RAM (Raymond Alf Museum, Claremont, California); UCMP (University of California Museum of Paleontology, Berkeley, California); UF/VP (Florida Museum of Natural History, University of Florida, Gainesville, Florida); UF/FGS (Florida Geological Survey collection, currently housed in University of Florida); UOMNH F (University of Oregon Museum of Natural History Fossil, Eugene, Oregon).

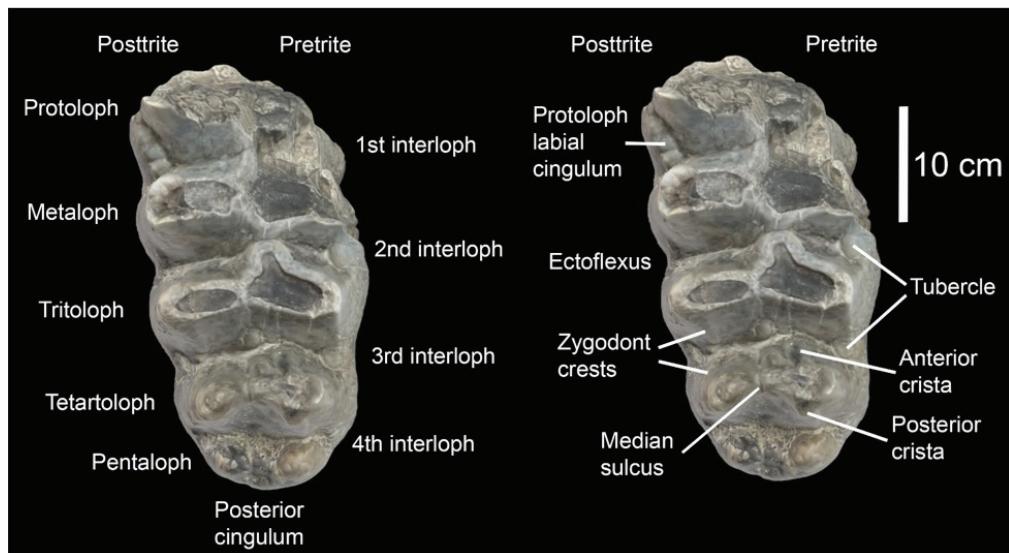


Figure 2. Right M3 of *Mammut matthewi*, LSUMG-V-17901, with major dental features labeled.

## Results

### Systematic Paleontology

Order PROBOSCIDEA Illiger 1811

Clade ELEPHANTIMORPHA Shoshani et al., 1998

Family MAMMUTIDAE Hay 1922

Genus *MAMMUT* Blumenbach 1799

*Mammut matthewi* (Osborn 1921)

*Referred Specimen.* LSUMG-V-17901 is composed of a partial cranium that contains the posterior-most section of the palate with both left and right M3, an associated and incomplete right M2, and two associated complete upper tusks (Fig. 3). LSUMG-V-17937, is composed of a partial vertebra with a neural spine and three fragments of the vertebra centrum (Fig. 4). Both specimens are currently housed in the Louisiana State University Museum of Natural Science (LSUMNS) Vertebrate Paleontology Collection in Baton Rouge, Louisiana. The prefix, LSUMG-V, refers to the old Louisiana State University Museum of Geology (LSUMG) whose collection was accessioned in the Louisiana State University Museum of Natural Science (LSUMNS) in 1992, but the old prefix was retained.

*Locality.* LSUMG-V-17901 and LSUMG-V-17937 were found in the Thompson Creek site, locality number LSUMG-VL-1057. The fossils were discovered *in situ* in what is considered to be the Pascagoula Formation.

*Partial Cranium.* The partial cranium of LSUMG-V-17901 only contains the posterior-most section of the palate. The palate is comprised of portions of the maxillae and palatines. Both the right and left maxillae are broken anterior to the M3s with just the posterior-most section of the maxilla preserved. Nearly all of the palatine bones are preserved. The upper left and right M3 are preserved *in situ* in the maxilla (Fig. 3). The cranium is heavily pneumatized. Very little of the orbit is preserved, as the cranium is broken below the lacrimal bone and only the maxilla and infraorbital foramen are preserved. There is a line of plaster down the midline of the palatines connecting the two halves and the whole palate is held together on a plaster stand. It is possible that the palate was broken along this midline or that it was unfused. The plaster does not affect the length measurements of the palate, as the two halves do connect while the plaster is used to hold the two pieces together and fill in missing parts. The posterior section of the palatine bones are preserved and form a half circle at the posterior palate. The M3 in the maxilla are posteriorly convergent at an angle of around 50°, forming a weak “V shape.” The width of the palate at the anterior-most side of the M3 is 178 mm, and the width of the palate from posterior most side of the M3 is 126.8 mm.

*Dentition.* LSUMG-V-17901 has the right M2 and both M3s preserved (Fig. 3; Table 1). The occlusal surface of the M2 is heavily worn and almost completely flat. The M2 is trilophodont based on the preserved labial and lingual margins of the protoloph, metaloph, and tritoloph. The M2 is missing the pretrite cusp of the protoloph, which has been reconstructed with plaster. There is an identifiable ectoflexus on the labial side of the interloph between the margins of the metaloph and the tritoloph. The roots of the M2 are not well-preserved, with only a small piece of the posterior roots preserved under the posttrite cusp of the tritoloph. The entire ventral surface of the M2 has postmortem breakage. There does not appear to be evidence of root resorption on the posterior tritoloph root, as the root is not pitted and is still thick. The posterior-most section of the alveolus for the M2 was still preserved on the maxilla, and the M2 fits perfectly in it and against the M3 (Fig. 5). This tight articulation, lack of root resorption, and the amount of postmortem damage to the M2 indicates that the M2 was separated from the rest of the palate postmortem.

Both M3s are pentalophodont and included the protoloph, metaloph, tritoloph, tetartoloph, and a reduced pentaloph. The post-tetartoloph structure was identified as a true pentaloph rather than the posterior cingulum due to the presence of distinct pretrite and posttrite cusps that are separated by a median sulcus and the presence of a cingulum posterior to the pentaloph. Typically, in mastodon lower teeth that are pentalophodont, the fifth loph has either the same crown height or half the height of the other lophs (Dooley et al. 2019, Saunders 1977). However, Saunders (1977) noted that the fifth ridge is less developed on mastodon upper M3s compared to the lower m3s. Directly posterior to the pentaloph on the left M3 is a very small ridge identified as the posterior cingulum of the pentaloph. Its presence provides further evidence that the fifth ridge is a true pentaloph and not the posterior cingulum. The lophs are perpendicular to the long axis of the tooth, which is characteristic

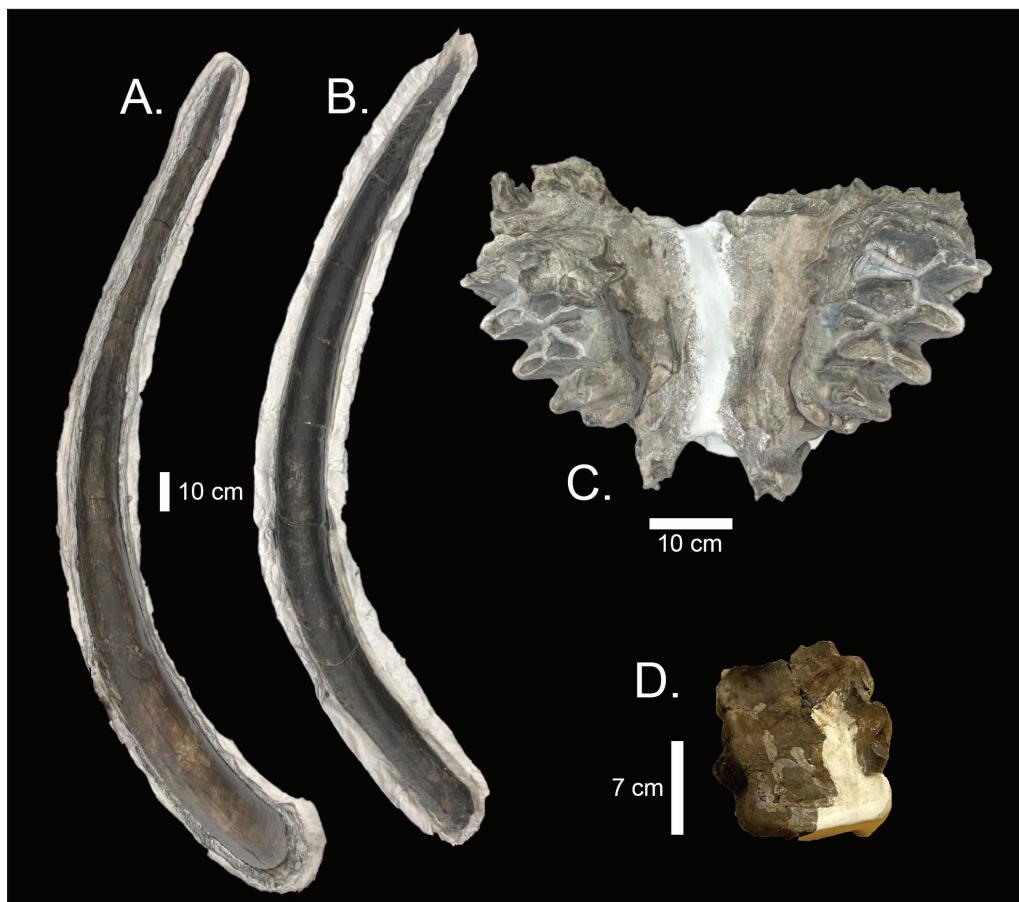


Figure 3. *Mammut matthewi*, LSUMG-V-17901, tusks, palate, and isolated upper right M2 of Thompson Creek mastodon from Pascagoula Formation, Thompson Creek site, West Feliciana Parish, Louisiana. **A.** left tusk; **B.** right tusk; **C.** partial cranium with upper M3s, ventral view; **D.** upper right M2, occlusal view (Note: anterior side of the tooth is towards the bottom of the picture, and the posterior side is towards the top of the picture). All specimens are housed at the Louisiana State University Museum of Natural Science Vertebrate Paleontology Collection. **A-C** are orthographic views of photogrammetric models created by Alton Dooley on Agisoft Metashape 1.8.4.

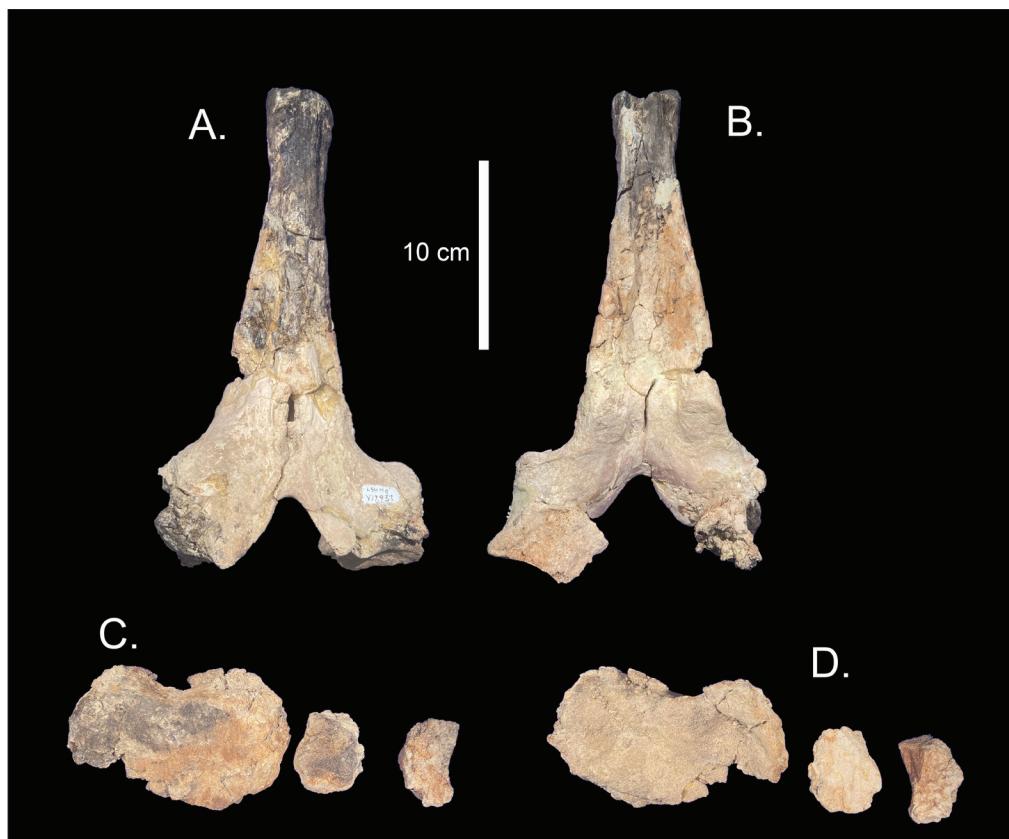


Figure 4. *Mammut matthewi*, LSUMG-V-17937, partial anterior thoracic vertebra of Thompson Creek mastodon from Pascagoula Formation, Thompson Creek site, West Feliciana Parish, Louisiana. **A.** anterior view of partial neural spine; **B.** posterior view of partial neural spine; **C.** anterior view of centrum fragments (3); **D.** posterior view of centrum fragments (3). Photographs taken by Mason Kirkland.

Table 1. Measurements of the length and width of the upper molars of the Thompson Creek mastodon. All measurements taken in mm. \*Lophs were damaged, and the width measurement was calculated by adding the measured enamel thickness to the widest measured margins of the molar.

Thompson Creek Mastodon Molar Measurements									
Molar	Maximum Length (mm)	Maximum Width (mm)	Measured Enamel Thickness (mm)	1st loph Width (mm)	2nd loph Width (mm)	3rd loph Width (mm)	4th loph Width (mm)	5th loph Width (mm)	Length/Width Ratio
Left M3	166	96.15	5.29	94.41*	96.15*	88.52	76.85	50.52	1.73
Right M3	170	93.98	5.26	90.02*	93.98*	88.06	72.71	50.74	1.81
Right M2	93.86	79.68	-	-	-	-	-	-	1.18

of upper molars. There is no choerodonty (bumpy texture) or plication present on either M3. The overall weakly developed cristae, absent to weakly developed tubercles, and the smooth texture of the enamel due to the absence of choerodonty and plication, corresponds to the “smooth variety” cheek tooth morphotype (Saunders 1977). The 1<sup>st</sup> and 2<sup>nd</sup> interloph valleys on both M3 appear more restricted likely due to the extensive wear on the lophs and cristae.

On the right M3 the protoloph is broken postmortem, exposing the dentin with almost none of the enamel remaining on the pretrite. Approximately half of the anterior side of the posttrite is broken. The damage to the protoloph makes it impossible to directly observe the amount of wear. However, due to the way mastodon teeth are worn it can be assumed that the protoloph would be more worn than the metaloph. The metaloph is more intact with the anterior and lingual side of the pretrite worn down to the dentin with no enamel present, while the posttrite is fully intact. The pretrite cusps display moderate to heavy wear with an obliterated wear pattern, while the posttrite cusps display moderate wear and a trefoil wear pattern. There is still a band of enamel that separates the two pretrite and posttrite basins of the loph that has not been worn away. The tritoloph is fully intact with moderate wear on the pretrite cusps and light wear on the posttrite cusps. The pretrite cusps display a simple trefoil wear pattern, while the posttrite cusps display a simple oblong wear pattern. There is a distinct band of enamel that separates the pretrite and posttrite basins of the tritoloph that has not been worn away. The tetartoloph is fully intact with light wear and a small amount of dentin exposed on the pretrite cusps and with little to no wear on the posttrite cusps.

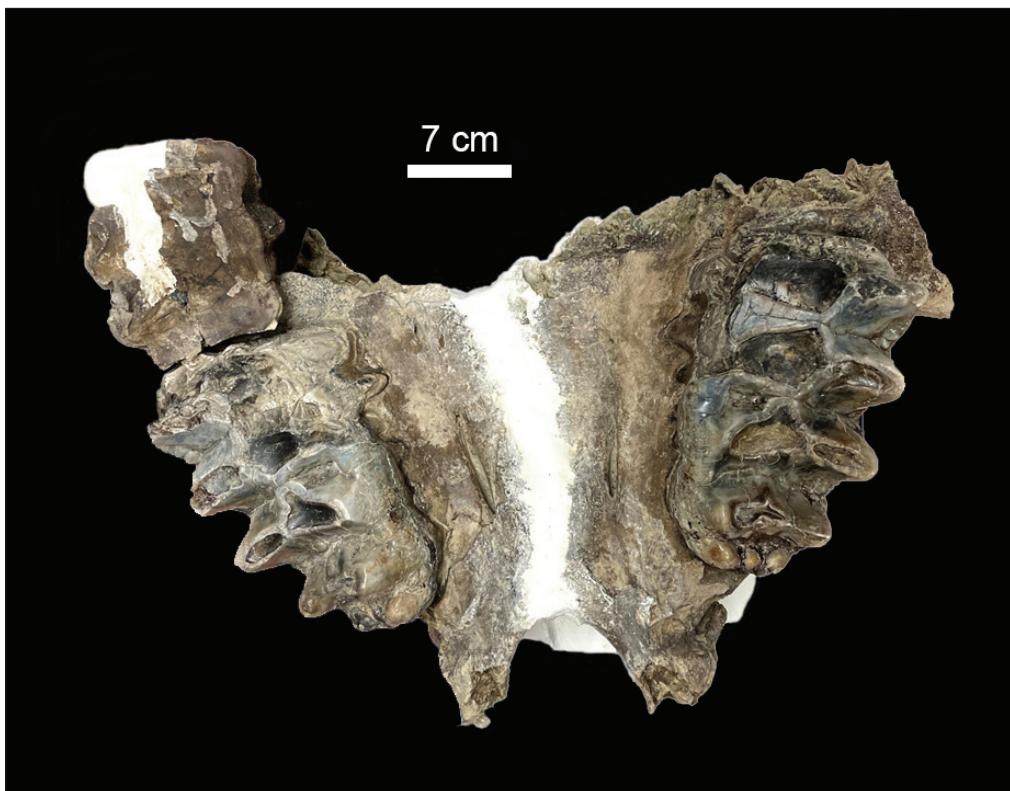


Figure 5. *Mammut matthewi*, LSUMG-V-17901, ventral view of palate with upper right M2 in place on Thompson Creek mastodon from Pascagoula Formation, Thompson Creek site, West Feliciana Parish, Louisiana.

The pentaloph is distinct and shows no sign of wear. It is less than half of the height of the tetartoloph, but the pretrite and posttrite cusps are separated by a median sulcus. There is a small shelf posterior to the pentaloph identified as the talon. There is a distinct ectoflexus present on the labial side of the first three interlophs, with a slight ectoflexus present on the 4<sup>th</sup> interloph separating the tetartoloph and the pentaloph. The anterior cristae on the pretrite side of the metaloph and tritoloph are strongly developed and help to form the strong trefoil wear pattern on the pretrite side of the two lophs. The pretrite anterior cristae are not as strongly developed on the tetartoloph and the pentaloph, which causes the 3<sup>rd</sup> and 4<sup>th</sup> interloph valleys to be more open than on the 1<sup>st</sup> and 2<sup>nd</sup> interloph valleys. The posttrite cristae, also referred to as the zygodont crests (Tobien 1975), are absent to very weakly developed in all interloph valleys. There is no cingulum on the lingual or labial margins of the molar, except for a weakly developed cingulum on the labial margin of the protoloph only. There are no tubercles on the labial side of the molar, but there is a weakly developed tubercle on the lingual margin of the 2<sup>nd</sup> interloph and a smaller weakly developed tubercle on the lingual margin of the 3<sup>rd</sup> interloph. There is a small amount of cementum in the 3<sup>rd</sup> and 4<sup>th</sup> interlophs.

The left M3 shares many of the same characteristics with the right M3, except for the following differences. On the left M3, the protoloph has all its anterior enamel and a small portion of the dentin broken off postmortem. The pretrite has enamel and dentin on the anterior side broken off and displays heavy wear with an obliterated wear pattern. The posttrite has the anterior side of its enamel missing and appears to display moderate wear with an oblong wear pattern, but it is too damaged to accurately determine the level of wear. The metaloph on the left M3 is much more intact than the right M3, with only a postmortem broken section on the lingual side of the pretrite. The pretrite cusps display heavy wear with an obliterated wear pattern, while the posttrite cusps display moderate wear and a trefoil wear pattern. There is a band of enamel that separates the two pretrite and posttrite basins on the metaloph that is worn down to the dentin only in the very middle. The tritoloph on the left M3 has similar levels of wear and wear patterns to the right M3. There is an intact band of enamel that separates the two pretrite and posttrite basins on the tritoloph, but it is more worn than on the right M3. The tetartoloph is fully intact with light wear on the pretrite cusps, which displays a small simple trefoil wear pattern, and little to no wear on the posttrite cusps. The pretrite cusp of the tetartoloph is more worn on the left M3 than on the right M3, as there is more dentin exposed on the cusps, creating a simple trefoil wear pattern. The left M3 pentaloph is similar to the right M3, except for a small cusp in between the pretrite and posttrite cusps and lingual to the median sulcus. It appears to be the mesoconelet of the pretrite. The pretrite anterior cristae are moderately developed on the tetartoloph and weakly developed on the pentaloph. The more developed cristae cause the 3rd and 4<sup>th</sup> interloph valleys to be slightly more restricted than on the right M3. However, the 3<sup>rd</sup> and 4<sup>th</sup> interloph valleys are still more open than the 1<sup>st</sup> and 2<sup>nd</sup> interloph valleys. There are no tubercles on the labial side of the molar, but there is a weakly developed tubercle that is worn almost flat on the lingual margin of the 2<sup>nd</sup> interloph.

*Upper Tusks.* The associated and complete left and right upper tusks of LSUMG-V-17901 were both isolated when they were recovered. The premaxillae where the tusks would have emerged from the skull were not preserved, so it was unknown exactly how the tusks would be oriented in the skull or the correct siding of the tusks. To determine the likely siding and orientation of the tusks, the 3D models of the tusks were attached to a scan of the Cohoes mastodon skull (NYSM VP101) from the New York State Museum in four possible orientations (Fig. 6). Based on these reconstructions, the mostly likely orientation of the tusks is the one shown in Figure 6A, which is consistent with the typically straight

to upward curvature of Pleistocene mastodon tusks. Multiple angles of this interpreted tusk orientation of Figure 6A are shown in Figure 7. Based on this interpretation, the tusks are thought to protrude straight out from the alveoli before immediately curving gently upwards for nearly their entire length to the curve flattens out slightly more horizontally at the tips. The tusks also flair out laterally to about half the length of the tusks, and then flair back medially until the end. There is a wear facet on the ventral surface of the left tusk that further supports the orientation of the tusks in Figure 6A and 7. It is consistent with other mastodon specimens, which typically have a wear facet on the ventral or antero-ventral surface of the tusk depending on the curvature of the tusk (Smith 2010, Smith and Fisher 2011, Smith and Fisher 2013). Based on this interpretation, the tusk in Figure 3A is the right tusk and the one in Figure 3B is the left tusk.

While both upper tusks are mostly complete, there is noticeable asymmetry between the two and a difference in how well they are preserved. The lengths of both tusks were recorded in Table 2. By measuring the diameter of the tusk at every 10 cm along the full length of the tusk, the circumference of each measured point could be calculated assuming a circular cross area of the tusk (Table 3). By plotting the circumference and the length of the tusk, a tusk girth profile was created (Fig. 8). The tusks are fractured in several locations and are held together in their plaster jacket, so it was decided to not remove the tusks from their jackets for fear of further damaging the specimens. According to pictures taken during the excavation, the ventral side of the left tusk appears to have been heavily eroded (Schiebout et al. 2006; see photos taken by Ray Wilhite on file in the Vertebrate Paleontology Collection). The left tusk is more dorsoventrally compressed, with the right tusk having more of a flattened anteriorly pointing tip. There is no enamel band on either tusk. There appears to be a wear facet on the ventral surface of the right tusk, but not on the left tusk, due to breakage.

*Partial Vertebra.* The partial vertebra of LSUMG-V-17937 contains a neural spine and three fragments of the vertebral centrum. The base of the neural spine is mostly complete but displays moderate weathering, and it is unknown how much of the top of the neural spine is missing. The neural spine is broken where the neural arch attaches to the centrum, with the postzygapophyses and the dorsal most section of the neural canal preserved. Three fragments of the centrum are heavily worn and very incomplete. The largest centrum fragment appears to have both the anterior and posterior surfaces preserved. The posterior surface of the centrum has a rough texture, which indicates that posterior epiphysis of the centrum is unfused. This is very common in proboscidean vertebrae, as the centrum epiphyses typically either do not fuse within the animal's life or fuse very late in life (Haynes 2017). The partial vertebra compares more favorably to an anterior thoracic vertebra than a posterior thoracic vertebra, as the neural spine has a sharper anterior surface, and the posterior surface has a defined concavity (Hodgson et al. 2008).

## Discussion

### Identification

LSUMG-V-17901 and LSUMG-V-17937 are identified as *Mammut*. The morphology and measurements of the molars and tusks fall within *Mammut*, when compared to other North American Neogene proboscideans. The tooth morphology of LSUMG-V-17901 is typical of a mammutid and does not share the features of a gomphotherid. Gomphothere teeth are typically bunodont compared to the zygodont teeth of mammutids, and the interloph[id] valleys of gomphothere teeth are blocked due to the presence of the pretrite central conules (Osborn 1936, Saunders 1996, Shoshani and Tassy 1996, von Koenigswald

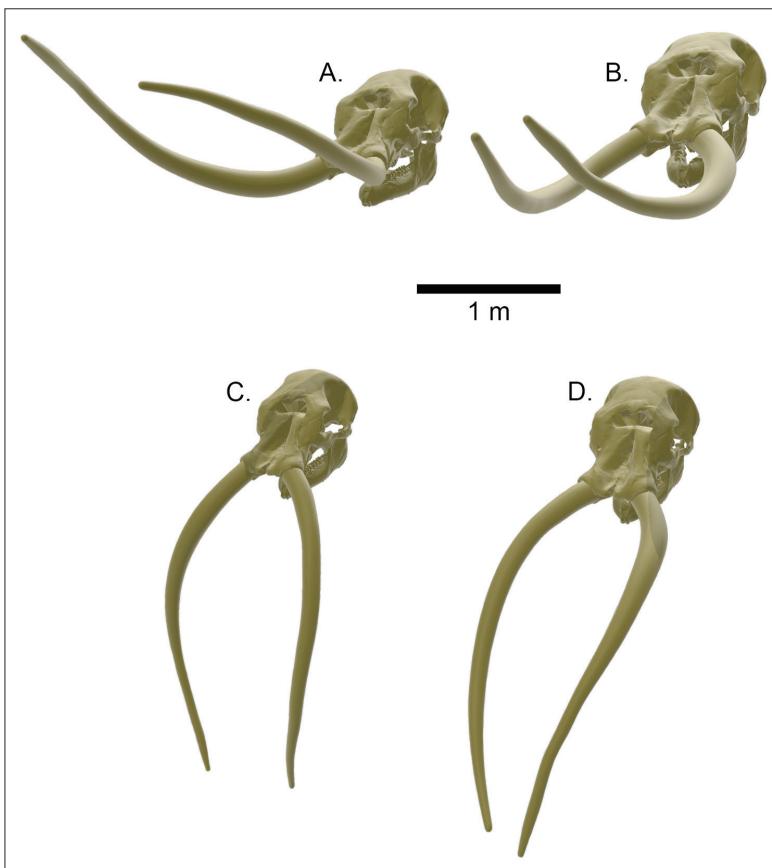


Figure 6. Four possible reconstructions of the orientation of the two isolated tusks of the Thompson Creek mastodon (LSUMG-V-17901) by paleoartist Nic Bushell. **A.** an upwards orientation of the tusks typical of most reconstructions of mastodon tusks. **B.** an upwards orientation of the tusks with the left and right tusks switched. **C.** a downwards orientation of the tusks. **D.** a downwards orientation of the tusks with the left and right tusks switched. Reconstruction A. is interpreted as the most accurate reconstruction of how the tusks would have appeared when the animal was alive. Due to a lack of preserved material in the Thompson Creek mastodon and the lack of complete Mio-Pliocene *Mammut* skulls, the 3D models of the Thompson Creek mastodon tusks were attached to the 3D model of the *Mammut americanum* Cohoes mastodon skull (NYSM VP101) which is representative of a typical Pleistocene *Mammut* skull. It is possible that the Thompson Creek mastodon's skull could have had a different morphology that would impact the reconstruction. The 3D model of the Cohoes mastodon skull (NYSM VP101) was scanned by the New York State Museum and was available on the Virtual Curation Lab's Sketchfab (<https://sketchfab.com/3d-models/cohoes-mastodon-skull-vcu-3d-3632-21cf1d2d26d4ca9963f9ad2a6cebab9>) and licensed under a Creative Commons CC BY-NC-ND 4.0. The 3D model of the Cohoes mastodon skull was modified from its original form by attaching the 3D models of the tusks of the Thompson Creek mastodon. The 3D model Cohoes mastodon skull is used with permission from Robert Feranec of the New York State Museum since the Creative Commons license for the Cohoes mastodon prevents derivatives.

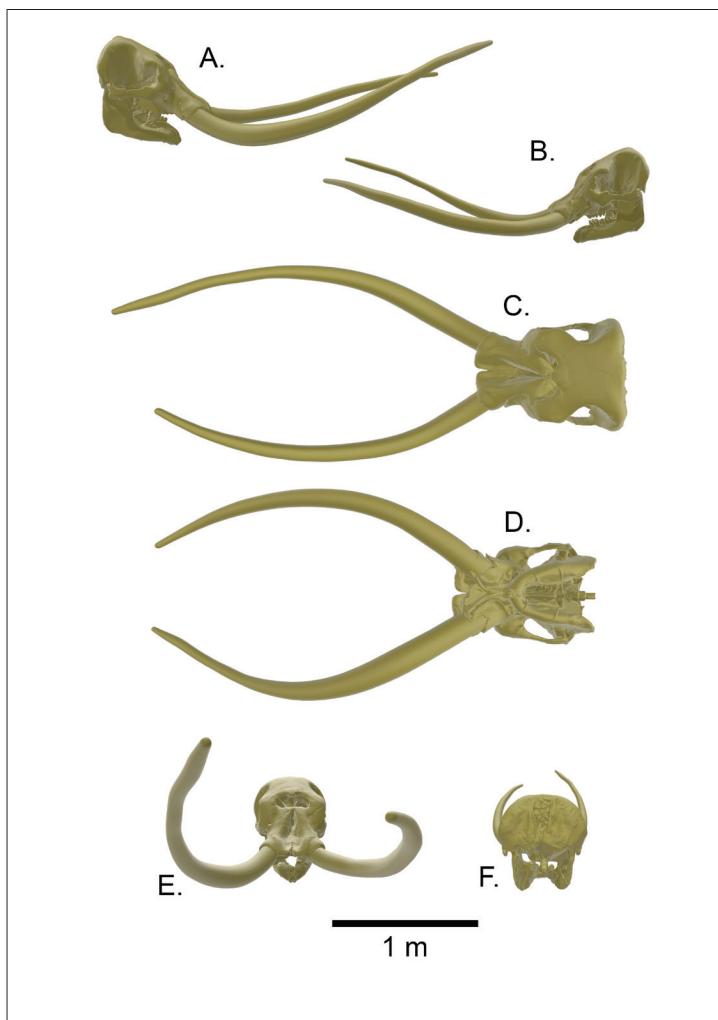


Figure 7. Reconstruction of the orientation of the two isolated tusks of the Thompson Creek mastodon (LSUMG-V-17901) by paleoartist Nic Bushell. **A.** right lateral view. **B.** left lateral view. **C.** dorsal view. **D.** ventral view. **E.** anterior view. **F.** posterior view. Due to a lack of preserved material in the Thompson Creek mastodon and the lack of complete Mio-Pliocene *Mammut* skulls, the 3D models of the Thompson Creek mastodon tusks were attached to the 3D model of the *Mammut americanum* Cohoes mastodon skull (NYSM VP101) which is representative of a typical Pleistocene *Mammut* skull. It is possible that the Thompson Creek mastodon's skull could have had a different morphology that would impact the reconstruction. The 3D model of the Cohoes mastodon skull (NYSM VP101) was scanned by the New York State Museum and was available on the Virtual Curation Lab's Sketchfab (<https://sketchfab.com/3d-models/cohoes-mastodon-skull-vcu-3d-3632-21cf1d2d26d4ca-9963f9ad2a6cebab9>) and licensed under a Creative Commons CC BY-NC-ND 4.0. The 3D model of the Cohoes mastodon skull was modified from its original form by attaching the 3D models of the tusks of the Thompson Creek mastodon. The 3D model Cohoes mastodon skull is used with permission from Robert Feranec of the New York State Museum since the Creative Commons license for the Cohoes mastodon prevents derivatives.

et al. 2023). When worn, these central conules give the gomphothere tooth a more complex trefoil pattern than mammutids (Saunders 1996). Nearly all North American gomphotheres, except *Stegomastodon*, have an enamel band present on their tusks, which is not present in LSUMG-V-17901 (Göhlich 1999, Lucas 2022, Osborn 1936, Shoshani and Tassy 1996.). LSUMG-V-17901 display zygodont molars that are typical of the two genera of Mio-Pliocene mammutids, *Zygododon* and *Mammut* (Tobien 1975, 1996). However, it is impossible to assign a specimen to one of these genera based on tooth morphology alone, due to their conservative morphology (von Koenigswald et al. 2023). It is possible to differentiate between *Mammut* and *Zygododon*, based on the morphology and measurements of the molars, mandible, maxilla, and upper tusks, as defined in von Koenigswald et al. (2023). *Zygododon* tusks are shorter than *Mammut* tusks, curve downward, and display an enamel band (von Koenigswald et al. 2023). *Mammut* tusks are enlarged, typically upwardly curving, and have no enamel band (von Koenigswald et al. 2023). The tusks of LSUMG-V-17901 are similar to the length of Pleistocene mastodon tusks. They are mostly straight with a slight curvature in two planes, and they have no enamel band. The partial vertebra of LSUMG-V-17937 compares favorably to a *Mammut* anterior thoracic vertebra, based on the robustness and posterior groove of the neural spine and the shallow curvature and large diameter of the largest centrum fragment. This paper considers LSUMG-V-17937 to be associated with LSUMG-V-17901, as both specimens were found at the same riverbank on the Thompson Creek site, both belong to *Mammut*, and there are no repeated elements which strongly indicate that both specimens are representative of the same individual. Based on the tooth and tusk morphology, LSUMG-V-17901 and LSUMG-V-17937, herein referred to as the “Thompson Creek mastodon,” are assigned to the genus *Mammut*.

Although it can be determined that the Thompson Creek mastodon belongs to the genus *Mammut*, determining its species is more complicated. Previous studies had attempted to identify the specimen to different levels of specificity. In Schiebout et al. (2006), the authors simply referred to the recovered material as a “mastodon” and stated that they were waiting until the preparation of the large tusk was complete before it was studied further. It was considered that the Thompson Creek mastodon could be assigned to *Pliomastodon* (*Mammut* syn.) *sellardsi* from the Palmetto Fauna in Bone Valley, Florida (Hulbert 2001, Simpson 1930), since both specimens were from similar geographic areas and geologic ages. Unfortunately, the holotype of *Mammut sellardsi* (UF/FGS 3822) is only a lower jaw with lower teeth that cannot be directly compared to the upper teeth of the Thompson Creek mastodon due to differences in morphology (Dooley et al. 2019, Saunders 1977). Also, *Mammut sellardsi* is no longer considered a valid taxon and was synonymized with *Mammut matthewi* (Hulbert 2015, Shoshani and Tassy 1996, von Koenigswald et al. 2023). In Yann (2010), LSUMG-V-17091 was identified as *Mammut* cf. *M. matthewi*, based on the

Table 2. The total length of both left and right tusks taken from along the outside curve of the tusk and from the tip to the end of the tusk. All measurements taken in cm.

Thompson Creek Mastodon Tusk Length

Specimen	Total Length of Tusk Along the Outside Curve (cm)	Total Length of Tusk from Tip to End (cm)
Left Tusk	216.2	190.8
Right Tusk	227	198.8

dental morphology of the specimen, the age of the site, similar specimens of Mio-Pliocene *Mammut* taxa that were synonymized with *M. matthewi*, and the geographic restriction of other valid Mio-Pliocene *Mammut* taxa. In order to determine the taxonomic assignment of the Thompson Creek mastodon, the maximum length, maximum width, and the L:W ratio of the upper M2 and upper M3s of the Thompson Creek mastodon are compared to the molars of other Mio-Pliocene mammutids (Figs. 9, 10, and 11). The data on Mio-Pliocene mammutids used in this study to compare to the Thompson Creek mastodon is from von Koenigswald et al. (2023), and can be seen in Tables 4 and 5.

In North American *Mammut*, comparisons of the lengths, widths, and L:W ratios of the M3s/m3s are useful morphologic features to separate the two recognized Pleistocene species (Dooley et al. 2019). Other teeth, including the deciduous premolars, M1/m1, and M2/m2, are not as reliable as the M3/m3 (Dooley et al. 2019). This also appears to be true for the Mio-Pliocene taxa, but the lack of specimens with preserved M2/m2 further prevents robust comparisons (Fig. 10). When compared to the Mio-Pliocene mammutid dataset in von Koe-

Table 3. Circumference of the tusk calculated from diameter measurement every 10 cm along the outside curve of the tusk, assuming a circular cross section. All measurements taken in cm.

Thompson Creek Mastodon Tusk Circumference

Total Distance (cm)	Circumference of Left Tusk (cm)	Circumference of Right Tusk (cm)
10	15.87	12.59
20	17.41	15.50
30	20.64	17.99
40	24.27	18.31
50	24.92	18.94
60	28.33	20.41
70	29.90	20.13
80	31.31	22.74
90	33.01	27.46
100	34.56	28.38
110	34.56	29.30
120	35.31	29.91
130	37.00	34.13
140	35.39	35.13
150	36.18	36.95
160	36.18	37.34
170	36.47	39.49
180	35.13	38.50
190	33.96	38.81
200	35.80	38.85
210	37.97	39.21
220	-	38.03

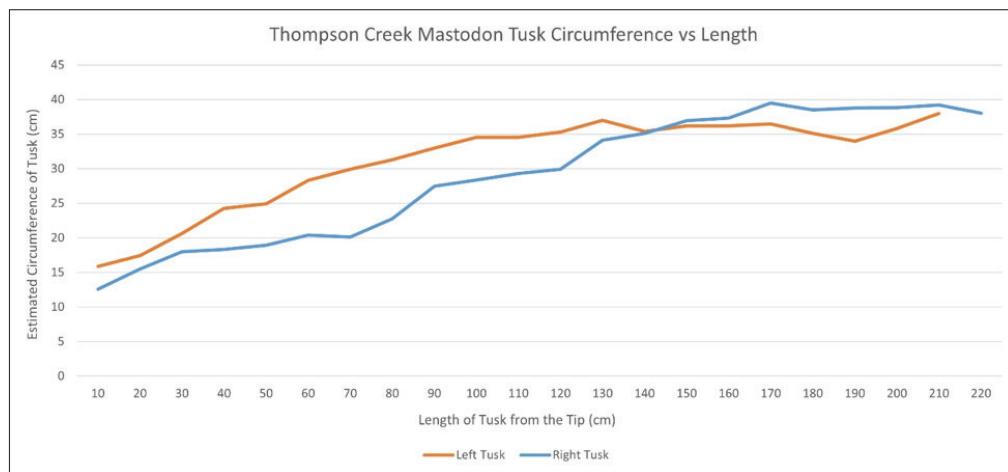


Figure 8. Relation between the circumference and the total length of both upper tusks for LSUMG-V-17901. Circumference was estimated from the measured diameter of the tusk taken every 10 cm. Total length of the tusk measured along the outside curve of the tusk.

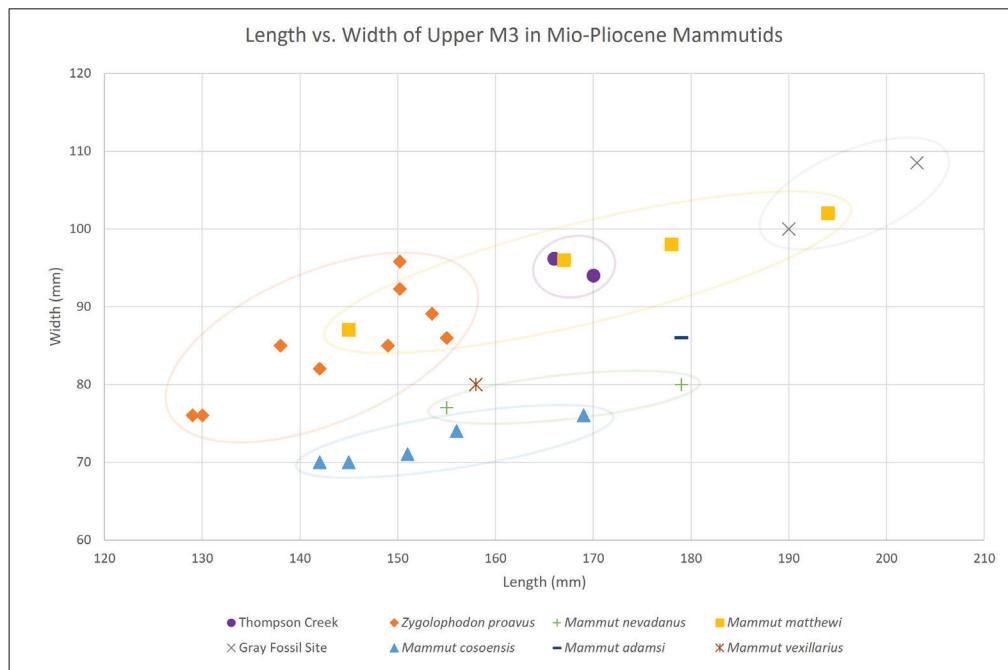


Figure 9. Length and width of Thompson Creek mastodon's upper M3s compared to other North American Mio-Pliocene mammutids. Length and width data for Mio-Pliocene mammutids from von Koenigswald et al. (2023).

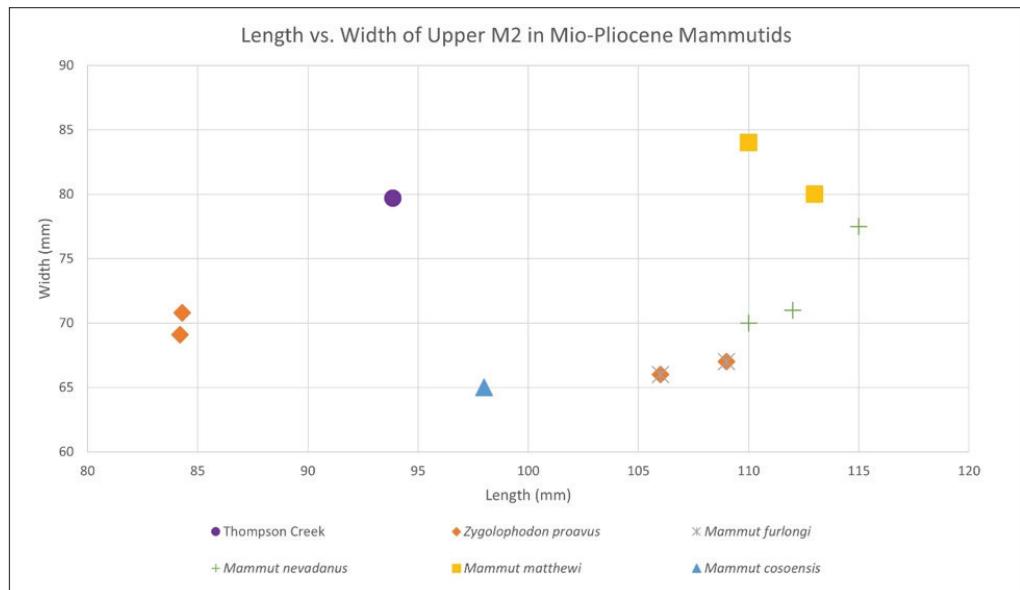


Figure 10. Length and width of Thompson Creek mastodon's upper M2s compared to other North American Mio-Pliocene mammutids. Length and width data for Mio-Pliocene mammutids from von Koenigswald et al. (2023).

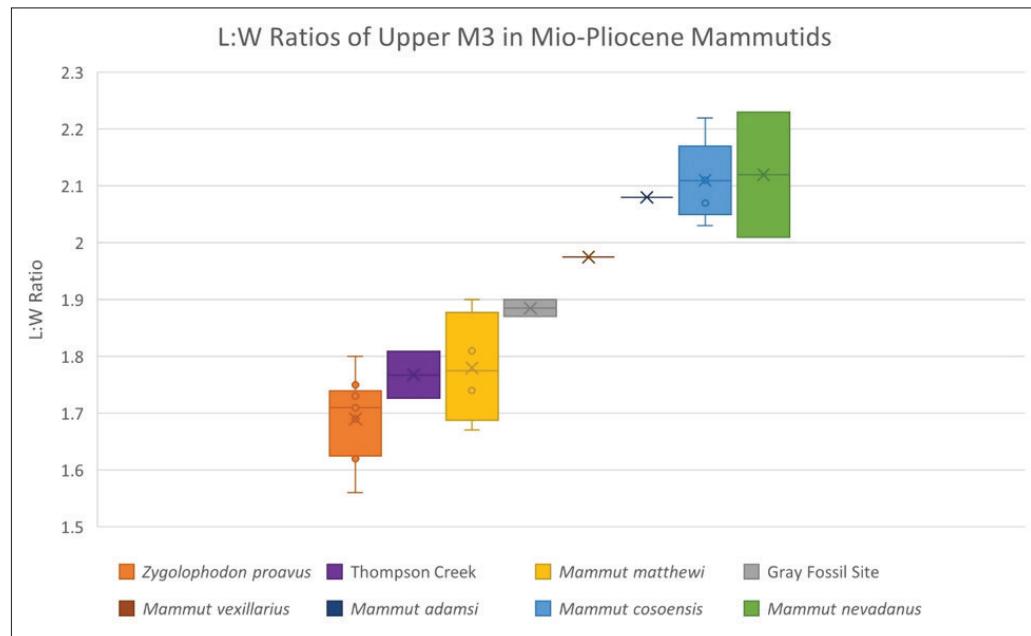


Figure 11. Length/Width ratios (L:W) of Thompson Creek mastodon's upper M3s compared to other North American Mio-Pliocene mammutids. L:W ratio data for Mio-Pliocene mammutids from von Koenigswald et al. (2023).

Table 4. Locality information and measurements of the maximum length, maximum width, and L:W ratios of upper M3s of Mio-Pliocene mammutids used in this study. \* Indicates specimens that were synonymized with *Mammut mathewi*. Data for Mio-Pliocene mammutids from von Koenigswald et al. (2023).

Genera	Age	Locality	State	Tooth Position	Specimen Number	Upper M3		
						Length (mm)	Width (mm)	L/W ratio
<i>Mammut mathewi</i>	Hemphillian	Thompson Creek	Louisiana	Left M3	LSUMG-V-17901	166	96.15	1.73
<i>Mammut mathewi</i>	Hemphillian	Thompson Creek	Louisiana	Right M3	LSUMG-V-17901	170	93.98	1.81
<i>Zygolophodon proavus</i>	Barstovian	Deep River	Minnesota	Right M3	AMNH FM 8137	150.2	95.8	1.56
<i>Zygolophodon proavus</i>	Barstovian	Virgin Valley	Nevada	M3	DMNS EVP 92	155	86	1.8
<i>Zygolophodon proavus</i>	Barstovian	Kingsford Mine	Florida	Right M3	UF/NP 116809	138	85	1.62
<i>Zygolophodon proavus</i>	Barstovian	Barstow	California	Left M3	RAM 908	129	76	1.69
<i>Zygolophodon proavus</i>	Barstovian	Barstow	California	Right M3	RAM 908	130	76	1.71
<i>Zygolophodon proavus</i>	Barstovian	Pawnee Creek	Colorado	Left M3	AMNH F:AM 23337	153.5	89.1	1.72
<i>Zygolophodon proavus</i>	Barstovian	Pawnee Creek	Colorado	Right M3	AMNH F:AM 23337	150.2	92.3	1.63
<i>Zygolophodon proavus</i>	Clarendonian	Unity	Oregon	Left M3	OMSI 1946.02.1026	149	85	1.75
<i>Zygolophodon proavus</i>	Clarendonian	Unity	Oregon	Right M3	OMSI 1946.02.1026	142	82	1.73
<i>Mammut nevadensis</i>	Hemphillian	Thousand Creek Beds	Nevada	Right M3	LACM (CIT) 63/1922	155	77	2.01
<i>Mammut nevadensis</i> *	Hemphillian	Upper Petrifield Canyon	Nevada	M3	UCMP 38645	179	80	2.23

Table 4 continued. Locality information and measurements of the maximum length, maximum width, and L:W ratios of upper M3s of Mio-Pliocene mammutids used in this study. \*Indicates specimens that were synonymized with *Mammut matthewi*. Data for Mio-Pliocene mammutids from von Koenigswald et al. (2023).

Genera	Age	Locality	State	Tooth Position	Specimen Number	Length (mm)	Width (mm)	L/W ratio
Upper M3								
<i>Mammut matthewi</i>	Hemphillian	Rattlesnake	Oregon	M3	JODA 1322	145	87	1.67
<i>Mammut matthewi</i>	Hemphillian	Optima	Oklahoma	M3		194	102	1.9
<i>Mammut matthewi</i>	Hemphillian	Hermiston	Oregon	Left M3	UOMNH F 7024	167	96	1.74
<i>Mammut matthewi</i>	Hemphillian	Hermiston	Oregon	Right M3	UOMNH F 7024	178	98	1.81
<i>Mammut adamst*</i>	Blancan	Saw Rock	Kansas	M3	KUVP 6788	179	86	2.08
<i>Mammut vexillarius*</i>	Blancan	Elephant Hill	California	M3	UCMP 28301	158	80	1.98
<i>Mammut</i> sp.	Hemphillian	Gray Fossil	Tennessee	Right M3	ETMNH 305	190	100	1.9
<i>Mammut</i> sp.	Hemphillian	Gray Fossil	Tennessee	Right M3	ETMNH 22000	203.1	108.51	1.87
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Right M3	LACM (CIT) 284/1720	145	70	2.07
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Left M3	LACM (CIT) 284/1720	142	70	2.03
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Left M3	LACM (CIT) 284/2015	151	71	2.12
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Right M3	LACM (CIT) 284/2015	156	74	2.11
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Left M3	LACM (CIT) 284/855	169	76	2.22

Table 5. Locality information and measurements of the maximum length, maximum width, and L:W ratios of upper M2s of Mio-Pliocene mammutids used in this study. \* Indicates specimens that were synonymized with *Mammut matthewi*. Data for *Mammut matthewi* from von Koenigswald et al. (2023).

Genera	Age	Locality	State	Tooth Position	Specimen Number	Upper M2		
						Length (mm)	Width (mm)	L/W ratio
<i>Mammut matthewi</i>	Hemphillian	Thompson Creek	Louisiana	Right M2	LSUMG-V-17901	93.86	79.68	1.18
<i>Zygolophodon proavus</i>	Barstovian	Barstow	California	Left M2	RAM 908	84.3	70.8	1.19
<i>Zygolophodon proavus</i>	Barstovian	Barstow	California	Right M2	RAM 908	84.2	69.1	1.22
<i>Zygolophodon proavus</i>	Clarendonian	Unity	Oregon	Right M2	OMSI 1946.02.1026	109	67	1.62
<i>Zygolophodon proavus</i>	Clarendonian	Unity	Oregon	Left M2	OMSI 1946.02.1026	106	66	1.61
<i>Mammut furlongi</i>	Clarendonian	Black Butte	Oregon	Left M2	UOMNH F 10291/2	106	66	1.6
<i>Mammut furlongi</i>	Clarendonian	Black Butte	Oregon	Right M2	UOMNH F 10291/2	109	67	1.62
<i>Mammut nevadanus</i>	Hemphillian	Thousand Creek Beds	Nevada	Right M2	LACM (CIT) 63/1922	112	71	1.57
<i>Mammut nevadanus</i>	Hemphillian	Thousand Creek Beds	Nevada	Left M2	LACM (CIT) 63/1922	110	70	1.58
<i>Mammut nevadanus</i> *	Hemphillian	Upper Petrified Canyon	Nevada	M2	UCMP 38645	115	77.5	1.48
<i>Mammut matthewi</i>	Hemphillian	Hermiston	Oregon	Left M2	UOMNH F 7024	110	84	1.35
<i>Mammut matthewi</i>	Hemphillian	Hermiston	Oregon	Right M2	UOMNH F 7024	113	80	1.37
<i>Mammut cosoensis</i>	Blancan	Coso-Mountains	California	Left M2	LACM (CIT) 284/1720	98	65	1.51

nigswald et al. (2023), the Thompson Creek mastodon's M3s group more closely compare in length and width proportions to Hemphillian and Blancan *Mammut matthewi* specimens than to other mammutid taxa (Fig. 9). The L:W ratios of the Thompson Creek mastodon's M3 compare more favorably to the L:W ratios of *Mammut matthewi* and *Mammut* sp. from the Gray Fossil Site (Fig. 11). The length and width of the Thompson Creek mastodon's M3s are nearly identical in measurement to the upper left M3 of the Hermiston mastodon (UOMNH F 7024) which is identified as *Mammut matthewi*. The upper left M3s of the Thompson Creek and Hermiston mastodons have nearly identical measurements with about 1 mm difference in length, the same width, and a 0.01 difference in L:W ratios (Table 4). The upper right M3s of the Thompson Creek and Hermiston mastodons, while still similar, have slightly more discrepancies in measurements with about 8 mm difference in length, 4 mm difference in width, and nearly the same L:W ratios (Table 4). The length and width proportions and the L:W ratio of the Thompson Creek mastodon's M3 did not compare favorably to specimens of *Mammut cosoensis*, *M. nevadanus*, *M. vexillarius*, or *M. adamsi*. In addition to the geographic distance between known occurrences of these taxa and the Thompson Creek mastodon, these western specimens also tend to have higher L:W ratios in their 3<sup>rd</sup> molars (von Koenigswald et al. 2023). Due to this, the Thompson Creek mastodon is identified as *Mammut matthewi*.

The upper tusks of the Thompson Creek mastodon are compared to recovered upper tusks of other North American Mio-Pliocene mammutids. The specimen of *Mammut nevadanus* from Thousand Creek Beds, Nevada, LACM (CIT) 63/1922, has the complete right tusk *in situ* in the cranium (Stock 1936). The tusk points downwards, is very straight, and has a slight medial curve to the overall shape of the tusk. The tusk is 65 cm in length and has a transverse diameter of 61.4 mm at the third cross section (Stock 1936: Plate 1). Only a small portion of the right tusk of *Mammut nevadanus* from Upper Petrified Canyon, Nevada, UCMP 38645, was preserved in the skull (MacDonald 1959). The tusk is interpreted to curve downwards similar to the specimen from Thousand Creek Beds, but it is too fragmentary to determine anything else about its morphology. The tusk has a diameter of 68 mm at the alveolar opening. The tusks of the Thompson Creek mastodon are nearly double the diameter and triple the length of the tusks of *Mammut nevadanus*. The tusks of the Thompson Creek mastodon are not straight and do not point downward like the tusks of *Mammut nevadanus* (LACM [CIT] 63-1922).

The upper tusks of *Mammut cosoensis* are broken, preventing a detailed comparison. However, the preserved section of the upper tusks of *Mammut cosoensis* (LACM [CIT] 284/1720) appear to be relatively straight with a slight upwards curvature, while the comparable sections of the Thompson Creek mastodon's upper tusks have a more obvious upward and medial curvature.

The only specimen that the Thompson Creek mastodon's tusks display any similarities to is that of UOMNH F 7024, identified as *Mammut matthewi* from Hermiston, Oregon. A photo of the Hermiston mastodon excavation was compared to the interpreted orientation of the Thompson Creek mastodon (Fig. 12). UOMNH F 7024 was first formally described in von Koenigswald et al. (2023), and is currently housed in the paleontology collection at the University of Oregon in Eugene, Oregon. The material associated with UOMNH F 7024 includes a maxilla with the M2s and M3s *in situ* on both sides and the basieranium (von Koenigswald et al. 2023). It was also reported in field notes by J. A. Shotwell during the excavation, that two tusks and a femur were found associated with the specimen, but both the tusks and femur could not be relocated for study, and their current status and locations are unknown (von Koenigswald et al. 2023). A picture taken of the excavation of the Herm-

iston specimen that appeared in the newspaper *East Oregonian* on 7 July 1954 (Fig. 12A) and the field notes taken by J.A. Shotwell and H. Alvey are the only record of the tusks. In von Koenigswald et al. (2023), the authors stated that the photo indicates that the tusks were found *in situ*, and determined that the size and shape of the right alveolus indicated that the diameter of the right tusk was 20 cm at the base, and the plaster jacket of the left tusk had a length of 2.1 m, based on field notes by J. A. Shotwell from *East Oregonian* 22 July 1954, which are on file at the University of Oregon.

Since the Hermiston mastodon's tusk are only known from the press photograph from the *East Oregonian* and the field notes, it is unclear whether the tusks were in their original orientation or if they had shifted in the tusk alveoli from taphonomic processes when they were recovered and photographed. It is possible that the orientation of the Hermiston mastodon's tusks, as seen in the *East Oregonian* photo, does not match their original position in life. If the Hermiston mastodon's tusk were found *in situ*, as stated in J. A. Shotwell's field notes, then the interpreted orientation of the Thompson Creek mastodon's tusks (Fig. 7) is very similar to how the tusks are orientated in the photo of the excavation of the Hermiston mastodon from the *East Oregonian* (Fig. 12A). Both the Hermiston and the Thompson creek mastodons' tusks project straight out from the cranium while flaring laterally. The tusks then flare slightly upwards and medially toward the tips, which are not visible in the Hermiston mastodon photo (Fig. 12A).

As mentioned previously, the Thompson Creek mastodon and Hermiston mastodon have nearly identical length and width measurements of the upper left M3, and similar length and width measurements of the upper right M3. The measurements of the Hermiston mastodon's tusks indicate that the Hermiston mastodon had thicker tusks of very similar length to the Thompson Creek mastodon (von Koenigswald et al. 2023). The similarities in the measurements of the upper M3s and the overall similarities in the shape and curvature of

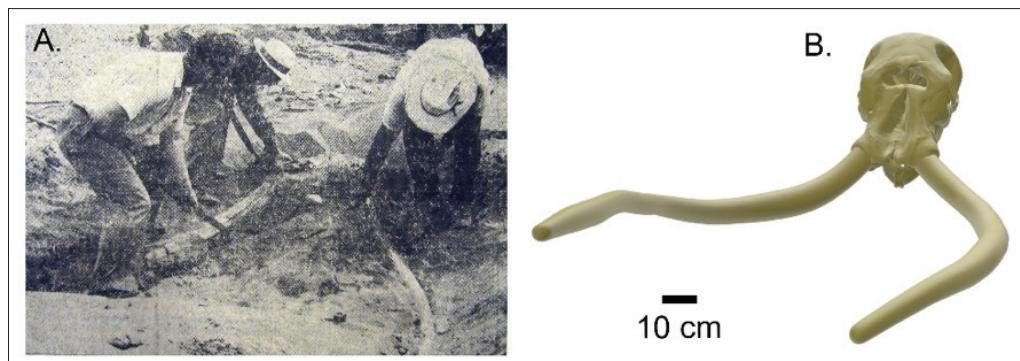


Figure 12. A side-by-side comparison of the Hermiston mastodon (UOMNH F 7024) and the Thompson Creek mastodon (LSUMG-V-17901). Note the similarities in the thickness, curvature, and orientation of the tusks in the skull could indicate that *Mammut matthewi* had proportionally thinner and straighter upcurved tusks than later Pleistocene mastodons. **A.** photo of the excavation of the Hermiston mastodon published in the newspaper *East Oregonian* on July 7<sup>th</sup>, 1954. Both tusks are visible and *in situ* in the skull, which is heavily eroded to the point that the dorsal roof is not visible. Image used with permission of *East Oregonian*. **B.** reconstruction of the Thompson Creek mastodon in a similar orientation to the Hermiston mastodon.

the tusks indicate that both the Thompson Creek mastodon and the Hermiston mastodon are likely two individuals of the same taxon. Since the Hermiston mastodon was assigned to *Mammut matthewi* (von Koenigswald et al. 2023), this further strengthens the assignment of the Thompson Creek mastodon to *Mammut matthewi*. Therefore, the Thompson Creek mastodon is assigned to *Mammut matthewi* based on the morphology of its M3s and upper tusks compared to other contemporary *Mammut* species.

*Dentition of Neogene mammutids.* The Thompson Creek mastodon's upper M3s compare favorably to referred specimens of *Mammut matthewi*. Unfortunately, direct comparisons to the holotype and paratypes of *M. matthewi* is complicated. Osborn (1921) assigned AMNH FM 18237 as the holotype for *M. matthewi*, which he identified as an incomplete upper right M3 that is missing the anterior and labial margins of the protolophid. For the three paratypes Osborn assigned to *M. matthewi*, he identified AMNH FM 17217 as a complete lower right m2, and he did not identify the incomplete teeth of AMNH FM 18239 or AMNH FM 18238 (Osborn 1921). However, his identification of the teeth does not match the illustration of the specimens (See Figure 1 in Osborn 1921.) A later study stated that the holotype (AMNH FM 18237) was incorrectly identified and was actually an incomplete lower right m3 (Tobien 1975). AMNH FM 17217 is illustrated as lower left m2, despite being identified by Osborn as a lower right m2 (See Figure 1 in Osborn 1921.) The illustration of AMNH FM 18239 indicates that it is an incomplete lower right m2 that is missing the anterior margin of the protolophid, and AMNH FM 18238 is the posterior section of a lower right m3 (See Figure 1 in Osborn 1921.) This re-identification means that there are no upper M3s in the assigned type specimens to allow for a direct comparison to the Thompson Creek mastodon M3s. The fact that the crowns of all of the type specimens are incomplete, except AMNH FM 17217, means that no measurements for the specimens have been taken which prevents quantitative comparisons (von Koenigswald et al. 2023). The lack of measurements for the type specimens also means that it has not been established that posterior lophs/lophids of *Mammut matthewi* narrow at a statistically significant rate than other *Mammut* taxa. Therefore, the assignment of the Thompson Creek mastodon to *M. matthewi* cannot be based solely on a rather poor diagnostic character and incomplete types, but must be based on other lines of evidence and comparisons to more complete specimens that have been referred to *M. matthewi*.

The methods from Dooley et al. (2019), and von Koenigswald et al. (2023), to differentiate and identify the far more common Pleistocene mastodons, were used to assign the Thompson Creek mastodon to a species. This includes a comparison of the lengths, widths, and L:W ratios of the M3s/m3s. *Mammut pacificus* corresponds to narrow-toothed mastodons, while *M. americanum* corresponds to wide-toothed mastodons (Dooley et al. 2019). When a scatterplot of the lengths and widths of Mio-Pliocene mammutids upper M3s is created, there are similar trends (Fig. 9). Specimens referred to *M. matthewi*, including Rattlesnake Creek (JODA 1322), Optima (no catalog number), Hermiston (UOMNH F 7024), and two specimens of *Mammut* sp. from the Gray Fossil Site (ET-MNH 305 and 22000) group towards the top of the chart similar to *M. americanum* and correspond to the wide-toothed morphotype. Specimens of *Mammut cosoensis* from Coso Mountains (LACM [CIT] 284/1720, LACM [CIT] 284/2015, LACM [CIT] 284/855); *M. nevadanus* from Thousand Creek Beds (LACM [CIT] 63/1922) and Upper Petrified Canyon (UCMP 38645); and *M. vexillarius* from Elephant Hill (UCMP 28301) group towards the bottom of the chart similar to *M. pacificus* and correspond to the narrow-toothed morphotype. *Mammut adamsi* from Saw Rock (KUVP 6788) falls in between the groupings of narrow and wide toothed mastodon (Fig. 9). Dental measurements place the Thompson Creek mastodon towards the top of the graph which corresponds to the wide-toothed

mastodons, and *M. matthewi* is currently the only known Mio-Pliocene species that also corresponds to the wide-toothed mastodons.

The L:W ratio of the M3s/m3s is commonly used to differentiate between the narrow-toothed *Mammut pacificus* and the wide-toothed *M. americanum* (Dooley et al. 2019, McDonald et al. 2020, von Koeingswald et al. 2023). There is a documented trend that western specimens of *M. pacificus* typically have narrower M3s/m3s with a mean L:W ratio of  $1.98 \pm 0.14$  and a 95% confidence interval of 1.7–2.26 (Dooley et al. 2019). In comparison, mid-western and eastern specimens of *M. americanum* have wider M3s/m3s with a mean L:W ratio of  $1.77 \pm 0.10$  and a 95% confidence interval of 1.57–1.97 (Dooley et al. 2019). There is extensive overlap between the ranges of L:W ratios for *M. pacificus* and *M. americanum*, which makes it difficult to correctly identify isolated teeth. The Thompson Creek mastodon has a L:W ratio of 1.73 for the left M3 and 1.81 for the right M3. The Thompson Creek mastodon's upper M3s L:W ratios are compared to other Mio-Pliocene mammutid taxa using a box and whisker plot (Fig. 11). There are two obvious major groupings of the box and whisker plot of the mammutid taxa, which correspond to the wide and narrow tooth morphotypes. The wide-toothed mammutids have L:W ratios that do not exceed 1.9 and include *Zygodipodon proavus*, the Thompson Creek mastodon, *Mammut matthewi*, and *Mammut* sp. from the Gray Fossil Site (Fig. 11). The narrow-toothed mammutids have L:W ratios above 2 and include *M. adamsi*, *M. cosoensis*, and *M. nevadanus* (Fig. 11).

The L:W ratios of the Thompson Creek mastodon's M3s fall within both quartiles of known specimens of *Mammut matthewi*, and are similar to those of specimens of *M. matthewi* from Rattlesnake, Oregon and Optima, Oklahoma (Fig. 11). Interestingly, other taxa of mammutids that were synonymized with *M. matthewi* do not fall within the box and whisker plot of named specimens of *M. matthewi* (Fig. 11). The molar of *M. vexillarius* has a L:W ratio of 1.98 and falls in between the major groupings of wide-toothed and narrow-toothed mastodons. *Mammut vexillarius* does not overlap with the plots of *M. matthewi*, *M. cosoensis*, nor *M. nevadanus* but it is closer to the plots of *M. cosoensis* and *M. nevadanus* than the plot of *M. matthewi*. *Mammut adamsi* from Saw Rock, Kansas does not overlap with *M. matthewi* with its higher L:W ratio of 2.08, but instead overlaps with *M. cosoensis* and *M. nevadanus*. The teeth of *M. nevadanus* have a L:W ratio of 2.01 and 2.23, which plot much more closely to western mammutids like *M. cosoensis* and does not overlap with *M. matthewi*.

The fact that the specimens of Mio-Pliocene mammutids distinctly separate into the wide-toothed and narrow-toothed morphotypes that are seen in Pleistocene mastodons is potentially important for further defining the evolutionary lineages of mammutids in North America. This supports the hypothesis that *Mammut americanum* arose from the wide-toothed *M. matthewi*, and *M. pacificus* arose from one of the narrow-toothed western Mio-Pliocene *Mammut* species such as *M. cosoensis*, *M. nevadanus*, or *M. vexillarius*. However, due to the limited number of Mio-Pliocene mastodon specimens there is still too little data available at this time to make any definitive conclusions about the validity of taxa and the evolutionary lineages of the mastodons in North America.

Due to the difference in the L:W ratios of taxa synonymized with *Mammut matthewi* (i.e., *M. nevadanus*, *M. vexillarius*, and *M. adamsi*) and referred specimens of *M. matthewi* (Rattlesnake Creek, Optima, and Hermiston), it should not be automatically assumed that the synonymized taxa are the same species as *M. matthewi*. It must be noted that the data for *M. vexillarius* and *M. adamsi* are based on single specimens which should by no means be considered conclusive. There are too few specimens and data points of the various Mio-Pliocene mammutid taxa to make any conclusions about their taxonomic validity based solely on dental proportions. A more detailed study of the taxonomy of the Mio-Pliocene

mammutids is required, and the assumption that the taxa synonymized with *M. matthewi* are true representatives of the species should be questioned. With the current data, the L:W ratios of the Thompson Creek mastodon overlap the most with specimens identified as *M. matthewi*, which supports the taxonomic assignment of the Thompson Creek mastodon to *Mammut matthewi*.

The Thompson Creek mastodon is not considered to be *Mammut americanum* despite similar M3 tooth morphology due to temporal separation, as *M. americanum* has not been reported from the latest Hemphillian (Shoshani and Tassy 1996, von Koenigswald et al. 2023). Distinguishing *M. americanum* from *M. matthewi* is problematic, as there is a lack of distinct diagnostic characters that separate the two species. Both *M. americanum* and *M. matthewi* correspond to the wide-toothed mastodons with a lower L:W ratio in the M3/m3. *Mammut matthewi* was stated to be distinguished by a rapid decrease in the width of the tritoloph[id] and tetartoloph[id] of the third molars compared to the protoloph[id] and metaloph[id] (Osborn 1921). As previously stated, there has been no study to determine if the rapid narrowing of the posterior half of the M3/m3 is statistically significant, compared to other *Mammut* species, including *M. americanum*. Therefore, the main diagnostic character used to separate *M. matthewi* and *M. americanum* is temporal separation, with *M. matthewi* being reported from Miocene and Pliocene formations (Osborn 1921, Shoshani and Tassy 1996, von Koenigswald et al. 2023), and *M. americanum* being reported from late Pliocene and much more commonly from Pleistocene formations (Shoshani and Tassy 1996, von Koenigswald et al. 2023). Using geologic age as a diagnostic character is problematic as it falls into the circular reasoning fallacy and further reinforces the need for more diagnostic morphological characteristics to separate *Mammut* species. While the Thompson Creek mastodon is assigned to *M. matthewi*, based on its overall tooth morphology compared to all known latest Hemphillian *Mammut* species, the morphology of the Thompson Creek mastodon's upper tusks could potentially be a morphologically significant character that could be used to differentiate between *Mammut matthewi* and *M. americanum*.

*Upper tusk morphology of Neogene mammutids.* As stated previously, the orientation in Figure 6A is likely the most accurate reconstruction of the Thompson Creek mastodon tusks, as the tusks have an upwards curvature which is the typical curvature for *Mammut*. The orientation in Figure 6C and Figure 6D would be physically impossible for the animal, as the tusks would be longer than the skull is tall, assuming that the Thompson Creek mastodon has a body height and build similar to known specimens of *Mammut*. The orientation in Figure 6B, while physically possible, is a completely different orientation and shape than any known *Mammut* reconstruction and thus is considered less accurate than the orientation of Figure 6A.

Compared to later Pleistocene mastodons, the tusks of the Thompson Creek mastodon are far straighter and thinner for their length than either Pleistocene species of mastodon. Both *Mammut americanum* and *M. pacificus* have hyper-enlarged tusks that have a strong upward curvature (Dooley et al. 2019, Fisher 2009, Göhlich 1999, Osborn 1936). There is a pronounced sexual dimorphism in Pleistocene mastodon tusks, which makes it easier to identify male from female mastodons. Typically, adult males have tusks that are much longer and larger in diameter than adult females, who have tusks which are generally shorter and more slender (Fisher 2009; Smith 2010; Smith and Fisher 2011, 2013). The Thompson Creek mastodon's tusks are similar in length to adult male *M. americanum* tusks (Fisher 2009). However, the Thompson Creek mastodon's tusks are smaller than most of the inferred adult male tusk circumferences and larger than most of the adult female tusk circumferences (Fisher 2009). It is also unlikely that the Thompson Creek mastodon is a juvenile specimen, as the wear on the M3s indicates it is a mature adult (see Age Group below). It

cannot be determined if the Thompson Creek mastodon is a male or a female based on tusk morphology when compared to the typical ranges of adult Pleistocene *M. americanum*, nor through comparison of femur or pelvic bones, since none were recovered (Fisher 2009).

The difference in girth of the Thompson Creek mastodon's tusks compared to other specimens of *Mammut americanum* found in Louisiana is apparent. For comparison, there is an uncatalogued mastodon tusk from Little Bayou Sara, Louisiana on display in the Howe-Russell Geoscience Complex at LSU. The Little Bayou Sara Tusk belonged to an American Mastodon, which has been inferred to be a male due to its hyper-enlarged size (A. Dooley, Western Science Center, Hemet, CA, 2021, pers. comm.). Despite being only partially complete, the largest circumference of the Little Bayou Sara Tusk is 64.2 cm, which is a significantly larger circumference than either tusk of the Thompson Creek mastodon.

Despite the difference in length and girth proportions, the most unusual aspect of the Thompson Creek mastodon's tusks is their shape. The section of the tusks that fit within the alveoli are relatively straight. Once the tusks protrude from the alveoli, they immediately begin curving gently upwards for nearly the entire length of the tusks, to where the curve flattens out slightly more horizontally at the tips. The tusks also flair out laterally to about half the length of the tusks, and then flair back medially to the end. Among Pleistocene mastodon tusks, a strong upwards curvature with a slight flair laterally towards the base of the tusk before flaring medially towards the tips of the tusks is common. The tips of Pleistocene mastodon tusks usually either continue to flair upwards with nearly no lateral or medial curve, or the tusks will continue to flair upwards, and the tips have a very strong medial curve towards each other. The Thompson Creek mastodon's tusks do have the typical upwards curvature seen in most *Mammut*, but the tips of the tusks flatten out and point anteriorly, which is not very common in Pleistocene mastodon tusks. This gives the Thompson Creek mastodon more anteriorly straight pointing tusks, as opposed to tusks that have a strong upwards curvature. This is not a common tusk shape seen in either species of Pleistocene *Mammut*.

Unfortunately, differences in *Mammut* tusk morphology remain relatively poorly understood. Due to the highly individually variable nature of mastodon tusk morphology, studies focused on documenting the differences in the morphology of mastodon tusks have been mostly limited to determining the degree of sexual dimorphism between male and female Pleistocene mastodons (Fisher 2009; Smith 2010; Smith and Fisher 2011, 2013). As a result, tusk morphology is currently a poor trait to determine the taxonomic assignment of a *Mammut* specimen. Individual variation, age, genetic mutation, wear, and sex-linked morphology must be considered when making interpretations of the upper tusks of mastodons. It is unknown if the Thompson Creek mastodon's tusks shape and asymmetry represent normal tusk growth for the taxon, or if an external factor or genetic variation in this individual had altered the normal tusk growth. While it cannot be discounted, there does not appear to be any evidence to suggest that the shape of the Thompson Creek mastodon tusks was caused by pathological processes. Asymmetry between the tusks has been observed in specimens of mastodons and can be the result of some biological factor such as sex-linked morphology, individual variation, or simple wear (Smith 2010; Smith and Fisher 2011, 2013).

The long, narrow, and straight tusks of the Thompson Creek mastodon do fit with a possible pattern that is emerging about Mio-Pliocene mammutids. Mio-Pliocene mammutids' tusks appear to be proportionally thinner and straighter than Pleistocene mammutids' tusks, which are thicker and have a strong upward curvature. This could indicate a distinct difference in the morphology of the tusks of Mio-Pliocene and Pleistocene mastodons, which could potentially provide a new diagnostic character between *Mammut matthewi* and *M.*

*americanum*. *M. matthewi* having proportionally thinner and straighter tusks compared to *Mammut americanum* could be a potential diagnostic character used to separate the two species, rather than being based solely on temporal separation. The presence of two specimens assigned to *M. matthewi* with similar tusk morphology that is different from specimens of *M. americanum* does support this hypothesis. Ultimately, more specimens of Mio-Pliocene mammutids with upper tusks would have to be found to determine if this was a widespread and distinct morphological feature for *M. matthewi* as both the *East Oregonian* photo of the Hermiston mastodon's tusks and the current 3D reconstruction of the Thompson Creek mastodon's tusks may not match their original position in life. Therefore, due to the limited statistical data to support the interpretation that proportionally thinner and straighter tusks are a potential diagnostic character of Mio-Pliocene mammutids, the pattern should be considered tentative at best until more data is collected.

### Age group

Mastodons are thought to age similarly to modern African elephants (Saunders 1977). The age of African elephants can be estimated based on the wear states of the molars, and the age of the elephant is given in African Elephant Years (AEY; Laws 1966). Law's African Elephant Years are commonly used to determine the age of fossil proboscideans, and an analogous system, used to determine the age of mastodons, is given in Saunders (1977). The wear stage of the Thompson Creek mastodon's M3 corresponds to the mature age group defined by Saunders (1977). The mature age group states that the M2/m2 displays a heavy to an obliterated wear pattern, and the M3/m3 displays light to heavy wear on either just the anterior or all of the loph[ids] (Saunders 1977). The severe wear on the M2, the heavy wear on the protoloph and metaloph of the M3, and the moderate to light wear on the tritoloph and tetartoloph of the M3 indicate that the Thompson Creek mastodon belongs to the mature age group (Saunders 1977). Mastodons in the mature age group fall in between 32 to 36  $\pm$  2 AEY (Saunders 1977). Based on this, the Thompson Creek mastodon falls within the mature age group and is likely 32 to 36  $\pm$  2 AEY" (Laws 1966, Saunders 1977).

### Tooth wear and diet

The state of wear on the Thompson Creek mastodon's M2 is much more extreme than on the M3. The upper right M2 is very heavily worn to the point that the tooth is almost completely flat with no visible lophs or cusps. In comparison, despite the postmortem damage to the anterior side of both M3, the lophs on both M3 only show moderate wear. Differentiation in the degree of wear between mastodons of similar age has been documented. When compared to other specimens of similar age, such as specimen WSC 18743 *Mammut pacificus* (See Figure 1 in Dooley et al. 2019), the other specimens displayed far more wear on the M3 with similar wear on the M2. When comparing specimens of *M. americanum* from Trolinger Spring and Boney Spring, Saunders (1977) notes that an individual of the mature age group could display extensive to severe wear on the M2, while only displaying light to moderate wear on the M3. At this time, it is cautioned against drawing any definitive conclusions if the greater degree of wear on the M2 was related to the Thompson Creek mastodon's diet, or if it is simply individual variation in wear.

There was noticeable asymmetrical wear between the two M3s. The left M3 displayed more heavy wear on the same section of the molar than on the right M3. Asymmetrical wear between the left and right M3s/m3s has been observed in other mastodon teeth, although it is rarely reported as it is usually not considered a significant feature that requires discussion or mention within a description (Dooley et al. 2019, Saunders 1977, von Koenigswald et

al. 2023, White 2024). No formal explanation for the asymmetrical wear between M3s/m3s has been proposed, although a possible explanation is that favoring one side of the mouth through preferential chewing could cause this asymmetrical wear. Laterality, preference for one side of the body over the other, has been observed in a variety of species and the fossil record (Babcock 2005, Rogers 1989, Schneider et al. 2012). One aspect of laterality is a chewing side preference in which mastication is performed predominantly on either the left or right side of the mouth (Christensen and Radue 1985). A chewing side preference has been noted to cause differential wear in the teeth with a higher degree of tooth wear on the preferred side (Ibrová et al. 2017, Nygrén 2000, Parés-Casanova and Morros 2014, Samley et al. 2011). Therefore, it is likely that the asymmetrical wear on the left and right M3 of the Thompson Creek mastodon can be attributed to preferential chewing.

All mammutids have zygomorphodont dentition in which the lophids of the lower teeth interlock in the interlophs of the upper teeth, with the lophs/lophids only grinding against each other when the teeth are in heavy wear (von Koenigswald 2014, von Koenigswald et al. 2023). In the pattern of mastication for mammutids, the power stroke of the chewing cycle is typically divided into two phases. In phase I, the lower jaw moves in an orthal direction with central occlusion in which plant material is processed through compression with little to no shearing (von Koenigswald 2014, von Koenigswald et al. 2023). Phase II involves the lower jaw occluding in a lingual to antero-lingual direction (von Koenigswald 2014, von Koenigswald et al. 2023). Once the teeth become heavily worn and the loph/lophids obliterated, the enamel bands of the teeth function as a grinding surface (von Koenigswald 2014). In *Zygomorphodon* teeth both Phases I and II are distinct, while in *Mammut americanum* Phase II is less distinct, but still visible in some specimens, indicating that Phase I is more dominant (von Koenigswald 2014, von Koenigswald et al. 2023). The extensive wear on the M2 indicates that it was likely being used as a grinding surface, while the lophs on the M3s were used to compress plant material that was being eaten.

Like all mastodons, the Thompson Creek mastodon would have been a browser, consuming typical browse such as leaves, wood, bark, fruits, and nuts. However, they are known to also consume grass, herbaceous plants, and aquatic plants (Dreimanis 1968; Gobetz and Bozarth 2001; Green et al. 2017; Harrington 1986; Harrington et al. 1993; Haynes 1991; King and Saunders 1984; Newsom and Mihlbachler 2006; Saunders 1977, 1996; Widga et al. 2017). It has been proposed that if a mastodon tooth is of the smooth or rough morphotype, it corresponds to a spruce or pine dominated environment respectively (King and Saunders 1984, Saunders 1977). Even though the molars of the Thompson Creek mastodon correspond to the smooth variety morphotype defined by Saunders, there is currently no direct evidence that the Thompson Creek mastodon had a spruce dominated diet that Saunders ascribes to the Missouri smooth variety molars (Saunders 1977). At this time, it is currently unknown exactly what plants the Thompson Creek mastodon would have been consuming due to the lack of recovered pollen, phytoliths, or other plant remains.

## Conclusions

The Thompson Creek mastodon is identified as *Mammut matthewi*, making this the first specimen of the taxon from Louisiana and the only Mio-Pliocene mastodon reported from the state. This identification is based on the measurements and L:W ratios of the M3s and the morphology of the upper tusks, compared to all known latest Hemphillian *Mammut* species. More specimens of *M. matthewi* need to be recovered so that more quantitative and morphological data can be collected and compared to existing specimens. Mio-Pliocene

mastodons are not well understood, and more work needs to be done to accurately identify and describe mammutid taxa. The Thompson Creek mastodon has some of the most complete and well-preserved tusks of a Mio-Pliocene mammutid, and further comparison could reveal new insights into Mio-Pliocene mammutid tusk morphology.

More research needs to be done on the Pascagoula Formation in Thompson Creek Site. This paper, along with a paper by Yann (2010), determined that the age of the Pascagoula Formation in Thompson Creek is latest Hemphillian, corresponding to a geologic age of latest Miocene to earliest Pliocene. More paleo-environmental reconstructions should be pursued. Palynology samples should be collected from the sediment and processed to determine if any paleo-environmental reconstructions are possible. A comprehensive study of all of the paleontological specimens recovered from the site should be completed in order to better understand the prehistoric community in the Pascagoula Formation.

There are many paleontological specimens in the LSU Vertebrate Paleontology Collection that have not been published or studied. More work should be done to identify and record these specimens, as they are important in completing our understanding of prehistoric life in the Miocene and Pliocene of Louisiana and the Gulf Coast.

### Acknowledgements

I would like to thank Judith Schiebout, Suyin Ting, and Mason R. Kirkland for their work in the LSU Paleontology Collection and thanks also to Chris Austin and all the staff at the LSU Museum of Natural Science for allowing this project to be possible. Thank you to all the members of the LSU team that helped collect the specimens from Thompson Creek in 2005. I would like to thank my committee members Brooks Ellwood, Suyin Ting, Alton Dooley, and Achim Herrmann for all their help and guidance. Special thanks to Alton Dooley who helped with many aspects of the project and for creating the 3D models. Thanks to Chris Widga who helped with edits and provided new data and information for the project. Thanks to Blaine Schubert, Jim Mead, and the anonymous reviewers of *Pan-American Paleontology*, whose advice and edits helped improve the quality of this paper. Special thanks to Nic Bushell for his artistic reconstructions of the possible orientations of the tusks, and to Robert Feranec for granting permission to use the 3D model of the Cohoes Mastodon skull in the reconstruction. Thank you to my friends Robert “Dylan” Heifner and Cole Quinby, who graciously donated their time to help me with this project. Thank you to my family for their help and continued support.

### Literature Cited

Babcock, L.E. 2005. Asymmetry in the Fossil Record. *European Review* 13:135–143.

Bell, C.J., E.L. Lundelius Jr, A.D. Barnosky, R.W. Graham, E.H. Lindsay, D.R. Ruez Jr, H.A. Semken Jr, S.D. Webb, and R.J. Zakrzewski. 2004. The Blancan, Irvingtonian, and Rancholabrean Mammal Ages. Pp. 232–314, *In* M.O. Woodburne (Ed.). Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, NY. 400 pp.

Blumenbach, J.F. 1799. *Handbuch der Naturgeschichte*. 6<sup>th</sup> Edition. Johann Christian Ditterich, Göttingen, Germany. 748 pp.

Chandler, R.M. 1998. Fossil birds of the Tunica Hills and first record of ruffed grouse (*Bonasa umbellus*) for Louisiana. *Current Research in the Pleistocene* 15:103–104.

Christensen, L.V., and J.T. Radue. 1985. Lateral preference in mastication: A feasibility study. *Journal of Oral Rehabilitation* 12:421–427.

Cope, E.D. 1873. Synopsis of New Vertebrata from the Tertiary of Colorado, Obtained During the Summer of 1873. U.S. Geological and Geographical Survey of the Territories. Government Printing Office, Washington, D.C. 19 pp.

Cope, E.D. 1889. The Proboscidea. *The American Naturalist* 23:191–211.

Domning, D.P. 1969. A list, bibliography, and index of the fossil vertebrates of Louisiana and Mississippi. *Gulf Coast Association of the Geological Societies Transactions* 19:385–422.

Dooley, A.C. Jr, E. Scott, J. Green, K.B. Springer, B.S. Dooley, and G.J. Smith. 2019. *Mammut pacificus* sp. nov., a newly recognized species of mastodon from the Pleistocene of western North America. *PeerJ* 7:e6614.

Dooley, A.C. Jr, C. Widga, B.E. Stoneburg, C. Jass, V.M. Bravo-Cuevas, A. Boehm, E. Scott, A.T. McDonald, and M. Volmut. 2025a. Re-evaluation of mastodon material from Oregon and Washington, USA, Alberta, Canada, and Hidalgo and Jalisco, Mexico. *PeerJ* 13:e18848.

Dooley, A.C. Jr, C.D. White, B.E. Stoneburg, B.S. Dooley. 2025b. Mammalia: Proboscidea. Pp. 353–374, *In* S. Ting, L.E. Smith, C.D. White, and I.M. Gil (Eds.). *Vertebrate Fossils of Louisiana*. Special Publication of the Museum of Natural Science, Baton Rouge, LA. 441 pp.

Dreimanis, A. 1968. Extinction of mastodons in eastern North America: Testing a new climatic-environmental hypothesis. *The Ohio Journal of Science* 68:257–272.

Fisher, D.C. 2009. Paleobiology and extinction of proboscideans in the Great Lakes region of North America. Pp. 55–75, *In* G. Haynes (Ed.) *American Megafaunal Extinctions at the End of the Pleistocene*. Springer, Berlin, Germany. 208 pp.

Fisher, D.C. 2018. Paleobiology of Pleistocene Proboscideans. *Annual Review of Earth and Planetary Sciences* 46:229–260.

Frick, C. 1933. New remains of trilophodont-tetrabelodont mastodons. *American Museum of Natural History* 59:505–652.

Gilbert, C., A. Ropiquet, and A. Hassanin. 2006. Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): Systematics, morphology, and biogeography. *Molecular Phylogenetics and Evolution* 40:101–117.

Gillette, D.D., and D.B. Madsen. 1993. The Columbian mammoth, *Mammuthus columbi*, from the Wasatch Mountains of central Utah. *Journal of Paleontology* 67:669–680.

Göhlich, U.B. 1999. Order Proboscidea. Pp. 157–168, *In* G.E. Rössner and K. Heissig (Eds.). *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, Munich, Germany. 515 pp.

Gobetz, K.E., and S.R. Bozarth. 2001. Implications for late Pleistocene mastodon diet from opal phytoliths in tooth calculus. *Quaternary Research* 55:115–122.

Green, J.L., L.R. DeSantis, and G.J. Smith. 2017. Regional variation in the browsing diet of Pleistocene *Mammut americanum* (Mammalia, Proboscidea) as recorded by dental microwear textures. *Palaeogeography, Palaeoclimatology, Palaeoecology* 487:59–70.

Harington, C.R. 1986. The American mastodon. *Neotoma* 19:1–3.

Harington, C.R., D.R. Grant, and R.J. Mott. 1993. The Hillsborough, New Brunswick, mastodon and comments on other Pleistocene mastodon fossils from Nova Scotia. *Canadian Journal of Earth Sciences* 30:1242–1253.

Hay, O.P. 1922. Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington* 35:97–102.

Haynes, G. 1991. *Mammoths, mastodonts, and elephants: Biology, Behavior and the Fossil Record*. Cambridge University Press, Cambridge, U.K. 428 pp.

Haynes, G. 2017. Finding meaning in mammoth age profiles. *Quaternary International* 443:65–78.

Hibbard, C.W. 1944. Two new mammals from the middle Pliocene of Seward County, Kansas. *University of Kansas Science Bulletin* 30:107–116.

Hodgson, J.A., W.D. Allmon, P.L. Nester, J.M. Sherpa, and J.J. Chiment. 2008. Comparative osteology of late Pleistocene mammoth and mastodon remains from the Watkins Glen site, Chemung County, New York. Pp. 301–367. In W. Allmon and P.L. Nester (Eds.). *Mastodon Paleobiology, Taphonomy, and Paleoenvironment in the late Pleistocene of New York State: Studies on the Hyde Park, Chemung, and North Java Sites (Palaeontographica Americana, No. 61)*. Paleontological Research Institution, Ithaca, NY. 476 pp.

Hulbert, R.C. Jr. 2001. *The Fossil Vertebrates of Florida*. University Press of Florida, Gainesville, FL. 368 pp.

Hulbert, R.C. Jr. 2015. Palmetto Fauna. Available online at <https://www.floridamuseum.ufl.edu/florida-vertebrate-fossils/sites/palmetto-fauna/>. Accessed March 27, 2021.

Ibrová, A., J. Dupej, P. Stránská, P. Velemínský, L. Poláček, and J. Velemínská. 2017. Facial skeleton asymmetry and its relationship to mastication in the Early Medieval period (Great Moravian Empire, Mikulčice, 9th–10th Century). *Archives of Oral Biology* 84:64–73.

Illiger, J.K.W. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicas utriusque classis, eorumque versione germanica*. Berolini Sumptibus C. Salfeld, Berlin, Germany. 302 pp.

Inabinett, M. 2020. An Unusual Mastodon Revisited: Providing a regional focus for *Mammuthus americanus* (Proboscidea, Mammutidae) in the Southeast. Electronic Theses and Dissertations. East Tennessee State University. Johnson City, TN. 125 pp.

Karpinski, E., D. Hackenberger, G. Zazula, C. Widga, A.T. Duggan, G.B. Golding, M. Kuch, J. Klunk, C.N. Jass, and P. Groves. 2020. American mastodon mitochondrial genomes suggest multiple dispersal events in response to Pleistocene climate oscillations. *Nature Communications* 11:1–9.

Karpinski, E., C. Widga, A.R. Boehm, B.R. Peecook, M. Kuch, T.J. Murchie, and H.N. Poinar. 2023. Mastodon mitochondrial genomes from American falls, Idaho. *Quaternary International* 668:1–6.

King, J.E., and J.J. Saunders. 1984. Environmental insularity and the extinction of the American mastodont. Pp. 315–340, In P.S. Martin and R.G. Klein (Eds.). *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson, AZ. 892 pp.

Kurtén, B., and E. Anderson. 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York, NY. 442 pp.

Lambert, W.D., and J. Shoshani. 1998. Proboscidea. Pp. 606–621, In C.M. Janis, K.M. Scott, and L.L. Jacobs (Eds.). *Evolution of Tertiary Mammals of North America. Volume 1, Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge University Press, Cambridge, U.K. 708 pp.

Laws, R.M. 1966. Age criteria for the African elephant: *Loxodonta a. africana*. *African Journal of Ecology* 4:1–37.

Lucas, S.G. 2022. The Last North American Gomphotheres. Pp. 45–58, In G.S. Morgan, J.A. Baskin, N.J. Czaplewski, S.G. Lucas, H.G. McDonald, J.I. Mead, R.S. White Jr, A.J. Lichtig (Eds.). *Late Cenozoic Vertebrate Paleontology: Tribute to Arthur H. Harris*. New Mexico Museum of Natural History and Science Bulletin 88, Albuquerque, NM. 370 pp.

MacDonald, J.R. 1959. The middle Pliocene mammalian fauna from Smiths Valley, Nevada. *Journal of Paleontology* 33:872–887.

Matthew, W.D. 1930. A Pliocene mastodon skull from California, *Pliomastodon vexillarius*, n. sp. *University of California Publications on Geological Sciences* 19:335–348.

McCulloh, R.P. 2016. Tunica Hills Wildlife Management Area and Angola State Penitentiary. *Louisiana Geological Survey State Parks and Land Series* 3:1–28.

McDonald, A.T., A.L. Atwater, A.C. Dooley Jr, and C.J. Hohman. 2020. The easternmost occurrence of *Mammut pacificus* (Proboscidea: Mammutidae), based on a partial skull from eastern Montana, USA. *PeerJ* 8:e10030.

Newsom, L.A., and M.C. Mihlbachler. 2006. Mastodons (*Mammut americanum*) Diet Foraging Patterns Based on Analysis of Dung Deposits. Pp. 263–331, *In* S.D. Webb (Ed.). *First Floridians and Last Mastodons: The Page-Ladson Site in the Aucilla River*. Springer, Dordrecht, Netherlands. 588 pp.

Nygrén, K. 2000. Directional Asymmetry in Moose. *Alces: A journal devoted to the biology and management of moose* 36:147–154.

Olsen, S.J. 1972. American Mastodon and the Woolly Mammoth. Pp. 1–45, *In* S.J. Olsen (Ed.). *Osteology for the Archaeologist*, Number 3: American Mastodon and the Woolly Mammoth; Number 4: North American Birds. *Papers of the Peabody Museum of Archaeology and Ethnology*, Vol. 56. Cambridge, MA. 186 pp.

Osborn, H.F. 1921. First appearance of the true mastodon in America. *American Museum Novitates* 10:1–6.

Osborn, H.F. 1926. Additional new genera and species of the mastodontoid Proboscidea. *American Museum Novitates* 238:1–16.

Osborn, H.F. 1936. *Proboscidea: A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World*, Vol. 1. *Mœritherioidea, Deinotherioidea, Mastodontoidea*. American Museum Press, New York City, NY. 802 pp.

Parés-Casanova, P.M., and C. Morros. 2014. Molar asymmetry shows a chewing-side preference in horses. *Journal of Zoological and Bioscience Research* 1:14–18.

Rogers, L.J. 1989. Laterality in Animals. *International Journal of Comparative Psychology* 3:5–25.

Samley, K., J. Brown, R. Brooks, R. Splan, and C.A. Porr. 2011. Evaluation of Dental Wear Patterns and Preferred Chewing Direction in Horses. *Journal of Equine Veterinary Science* 31:287–288.

Saunders, J.J. 1977. Late Pleistocene Vertebrates of the Western Ozark Highland, Missouri. *Illinois State Museum Report of Investigations* 33:1–118.

Saunders, J.J. 1996. North American Mammutidae. Pp. 271–279, *In* J. Shoshani and P. Tassy (Eds.). *The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, U.K. 502 pp.

Schiebout, J. 1997. Paleofaunal survey, collecting, processing, and documentation at two locations on Fort Polk, Louisiana. Report prepared for U.S. Army Corps of Engineers, Fort Worth District, Fort Worth, TX. 93 pp.

Schiebout, J.A., J.H. Wrenn, S. Ting, J.L. Hill, M.D. Hagge, M.J. Williams, G.S. Boardman, and B.B. Ellwood. 2006. Miocene vertebrate fossils recovered from the Pascagoula Formation in southeastern Louisiana. *Gulf Coast Association of Geological Societies Transactions* 56:745–760.

Schneider, L.A., P.H. Delfabbro, and N.R. Burns. 2012. The influence of cerebral lateralisation on the behaviour of the racing greyhound. *Applied Animal Behaviour Science* 141:57–64.

Schultz, J.R. 1937. A late Cenozoic vertebrate fauna from the Coso Mountains, Inyo Canyon, California. Carnegie Institution of Washington Publication 487:75–109.

Shoshani, J., E.M. Golenberg, and H. Yang. 1998. Elephantidae phylogeny: Morphological versus molecular results. *Acta Theriologica* 43:89–122.

Shoshani, J., and P. Tassy. 1996. The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. Oxford University Press, Oxford, U.K. 502 pp.

Shotwell, J.A., and D.E. Russell. 1963. Mammalian fauna of the Upper Juntura Formation, the Black Butte local fauna. *Transactions of the American Philosophical Society* 53:42–69.

Simpson, G.G. 1930. Tertiary land mammals of Florida. *Bulletin of the American Museum of Natural History* 59:149–211.

Smith, K.M. 2010. Life histories of female American mastodons (*Mammut americanum*): Evidence from tusk morphology, stable isotope records, and growth increments. *Dissertations and Theses (Ph.D. and M.S.)*. University of Michigan, Ann Arbor, MI. 240 pp.

Smith, K.M., and Fisher, D.C. 2011. Sexual dimorphism of structures showing indeterminate growth: Tusks of American mastodons (*Mammut americanum*). *Paleobiology* 37:175–194.

Smith, K.M., and Fisher, D.C. 2013. Sexual dimorphism and inter-generic variation in proboscidean tusks: Multivariate assessment of American mastodons (*Mammut americanum*) and extant African elephants. *Journal of Mammalian Evolution* 20:337–355.

Stock, C. 1936. A *Pliomastodon* skull from the Thousand Creek beds, northwestern Nevada. *Contributions to Palaeontology* 3:35–39.

Tassy, P. 1996. Dental homologies and nomenclature in the Proboscidea. Pp. 21–25. *In* J. Shoshani and P. Tassy (Eds.). The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. Oxford University Press, Oxford, U.K. 502 pp.

Tedford, R.H., L.B. Albright, A.D. Barnosky, I. Ferrusquía-Villafranca, R.M. Hunt, J.E. Storer, C.C. Swisher, M.R. Voorhies, S.D. Webb, and D.P. Whistler. 2004. Mammalian Biochronology of the Arikareean Through Hemphillian Interval (Late Oligocene Through Early Pliocene Epochs). Pp. 169–231, *In* M.O. Woodburne (Ed.). Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, NY. 400 pp.

Tobien, H. 1975. The Structure of the Mastodont Molar (Proboscidea, Mammalia). Part 2, The Zygodont and Zygobunodont patterns. *Mainzer geowissenschaftliche Mitteilungen* 4:195–233.

Tobien, H. 1996. Evolution of zygodonts with emphasis on dentition. Pp. 76–85, *In* J. Shoshani and P. Tassy (Eds.). The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. Oxford University Press, Oxford, U.K. 502 pp.

von Koenigswald, W. 2014. Functional diversity in the masticatory patterns of Proboscidea. Pp. 1–41, *In* J. Rust and D. Kalthoff (Eds.). *Palaeontographica Abteilung A: Paläozoologie- Stratigraphie*, Vol. 307. Schweizerbart Science Publishers, Stuttgart, Germany. 147 pp.

von Koenigswald, W., C. Widga, and U. Göhlich. 2023. New mammutids (Proboscidea) from the Clarendonian and Hemphillian of Oregon—a survey of Mio-Pliocene mammutids from North America. *The Bulletin of the Museum of Natural History of the University of Oregon* 30:1–64.

Webb, S.D. 2000. Evolutionary history of New World Cervidae. Pp. 38–64, *In* E.S. Vrba and G.B. Schaller (Eds.). *Antelopes, Deer, and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*. Yale University Press, New Haven, CT. 356 pp.

Widga, C., J. Saunders, and J. Enk. 2017. Reconciling phylogenetic and morphological trends in North American *Mammuthus*. *Quaternary International* 443:32–39.

White, C.D. 2024. Descriptions of Interglacial Mastodons from Snowmass, Colorado. Electronic Theses and Dissertations. East Tennessee State University. Johnson City, TN. 187 pp.

Yann, L.T. 2010. Rare earth elements as an investigative tool into the source, age, and ecology of late Miocene to late Pleistocene fossils from the Tunica Hills, Louisiana. LSU M.S. Theses. Louisiana State University. Baton Rouge, LA. 91 pp.