UNIVERZITA KARLOVA V PRAZE

PŘÍRODOVĚDECKÁ FAKULTA

Ústav geologie a paleontologie

Studijní program: Geologie

Studijní obor: Praktická geobiologie

Evolution of Eurasian mammoths during the Quaternary with a focus on adaptations related to climate change

Vývoj euroasijských mamutů během kvartéru se zaměřením na adaptace související se změnami klimatu

Amín Bhija

Bakalářská práce

Vedoucí bakalářské práce: RNDr. Martin Mazuch, Ph.D.

Praha, 2023

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, dne ....

Podpis: ....

Poděkování

Velice rád bych zde poděkoval mému školiteli RNDr. Martinovi Mazuchovi Ph.D. za jeho trpělivost a pomoc během zpracování této práce.

Abstract

The main purpose of this work is to summarize the changing functional morphology of Eurasian mammoths throughout the Pleistocene, along with a short summarization of the Pleistocene environments of Eurasia. Dietary habits of mainland European mammoths are also be described, as the dental morphology and microwear analysis of mammoth teeth is often used as an environmental indicator. The transition between early mammoths such as *Mammuthus rumanus*, *Mammuthus meridionalis* and more derived grassland mammoths such as *Mammuthus trogontherii* and *Mammuthus primigenius* is illustrated through morphological adaptations and a change in their diet.

Key words: mammoth, Quaternary, Eurasia, climate change, adaptations

Abstrakt

Hlavním cílem této práce je shrnout změny ve funkční morfologii eurasijských mamutů během pleistocénu, společně s krátkým shrnutím pleistocenních prostředí Eurasie. Strava kontinentálních evropských mamutů je také popsaná, jelikož dentální morfologie mamutích zubů je často využita jako enviromentální indikátor. Přechod mezi rannými mamuty jako *Mammuthus rumanus* a *Mammuthus meridionalis* a více derivovanými stepními mamuty jako *Mammuthus trogontheri* a *Mammuthus primigenius* je ilustrována skrz morfologické adaptace a změnami v jejich stravování.

Klíčová slova: mamut, kvartér, Euroasie, klimatická změna, adaptace

Contents

Introduction

Mammoths are large mammals belonging to the order Proboscidea. They, along with their modern-day relatives, are easily recognizable thanks to their trunk, large size and prolonged incisors known as tusks. Mammoths as a group arose during the Upper Pliocene and survived through to the latest parts of the Pleistocene, with some population surviving into the Holocene (Arppe et al. 2019, Maglio 1973).

The Quaternary climate is very chaotic in nature, with shifts and anomalies being regular occurrence. Pleistocene glaciation cycles were greatly influential on the faunal and floral composition of Pleistocene landscapes, slowly transforming the forested Europe of the Plio-Pleistocene period to the more open grasslands known as the "mammoth steppe". As the name of the ecosystem implies mammoths were a key component of these grasslands. Major changes in mammoth diet and morphology corelated to the changes in vegetation (Guthrie 2001, Shoshani & Tassy 1996).

Mammoths come in several species, with the first mammoths evolving in Africa. Two African mammoths can be accredited with giving rise to European mammoths, *Mammuthus subplanifrons* and *Mammuthus africanavus*. Regardless of which one of these two was the ancestor of Eurasian mammoths, the first European mammoth was *Mammuthus rumanus*. This mammoth lived all throughout Eurasia during the Upper Pliocene and was mostly a browser. *Mammuthus meridionalis* appears at the starts of Pleistocene and is thought to have eaten more abrasive food than its ancestor. *Mammuthus trogontherii* is the first mammoth which can be considered a grazer and appears during the Middle Pleistocene. *Mammuthus primigenius* is the most derived mammoth whose diet was comprised mostly of abrasive grasses, it appeared during the Upper Pleistocene and survives all the way to the Holocene (Shoshani & Tassy 1996).

Early historical descriptions

Early research

The first record of a fossil mammoth from Europe comes from Gotha Germany in 1698 by Wilhelmus Ernestus Tentzelius. Tenzelius found and described parts of the skull, teeth and postcranial skeleton, he identified the bones as those of an elephant which has been buried during the mythical flood. Several more finds have been made during the 18^{th}, however they have not received a proper scientific name until 1799 when Johann Friedrich Blumenbach who named the animal *Elephas primigenius*. Three years prior Georges Cuvier had already recognised the fact that fossil mammoths were in fact not elephants lost in Europe but an extinct species, he described it as *Elephas mammoth* or *Elephas mammonteum*, however Blumenbach's name took its place instead. The name *Mammuthus* appears years later in 1828 by Joshua Brookes in a catalogue of his collection (Blumenbach 1799, Brookes 1828, Osborn 1942).

Osborn's taxonomy and further 20th century research

In 1942 proboscidean taxonomy received a large overhaul in scale and complexity with the release of Henry Farfield Osborn's posthumously released monography titled Proboscidea, it was released in two volumes and contained a complete summary of all of Osborn's knowledge on the namesake taxon. Within the second volume mammoths are discussed in detail, Osborn attempted to describe most of the relevant skeletal finds and to find lectotypes for his newly proposed diversity of Pleistocene proboscideans. Osborn divided mammoths into three genera*, Archdiskidon*, *Parelephas* and *Mammonteus*, these were all united a subfamily Mammontinae based on common cranial and hypsodont dental morphology (Osborn 1942).

While Osborn recognised that these genera were in fact related to each other, it wasn't until much later that the realisation of the fact that the vast majority of apomorphies used to define these genera fell within the range of interspecies variation (Maglio 1973, Shoshani & Tassy 1996).

In Maglio's Origin and evolution of the Elephantidae released in 1973 the taxonomy of mammoths was greatly streamlined, the name *Mammuthus* is used to describe a genus encompassing Osborn's subfamily Mammontinae and explains the previously embellished diversity as a mistake caused by fragmentary specimens being misidentified as new genera and the progressive changes in cranial and dental morphology as progression towards a grazing diet (Maglio 1973).

Along with and earlier description of the Pliocene mammoth *Mammuthus africanavus* from the year 1958 allowed researchers to recognise the progressive transition of mammoths radiating out of Africa to Eurasia and America. Following research only helped solidify the transition of former browsing types of African mammoth to later grazing dominant species, these trends can be seen described in

Shoshani's and Tassy's the Proboscidea (1996) where mandibular and dental morphology (such as progressive increase in number of lamellar plates, larger amount of cement and increased height) is thoroughly described and compared across the genus. Thus, we find ourselves in the current taxonomic situation with three properly established Eurasian species, *Mammuthus meridionalis*, *Mammuthus trogontherii* and *Mammuthus primigenius* (Arambourg 1952, Maglio 1973, Shoshani & Tassy 1996).

Research in the 21st century

Both genetic material and isotopic data have provided insight into ecology, environment, taxonomy and extinction of mammoths. Sadly, the vast amount of this data concerns only the woolly mammoth, *Mammuthus primigenius*. In 2008 genetic material of a male individual was sequenced, providing insight into population genetics. Isotopic data often provides great information about local environment, meaning mammoth remains can be used a paleo-indicators and even to reconstruct individual behaviour, such as migration or diet. Mammoths also made up a substation part within the diet of human hunters. Recently mammoth remains had allowed to interpret migration patterns of an individual animal. It is certain that mammoth will remain a relevant source of information for Quaternary research (Drucker et al. 2017, Miller et al. 2008, Tütken et al. 2007, Wooller 2019).

Environmental changes within Pleistocene

Whilst several mammoth species were present during the Pliocene, they weren't as proliferated and the shift in morphology such as lamellar frequency or hypsodonty are not nearly as extreme and reflective of environmental changes, thus Pliocene climate will be omitted.

The Pleistocene is defined by its climatic variability. During cyclical shifts of climate, the movement and thickness of ice sheets would vary Some of the cycles are associated with earths orbital parameters, specifically those of earlier Pleistocene, these cycles were shorter and less intense in glaciation. Middle to Upper Pleistocene is marked by change in glaciation, increasing the intensity of glaciation and the length of these cycles. Based on benthic oxygen data, we can describe the glacial cycles as stages based on marine isotopes – MIS, with these stages being dated as far as the start of Pleistocene and Upper Pliocene (Liebrand & Bakker 2019, Maslin & Ridgwell 2005, Pisias & Moore).

The Pleistocene epoch can be divided into three sub-epochs. The Lower Pleistocene begins roughly 2.6 Ma and ends about 0.8 Ma, this stage marks the beginning and expansion of ice sheets and the continual drying of northern landscapes. This led to ungulates and other herbivorous animals to switch from a browsing diet to a mixed feeding or grazing one. During Middle Pleistocene continental grasslands start to spread across the Europe and North America, Middle Pleistocene glaciations are more intense and occur more frequently, Middle Pleistocene ends roughly 0.129 Ma. During Upper Pleistocene the steppes and grasslands reach their peak distribution. The Upper Pleistocene ends 11.7 Ka and is succeeded by the Holocene epoch (Martin 2021, Strani et al. 2018).

The Upper Pleistocene marks the multi-continental spread of the mammoth steppe, this ecosystem was sustained by mega continental dryness and the presence of large megafauna, causing a reversal of today's conditions, where the arctic is dominated by bogs and mesic-adapted fauna and flora, whilst during the Upper Pleistocene arid-adapted fauna and flora prospered. The fauna and flora of this ecosystems must have been well adapted to this new, frigid and arid environment, with morphological changes such as increased height of the tooth crown and long coats of fur. During the climax of this period mesic fauna had to survive in refugia's, into which they retreated and propagated out of based on the climate fluctuation. The mammoth steppe disappears at the end of the Ice age along with the large mammals which thrived upon it (Guthrie 2001).

The latter part of the Cenozoic seems to have aimed towards a trend of climate cooling. This trend reaches its peak during the Pleistocene, dramatically changing the Plio-Pleistocene ecosystems. However even though the global climate was on average colder the local climates still vary, not only throughout glaciation but also seasonally and thanks to the shift during the MPR (Barrett 2008, Legrain et al. 2023).

Mammoth taphonomy and preservation

Taphonomy

Mammoth remains, like those of other large Pleistocene mammals are relatively resilient when it comes to preservation. The bones of these animals are large and hard to transport by either water or by carnivores. Mammoth fossils have been preserved in numerous ways due to the geographical distribution of the genus, including preservation in permafrost, channel deposits, caves, aeolian sediments, sink holes or asphalt sinks. All of these fossil sources differ greatly in preservation. The localities in more temperate regions tend to preserve far less organic material (Colleary et al. 2021, Péan & Patou-Mathis 2003).

Remains *Mammuthus meridional*is were found in Mygdonia Basin within the Platanachori Formation which is dominated by sandstones, conglomerates, clays, silts, limestone and marls. This infers that the mammoth lived in a marsh like environment (Konidaris et al 2020).

Mammuthus trogontherii and *Mammuthus primigenius* have been both found in loess-like sediment.

Loess is an aeolian or periglacial porous sediment capable of bearing megafaunal remains. An example of a loessal mammoth bearing paleosol is the locality Milovice (Péan & Patou-Mathis 2003, Vasiljevic et al. 2011).

Mammoth bones and teeth have been found near human remains and caves. The cave remains must have been transported here by human hunters as other (Péan & Patou-Mathis 2003).

Upper Pleistocene mammoths have been found with their genetic material intact within several conditions. The degradation of DNA within periglacial conditions is much less severe than in temperate climate. Permafrost remains have shown far lesser degrees of maturation than temperate deposits, such as channel or hot spring-fed sink holes, permafrost shows values closer to bones of extant elephants (Colleary et al. 2021).

By far the most durable part of the mammoth skeleton are its teeth. As the teeth of mammals are often very directly specialised towards its diet. Not only does the morphology of a mammal's tooth allow us to infer its diet, but it also preserves abrasion left by feeding on the surface of the tooth. If the enamel has more scratches on its surface rather than pits it means that the animal consumed a substantial amount of rougher vegetation such as grass, whilst a higher number of pits means that the animal was likely reliant on soft vegetation and browsing (Rivals et al 2012, Smith & DeSantis 2018).

Permafrost mummies

The Adams mammoth found in 1799 and excavated by the year 1806 was one of the first and more complete finds. In the end the skeleton was almost complete only lacking one foreleg whilst still containing large quantities of hair and soft tissue such as a dried-up brain. This skeleton led to one of the first attempts to reconstruct a mammoth (fig.1) (Adams 1807, Lister & Bahn 2007, Osborn 1942).

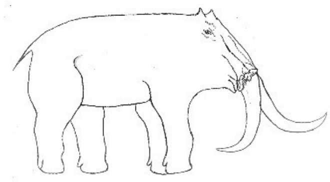


Figure 1 – The first attempt at reconstructing the Adams mammoth

In 1901 another notable mummy was found, the Berezovsky mammoth was a male which had died due to a fall into a small fissure which killed and later buried the animal rather quickly. Its internal organs had rotten away along with large amount of other soft tissue, parts of the trunk and tongue were recovered. In 1908 a mammoth with a preserved trunk was found near Sanga-Yurakh River. A small male with an almost complete skeleton and some soft tissue was found 1948 and had been designated as a standard for the woolly mammoth. Notably many mammoth calf's have been also found, often in good condition, preserving soft tissues (Garutt & Dubinin 1951, Lister & Bahn 2007, Mashchenko et al. 2013).

Taxonomy

Proboscidea

Proboscideans are a group of large afrotherian mammals containing two members of the family Elephantidae and many more extinct groups. In recent past Proboscidea have been an extremely successful group with its many members dominating the niches of large terrestrial herbivores, with fossil species being found everywhere expect Australia and Antarctica (Shoshani & Tassy 1996, Tabuce et al. 2008).

Proboscidea can be easily identified by their dentition, it is often remarkably preserved and easy to differentiate from other groups of mammals. The teeth of most proboscideans are lophodont (sometimes bunodont in basal genera), with most of the group's members possessing only decidual premolars, full grown molars and incisors in the form of tusks, which in many groups such as mammoths or mastodonts could reach up to several meters in length, few of the earliest members of the group also possess short primitive canines. The other defining trait of proboscideans is their trunk, the proboscis is a merging of the muscles of the upper lip and the nose, forming into a pseudo-limb of sorts, however as the trunk is formed entirely of muscle it is preserved only in extremely rare cases. Other notable characteristics present in the more derived forms include large pillar like legs, long humerus and femur, expanded ilium and broad digitigrade feet with five toes and a pad in-between as well as a very large skull (Maglio 1973, Shoshani & Tassy 1996).

Earliest known proboscideans can be dated as far as the Selandian. Proboscidea is a group of mammals undoubtedly bound to Africa, however several groups managed to migrate out of in the Lower Miocene (gomphotheres, mastodonts and dinothere's) and Upper Pliocene (mammoths and elephants). Out of these migrations the gomphotheres were the most successful with some species being found as far as South America. Gomphotheres was however outcompeted by elephants almost everywhere else after the Pliocene migration, the three surviving species of elephant are one of these migrants (Gheerbrant 2009, Shoshani & Tassy 1996).

We can split Proboscidea into two main branches: Elephantiformes (fig.2) and

Plesielephantiformes, with the former containing extant elephants and groups such as mastodonts or gomphotheres, the latter encompasses all dinotheres and other basal taxa (Shoshani 2001).

Distribution: Palaeocene to recent Africa / Miocene to recent of Eurasia / Miocene to Holocene of North and South America (Maglio 1973).

Taxonomy after 2020

1 Proboscidea Illiger 1811

- 1.1 *Eritherium* Gheerbrant, 2009
- 1.2 *Moeritheirum* Andrews, 1901
- 1.3 *Saloumia* Tabuce et al., 2020
- 1.4 Plesielehpantiformes Shoshani et al., 2001
- 1.5 Elephantiformes (Tassy, 1988)
    1.41 Mammutidae Hay, 1922
    1.42 Gomphotheriidae Hay, 1922
    1.43 Stegodontidae Osborn 1918
    1.44 Elephantidae Gray, 1821
-

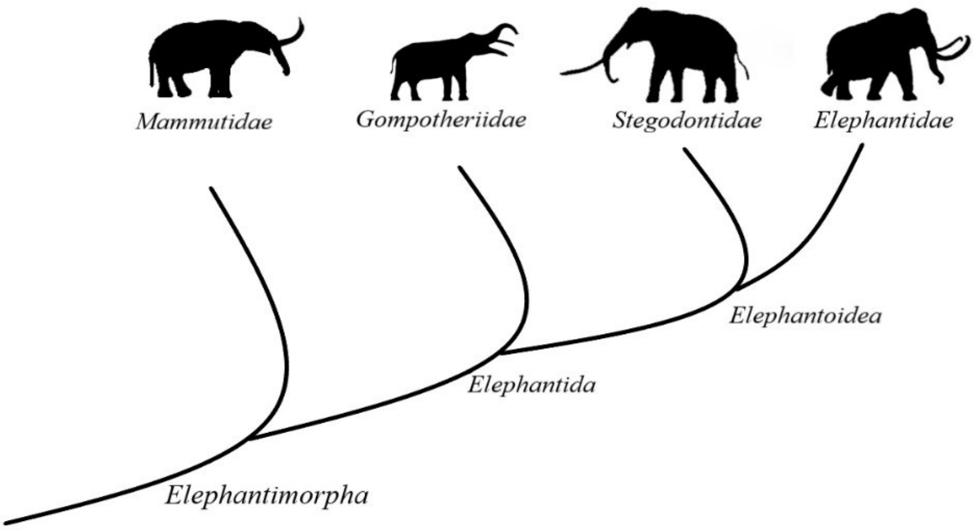


Figure 2 – Systematic classification of Elephantiformes (Shoshani et al. 2007)

Elephantidae

Elephantidae includes to extant genera and several extinct ones closely related to their modern cousins, the group encompasses all animals all the way from the basal genus *Primelephas* to the more derived forms such as extant *Elephas* or the extinct *Mammuthus*. The family was first described by John Edward Gray (Gray 1821, Shoshani et al. 2007).

Elephantidae can be easily identified by their derived teeth structure, all members of the group possess lophodont teeth with their cusps being morphed into at least several laminae. Elephants only possess molars and premolars evolved into a molar like structure, as well as one or two pairs of elongated incisors protruding out of the mouth in the form of tusks, the enamel on the surface of these tusks eventually withers away. Thanks to the number of plates on individual generations of teeth and a correlation to the height of the tooth crown of the animal we can effectively identify individual species of each new specimen. The numbers of plates correlated to the size of the lower third molar (From now on referred to as M3) can be used to interpret the diet of individual genera and species. Other notable features include their large size, pillar like legs with cushioning, rather large brain, compact and durable cranium with a rigid mandible, long marrow-lacking bones, digitigrade feet and a developed trunk or proboscis, this organ is made up entirely of musculature (Shoshani & Tassy 1996, Maglio 1973).

A notable factor among all herbivores is the hypsodonty index, which is a ratio of a tooths height compared to its length or width. This ratio highlights the capability of the teeth to sustain abrasion, without a cost at life expectancy of the animal. Development of this index among Elephantidae leads to a broadening of dietary niches. A measurement specific to Elephantidae is the lamellar index, which is the ratio of the number of laminae and the surface of the tooth (Kubo & Yamada 2014, Maglio 1973).

The first appearance of Elephantidae is uncertain, but we can be sure that the most basal members of the group were present in Africa in Upper Miocene roughly as far as 7 Ma. The group produced several cosmopolitan species throughout the Middle to Upper Pliocene, with *Mammuthus* being by far the most successful in terms of expansion, reaching peak distribution during Middle Pleistocene, with fossils being found as far as central Africa (Bibi et al. 2012, Shoshani & Tassy 1996).

Origin of Elephantidae can be traced back to the Upper Miocene with two genera *Stegotetrabelodon* and *Primelephas*. Both share several traits which the more derived elephants lack such as lower tusks and an extended lower jaw. These were originally seen as traits of gomphothere-like animals however further inspection of the teeth shows that both genera are true elephants. Both genera were distributed across Africa through several species, ranging from central Africa all the way to the levant. Maglio proposed that *Stegotetrabelodon* was ancestral to the smaller *Primelephas*, which would subsequently give rise to the four main branches within Elephantidae (fig.3) (Maglio 1973, Osborn 1942, Shoshani & Tassy 1996).

Four genera arose from basal Elephantidae such as *Primelephas* during the Pliocene, *Loxodonta, Palaeoloxodon, Elephas* and *Mammuthus*. The taxonomic relationship between these groups is often debated upon, generally *Loxodonta* is agreed upon as the most basal with *Palaeoloxodon* following and *Elepha*s and *Mammuthus* forming sister groups of the most derived elephants. (Palkopoulou et al. 2018, Shoshani et al. 2001).

Distribution: Upper Pliocene to recent Africa / Middle Pliocene to recent of Eurasia / Lower to Middle Pleistocene to Holocene of North America (Maglio 1973).

Taxonomy after 2018

1 Elephantidae Gray, 1826

- 1.1 *Loxodonta* Anonymous 1827
  Synonyms include - *Loxodonte*
- 1.2 *Palaeoloxodon* Makiyama, 1924
- 1.3 *Elephas* Linnaeus, 1758
  Synonyms include – *Elephantus, Eulephas, Leithadamsia, Hypselephas*
- 1.4 *Mammuthus* Brookes, 1828
  Synonyms include – *Archidiskodon, Metarchidiskidon, Mammonteus, Mammonteum,Parelephas, Dicyclotherium, Cheirolites*

Mammuthus

Mammuthus is a genus belonging to the family Elephantidae. Mammoths are often thought of as being all adapted to grazing, capable of living on a sprawling grassland with their dentition possessing higher hypsodonty index and lamellar frequency, however the mammoths of Lower and Middle Pleistocene were browsers and mixed feeders (Lister 2001, Lister et al. 2005, Maglio 1973, Shoshani & Tassy 1996).

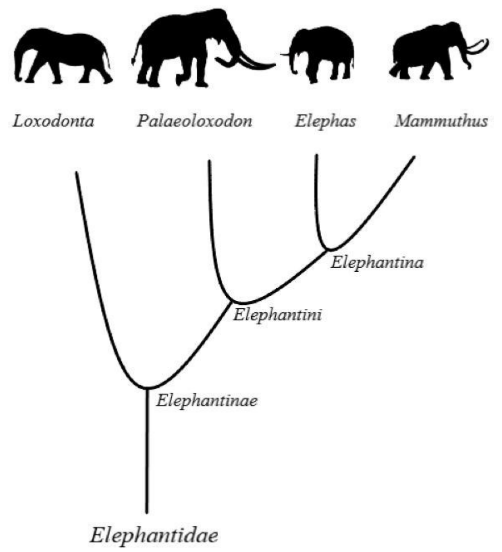


Figure 3 – Systematic classification of Elephantidae according to both hyoid and genetical comparisons, (Palkopoulou et al. 2018)

The teeth of *Mammuthus* come in 6 generations, with the first 3 being three deciduous premolars and the latter 3 being true molars. The last generation molars M3 can reach up to a size of 40 centimetres. These last molars also possess the most lamellar plates per species, ranging from 8 (*M. subplanifrons*) to 27 (*M. primigenius*). A trend of tooth crown heightening (fig.4). is also seen throughout mammoth evolution. This along with several other adaptations can be summarised as a progressive transition to a grazing diet. Mammoths lacked mandibular tusks (Rivals et al 2015, Maglio 1973, Lister 2001).

Some later species possess significantly dorso-ventraly elongated skulls, which tend to be slightly shorter on the anterior-posterior plane, cranium possesses concaves within the parietal range to a varying degree. Parietals are expanded to the sides (Maglio 1973).

Soft tissue of woolly mammoths shows that its proboscis possessed two elongated tips similar to *Elephas*. Upper Pleistocene forms also possessed fur. The earliest mammoth fossils can be dated back to Upper Pliocene Africa. The two earliest known members *Mammuthus subplanifrons* and *Mammuthus africanavus* are known from a few fragmentary cranial remains, several sets of teeth and very few parts of the postcranial skeleton. Their expansion to Eurasia is rather rapid, sporadic mentions of mammoth like material being found in Mediterranean and eastern Europe are sometimes dated to the Plio-Pleistocene boundary, however these reports are often disputed, and the taxonomy of the material is often discussed as several synonyms are often utilised to describe these species. By the Lower to Middle Pleistocene however mammoths are already present in Europe in the form of *Mammuthus rumanus* which evolved into the Lower Pleistocene *Mammuthus meridionali*s which possessed from 11 up to 14 lamellar plates, the Middle Pleistocene *Mammuthus trogontherii* follows with between 15 to 21 narrow plates and lastly the derived *Mammuthus primigenius* with up to 27 plates. Notably, *Mammuthus trogontherii* migrated all the way to the Americas and gave rise to *Mammuthus columbi*. These species often overlapped in distribution and differentiation between them can be quite difficult. The fluctuating sea levels of the Pleistocene also isolated Several Mammoth populations giving rise to several species of dwarf mammoths (Lister et al. 2005, Maglio 1973, Plotnikov et al. 2015, Shoshani & Tassy 1996).

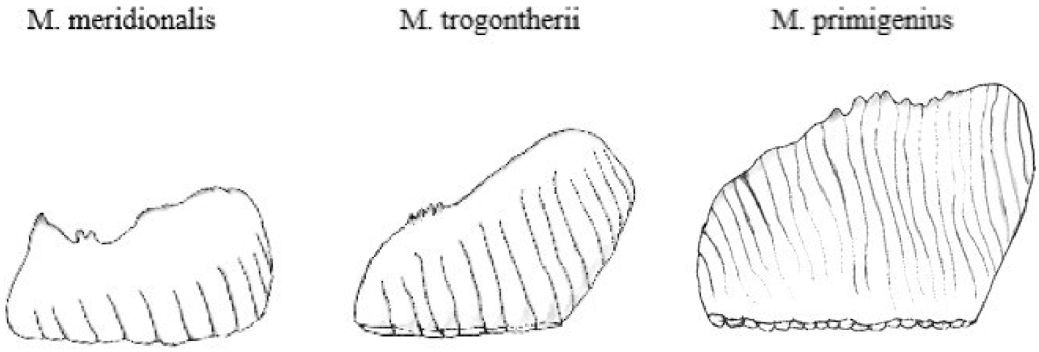


Figure 4 – The transition between upper M3 in Pleistocene European mammoths

Description: Upper Pliocene to Lower Pleistocene Africa / Lower Pliocene to Holocene of Eurasia / Lower to Middle Pleistocene to Holocene of North America (Maglio 1973).

Taxonomy as of 2010

1 *Mammuthus* Brookes, 1828

- 1.1 *Mammuthus subplanifrons* Osborn, 1928
  Synonyms include – *Loxodonta adaurora, Archidiskodon subplanifrons*
- 1.2 *Mammuthus africanavus* Arambourg, 1952
- 1.3 *Mammuthus rummanus* Ştefănescu, 1924
  Synonyms include – *Loxodonta antiquus rumanus, Archidiskodon rumanus*
- 1.4 *Mammuthus meridionalis* Nesti, 1825
  Synonyms include – *Archidiskodon meridionalis, Elephas meridionalis, Elephas lyrodon, Elephas moghrebiensis, Mammuthus gromovi*
- 1.5 *Mammuthus trogontherii* Pohlig, 1885
  Synonyms include – *Mammuthus armeniacus, Archidiskodon trogontherii, Mammonteus trogontherii, Parelephas trogontherii, Elephas trogontherii*
- 1.6 *Mammuthus creticus* Bate, 1907
  Synonyms include – *Elephas creticus*
- 1.7 *Mammuthus lamarmorai* Forsyth Major, 1883
  Synonyms include – *Elephas lamarmorae*
- 1.8 *Mammuthus exilis* Stock & Furlong, 1928
  Synonyms include – *Elephas exilis*
- 1.9 *Mammuthus columbi* Falconer, 1857
  Synonyms include – *Mammuthus imperator, Mammuthus hayi*
- 1.10 *Mammuthus primigenius* Blumenbach, 1799
  Synonyms include – *Mammonteus primigenius, Elephas primigenius*

Mammuthus africanavus

Mammuthus africanavus was a species of Upper Pliocene mammoth from northern Africa. It was a medium-sized mammoth know from only a fragmentary specimen of the skull and a few dozens of teeth. The teeth of this mammoth could possess from 9 to up to 12 laminae, its enamel being thinner than that of *Mammuthus subplanifrons* and the teeth overall being far less broad. Validity of the succession from *Mammuthus africanavus* has been questioned by several authors, with its small size and divergence of the tusks from the skull being wider than in later forms. This coupled with reported findings of mammoths from the Hadar formation, apparently closely resembling the early European mammoth *Mammothus rummanus* lead to some describing *M.africanavus* as a dead end, as well as of many of the molars being thought to have been those of *Loxodonta* (Lister & Bahn 2007, Maglio 1973, Markov 2012).

Mammuthus subplanifrons

Mammuthus sublanifrons holds an ancestral position to all Eurasian mammoths, it was a large animal with an estimated shoulder height of about 3,6 meters and weighing up to 9 tonnes. *M. Subplanifrons* could possess somewhere between 7 to 9 laminae, with its molars being described as primitive and very broad for a mammoth, laminae remain thick whilst being less frequent than in more derived forms. Layers of both cement and enamel remain thick. The jaw of M*ammuthus subplanifrons* is described as rather narrow and slender for a mammoth (Larramendi 2016, Lister & Bahn 2007, Maglio 1973).

Mammuthus subplanifrons appears in the Lower Pliocene roughly 5 million years ago and proceeded to migrate to south-east Africa as well. These mammoths later evolve into *Mammuthus africanavus*. *Mammuthus subplanifrons* seemed to have been able to consume more abrasive vegetation than other elephants, this was likely caused by dietary partitioning as other large proboscideans shared its environment (Groenewald et al 2020, Maglio 1973).

Mammuthus rumanus

Mammuthus rumanus was a large mammoth that could reach up to 10 to 11 tonnes in weigh. It the first mammoth to migrate into Eurasia. Fragmentary finds of molars, tusks and sometimes limbs have been found as far as east Asia and suggest pan-Eurasian presence, however these findings are somewhat controversial and the exact taxonomy and place within the genus is currently not well known. *M. Rumanus* has been accepted as valid quite recently, material belonging to *M. rumanus* has most likely been identified as other members of *Mammuthus* (*M. meridionalis* mostly). Dental remains of *M. rumanus* mostly consist of last generation molars which allow us to distinguish it from latter Eurasian species quite easily as these mammoths possess from 8–10 laminae on lower molars and up to 10 on upper molars (Larramendi 2016, Lister 2004, Lister et al. 2005, Markov 2012, Rabinovich & Lister 2017).

Morphology

Morphology of *Mammuthus rumanus* is poorly understood, as most of the postcranial skeleton has not been found, and only a couple of molars can be identified as *M. rumanus* with certainty. The molars of *M. rumanus* are more progressive than those of *M. subplanifrons* but less derived than those of *M. africanavus*, possessing from 8–10 lamellas and a hypsodonty index surpassing *M. subplanifrons*. The enamel of these molars is rather thick compared to the later forms of *Mammuthus* with its mean thickness being up to 3.9 mm. The composition of enamel layers is rather primitive, whilst the iddle layer is proliferated the most, compared to later forms it is not as thick, whilst the outer layer is thicker than in derived mammoths such as *M. meridionalis*, the inner layer is comparable to that of Middle Pleistocene mammoths but still rather thick compared to Upper Pleistocene mammoths. Median folds located on enamel folds are still present. The tusks of this mammoth were huge, one of the found tusks was measured to a total of 335 cm in length. Reports from Montopoli Italy include material that contains partial remains of *Mammuthus* tibia, third metacarpal, tusks and a very poorly preserved femur, it is still somewhat contested if these certainly belong to *M. rumanus* as these could be remains of very basal *M. meridionalis*. The humerus although formerly very fragmentary was restored to length of up to 1450 mm, making *M. rumanus* a rather large mammoth comparatively to more derived forms such *as M. primigenius* (Ferretti 2003, Larramendi 2016, Lister & Essen 2004, Markov 2012).

Ecology

Formerly evolving in Africa, as the first mammoth which established a permanent population in Eurasia, *Mammuthus rumanus* is often used as evidence of an ecological shift. *M. rumanus* has been described most often from south and eastern Europe, north-eastern Africa and the Levant and several controversial reports coming all the way from China. Oldest remains of a European elephantid come from Dacic basin, Romania, with these likely being those of *M. rumanus*, meaning that this species of mammoth was present in Europe possibly as far as 3.5–3.0 Ma, with earliest forms of *Mammuthus meridionalis* replacing *M. rumanus* completely by 2.6 Ma (Lister et al. 2005, Lister & Essen 2004, Rabinovich & Lister 2017).

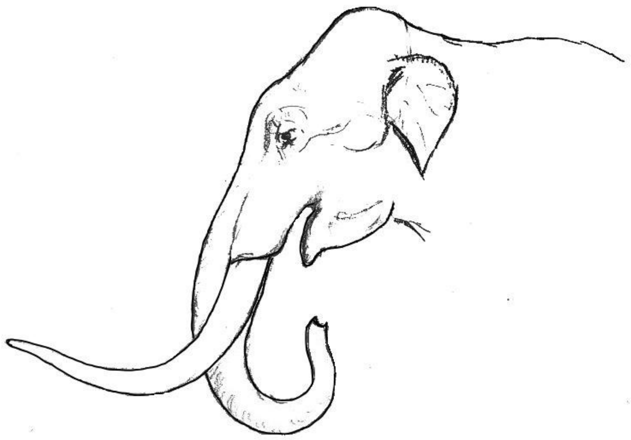
Appearance of mammoths is often associated with floral and climatic shifts in floral composition.

Mammuthus rumanus shared its ecosystem with several proboscidean genera such as *Anancus, Loxodonta* and *Elephas.* The idea that *M. rumanus* subsided of a diet consisting of more coarse vegetation than the other browsing Elephantidae is not unfounded, as compared to its predecessors and other elephants the crown of its teeth was somewhat higher and the increasing number of laminae would suggest a shift in diet towards its descendants (Rivals et al. 2015, Rook & Martínez-Navarro 2010).
Analysis of *M. rumanus* teeth microwear however showcased that whilst the diet of primitive mammoths differed from those of other browsing Elephantidae, it had not been until later more derived forms such as *Mammuthus trogontherii* that mammoths became grazers. Contemporary large herbivores such as *Anancus arvernensis* seemed to have focused on much softer and easily digestible vegetation, making them somewhat unable to subside off the soon to be dominant grassy more open areas (Rivals et al. 2015, Virág et al 2014).

The arrival of Mammoths in Europe and eventual spreading is likely related to the climatic shift at the beginning of Pleistocene (appearance of mammoths and some horses is often described as the elephant-equus event). Southern European vegetation during the Plio-Pleistocene boundary could be characterised as composed of woodlands and some mesic-grassland. With the vegetation distribution being comparable to today (Rook & Martínez-Navarro 2010, Szabó et al 2022).

M. rumanus disappears following the Plio-Pleistocene transition, having been replaced by their descendant *Mammuthus meridionalis.*

Figure 5 – Drawing of a *M. meridionalis*



Mammuthus meridionalis

Mammuthus meridionalis (fig.5) serves as an intermediary between still browsing mammoths of Africa and obligate grazing mammoths of Eurasia. Even the earliest forms of *M. meridionalis* from Italy possess several traits which suggest partial grazing. It was likely a mixed feeder, with higher crowned teeth than *Mammuthus rumanus* and an increased hypsodonty and lamellar index. *M. meridionalis* was also one of the largest species of mammoth (Maglio 1973, Rivals et al. 2015).

Morphology

M. meridionalis was incredibly large with adult males reaching up to 4 meters of height and 11 tonnes in weight (Larramendi 2016). As a direct descendent of *Mammuthus rumanus*, it possessed more developed dentition, with increased hypsodonty and lamellar index, with the number of laminae of the molar M3 ranging between 12–14 laminae. The tooth crown of the mammoth is higher compared to tooth width than those of its predecessors. The teeth also have thinner enamel than that of *M. rumanus (*Lister 2001). Enamel thickness ranges between 2.6 mm to 4 mm, with the middle layer being the thickest, and the outer layer is significantly thinner than that of *M. rumanus*, whilst the inner layer comprises a similar portion of the teeth enamel to that of *M. rumanus* or *M. trogontherii* (Ferretti 2003). The tusks of *M. meridionalis* also reach larger sizes than those of *M. rumanus*. The molars still are relatively broad compared to its descendants (Ferretti 2003, Lister & Essen 2004, Maglio 1973, Shoshani & Tassy 1996, Rossi et al. 2017).

The morphology of the skull of *M. meridionalis* is highly variable, depending on stratigraphical and geographical distribution, however certain traits distinguish this species from its predecessors and the species that follow, such as a fairly large zygomatic arch, premaxillaries are not entirely fused in all places and the corpus of the mandible is still fairly long, the entire shape of the skull is concave with a dome extending from the rest of the cranium (Ferretti 1999, Lister et al. 2004).

M. meridionalis established its presence across a rather large part of Eurasia, splitting off into several subgroups which map the progressive evolution of the species into *Mammuthus trogontherii*, especially differing in cranial morphology (Ferretti 1999).

M. gromovi differs from later forms of *M. meridionalis* only through slightly thicker enamel and a different way of folding, the dental formula otherwise falls within the measurements of *M. meridionalis. M. m. vestinus* is a subspecies of mammoth coming from Lower Pleistocene Italy and showcases a so called an extreme "meridionaloid" shape of the skull, posteriorly extending the crown point of the cranium, with the front of the skull being far more concave than in other *M. meridionalis.* Remains of this subspecies also often reach larger size than other *M. meridionalis* specimens. The teeth of these mammoths also remain rather primitive in structure. *M. m tamanensis* belongs to the group of mammoths which likely gave rise to *M. trogontherii*. This mammoth did not evolve the derived cranial features of M. m vestinus and kept a less domed skull, however the dental characteristics of this mammoth showcase growth of additional dental laminae, serving as an intermediary between early Italian *M. meridionalis* and the first *M. trogontherii* of central Europe. Reports of this mammoth come from European sediment of roughly 1.0 Ma (Ferretti & Croitor 2001, Lister & Essen 2004, Ferretti 1999, Maglio 1973, Rossi et al. 2017).

Ecology

Mammuthus meridionalis appears in Lower Pleistocene Europe roughly 2.5 Ma and proceeds to spread throughout the entirety of Europe and western Asia. *M. meridionalis* expands on the niches occupied by *Mammuthus rumanus*. Like the mammoths before it, *M. meridionalis* is still bound to the temperate forests of Southern Europe, however it was capable of expanding into open areas less ideal for browsing, the increase in in molar laminae, and the increased hypsodonty along with thinner layer of outer enamel suggest this mammoth could consume a larger variety of food than other proboscideans of its time. Along with the dental characteristics, the variety within the skull shape could also suggest different feeding habits as the morphological differences seemed to have affected the way in which these animals could manoeuvre their heads as the musculature connecting the thoracic hump and the back of the neck would allow for different head posture in individual subspecies, this is also likely linked to the size of the tusks as well as the posture of these animals must have accounted for their weight (Ferretti 1999, Ferretti & Croitor 2001, Maglio 1973).

Microwears analysis suggest that dietary habits were much more diverse among populations of *M. meridionalis* than in those of *M. rumanus*, with certain populations already specialising in grazing. This may however be due to the lack of *M. rumanus* material. More populations of this mammoth however still seem to be more browsing oriented with occasional grazing. This is likely due to the fact that whilst the teeth of this mammoth do fall within hypsodont range, the molars of the animal are still rather broad, and the crown is still flatter than those of later mammoths. This suggest that the environment of *M. meridionalis* may not have been as open as once though, likely still being living within forests or mesic grasslands (Rivals et al. 2015, Virág et al. 2014).

M. meridionalis migrates east into Eurasia from central Europe, where forms such as *M. m. tamanensis* give rise to mammoths more capable of grazing, being completely replaced by its descendant *Mammuthus trogontherii* by 0.6 Ma (Ferretti 1999, Lister et al. 2005).

Mammuthus trogontherii

Often called the "Steppe mammoth" *Mammuthus trogontherii* was described at Süßenborn by Pohlig in 1885. This name is synonymous with *Mammuthus armeniacus* but due to a more prolific use of *M. trogontherii*, the later name was given priority. *M. trogontherii*. It was the largest mammoth ever discovered, with individuals reaching up to 4 meters in height quite regularly, males could reach up to huge sizes with certain specimens remains ranging up to 4 and a half meters in height and estimated 12.5 tonnes in weight. This species of mammoth is known to have been very far spread, rapidly expanding into new areas of Eurasia and even north America soon after it appears in eastern Europe. Unlike its predecessors this mammoth lived within a much colder environment, with far more open grass dominated areas and only sparse forests, establishing a niche for mammoths which other elephants simply could not compete in, this can be seen in several aspects of *M. trogontherii* cranial morphology, such as a shortening of its mandible's rostrum, increased hypsodonty, increased lamellar frequency and even more shortening of the skull, however the extreme concave shape and doming of the skull present in *Mammuthus meridionalis* is not seen in *M. trogontherii* (Larramendi 2016, Lister et al. 2005, Maglio 1973, Pohlig 1885, Shoshani & Tassy 1996).

The teeth of *M. trogontherii* possess even more laminae, with M3s lamellar number ranging from 17 to 21. The teeth are narrower than those of *M. meridionalis* and all together their shearing capabilities are greater. The hypsodonty (roughly 1.2–1.8) of these teeth has greatly increased, with an increase of about 0.5 compared to *M. meridionalis* (1.3), reflecting a large shift in the diet of Eurasian mammoths. The enamel of the teeth is also thinner (Lister et al. 2005, Maglio 1973).

The expansion of *M. trogontherii* also gives rise to several new species, such as *Mammuthus columbi* in north America and *Mammuthus primigenius* in eastern Asia, and likely is the predecessor of *Mammuthus lamarmorai*. Shortly after *M. trogontherii* is replaced by its descendants (Lister et al. 2005).

Morphology

As stated above, whilst not the largest proboscidean, *M. trogontherii* is the largest mammoth to have ever existed. Likely surpassing even, the extremely large skeleton of *Mammuthus meridionalis* from Scoppito (Italy), with an individual from Azov estimated to have measured up to 12.7 tonnes in weight and its radius being 985 cm long. A description of the mammoth's spinal column from inner Mongolia places the total vertebral count of the thoracic region at 19 with the spines forming a sloping appearance in the back, creating a hump behind the neck. There are 4 thick lumbar vertebra, 4 to 6 sacral vertebra and 23 caudal vertebrae. The tail is shorter than that of *M. meridionalis* (Larramendi 2014, Larramendi 2016, Maglio 1973).

The cranium of *Mammuthus trogontherii* underwent several changes to accommodate for the changes in dentition, notably changing the shape of the maxilla and mandible to accommodate for the more hypsodont teeth. As mentioned before, it lacked the extreme modifications of southern mammoths, it is likely because *M. trogontherii* is derived from the more northern populations which had their crania less specialised. The skull is further shortened anterio-posterally, and the concave shape of the skull is reduced (Larramendi 2014, Lister et al. 2005 , Maglio 1973).

Dentition of *M. meridionalis* falls well within the range of hypsodonty, it is the first mammoth that has noticeably high crowned teeth which are narrow in comparison to its predecessor. The number of laminae is almost double of Lower Pleistocene mammoths, ranging between 17 to 21 laminae on mature molar M3. Individual plates are thin and spaced closely together, their distribution also increases the lamellar frequency. The ratio of enamel distribution across the individual layers remains similar to *M. meridionalis*, however the enamel is overall thinner, its mean thickness ranging from 1.9 to 3 mm. Enamel lacks median loops and is wrinkled. The tusks of the mammoth are long and slightly curved, one individual was found with tusks of about 250 mm in diameter (Ferretti 2003, Larramendi 2014).

It is unknown if *Mammuthus trogontherii* possessed any sort of hair or a long coat of fur. Since the tail is rather short and that remains of this mammoth have been found in arctic locations it is possible that the steppe mammoth was covered in fur (Larramendi 2016).

Ecology

Mammuthus trogontherii is the first grazing mammoth. Its dentition is specifically adapted to the open grasslands of Middle to Upper Pleistocene. This is likely thanks to the less specialised nature of central European *M. meridionalis*, allowing its descendants to feed on a broader diet including grasses. Whilst grasses do take up a large part of *M. trogontherii's* diet, it was not an obligate grazer by any means. Molars from Romania show that at least a substantial amount of eastern European mammoth's diet constituted of softer foliage such as leaves and fruits, and other sources such as twigs and tree bark (Rivals et al. 2012, Virág et al. 2014).

M. trogontherii spread throughout out most of Eurasia along with other elements of grassland fauna, such as large deer, rhinos and bovids. The larger inclusion of more abrasive vegetation and its association with other large grassland herbivores shows that this mammoth was preferred open landscapes (Magri & Palombo 2013).

Adult steppe mammoths did not have any natural predators at the time. Pleistocene felines such as *Homotherium latidens* or *Panthera Leo spalea* could have hunted prey ranging up to a ton, which would allow them to hunt young juveniles as well. Human hunting is speculative. Several sites are believed to show signs of animal butchering (Pawłowska et al. 2014, Valkenburgh et al. 2016).

M. trogontherii dominated the scrub grasslands of Middle Pleistocene all the way to Lower Pleistocene. Its rapid expansion gave rise to species such as *M. columbi* and *M. primigenius* which outlast in and occupy its niche until the end of the last glacial period. *M. trogontherii* is replaced by its descendants by 0.6 Ma. The last population of these mammoths survive in eastern Asia until the species extinction (Shoshani & Tassy 1996).

Mammuthus primigenius

Named by Blumenbach in 1799 *Mammuthus primigenius* (fig.6) was a staple of the Middle to Upper Pleistocene megafauna and is by far the most recognisable member of the genus *Mammuthus*. *M. primigenius* appears during the Upper Pleistocene and replaces transitionary forms of *Mammuthus trogontherii* by roughly 0.10 Ma. *M. primigenius* quickly spreads across Eurasia, all the way from northern Siberia to western Europe and even to north America. It continues the trend of including more and more grass within its diet, some inland populations even becoming obligate grazers. Unlike its ancestors *M. primigenius* is of a comparably small size, with the largest European individual approaching 9 tonnes in weight and around 3 meters in height, mammoths from northern Siberia were smaller. *M. primigenius* is the only mammoth to have its carcasses preserved within the permafrost of the northern tundra, offering unique insights into both its diet, soft tissue anatomy and behaviour. Mammoth evolution reaches its peak within the Upper Pleistocene forms, reaching the typical *Mammuthus* type triangle shaped skull, its molars having the highest crown of all other mammoths, the highest number of laminae at a maximum of 27 laminae on lower molar M3, thinnest enamel, a high hypsodonty index and high lamellar frequency (Larramendi 2016, Lister et al. 2005, Maglio 1973, Rivals et al. 2012, Shoshani & Tassy 1996).

Woolly mammoths were a stable of neolithic cultures, with butchering marks and other signs of hunting being rather common. It is often questioned whether human hunting is the reason for extinction of megafauna such as *M. primigenius*, several other factors such as the end of the last ice age or in some cases an impact of a small comet have also been attributed as the cause (Meltzer 2020).

Morphology

Unlike other mammoths mentioned above the morphological details of *M. primigenius* are well known. Not only are skeletal remains abundant compared to other large animals in general as woolly mammoths were a cosmopolitan species, their distribution and choice of habitat allowed for preservation of soft tissues within perma-frost (Lister & Bahn 2007, Osborn 1942, Shoshani & & Tassy 1996).

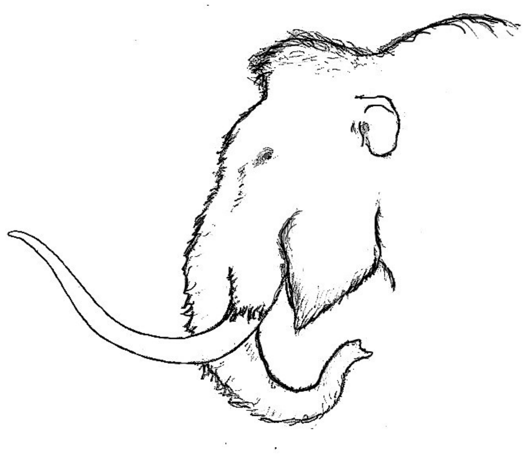


Figure 6 – Drawing of a *M. primigenius*

M. primigenius was smaller than the mammoths of Middle Pleistocene, standing up to around 3 meters in height and weighing up to 8 tonnes, with males generally being larger. The spine was made up of around 7 cervical vertebrae, 20 thoracic vertebrae, 4 lumbar vertebrae, around 21 caudal vertebrae and a fused sacrum, about 40 ribs are attached to the spine. The thoracic spine prosses processes high enough to form a hump in-between the shoulder blades (). The limbs of *M. primigenius* were of a similar shape to that of modern-day elephants, the radius could be up to 800 cm long, the trapezoid and lunar do no overlap as well as in more primitive mammoths and the bones are smaller in general (Larramendi 2016, Lister 2009, Mashchenko et al. 2017, Mashchenko et al 2021, Shoshani & Tassy 1996).

Cranium of *M. primigenius* is less concave than those *M. meridionalis* and *M. trogontherii*. Its parietals are elevated, and the occipital plane is flat. It is shortened anterio-posterioraly and does not expand into a large dome, however it is elevated in the vertical plane. The mandible is shortened, and the alveoli are accommodated for the higher crowned teeth (Lister 2009, Maglio 1973, Shoshani & Tassy 1996).

M. primigenius possessed highly hypsodont teeth with a very high crown compared to the width of the molars. Its lower molar M3 is relatively longer than those of its predecessors, possess more laminae, reaching the peak of lamellar range at 21 to 27 laminae per lower molar M3. The hypsodonty index does not shift or increase at rapidly as it did throughout the evolution of the mammoth stages however the lamellar frequency does. Teeth enamel is even thinner than that of *M. trogontherii,* with the inner and outer layer being proportionally the thinnest out of all mammoths, the mean thickness of enamel ranges between 1.5–2.3 mm. Tusks of *M. primigenius* were huge, comprising a major part of the skulls weight, one male tusk was reported to have been up to 3,8 meters long and weighing up to 86kg (Boeskorov et al. 2020, Ferretti 2003, Maglio 1973).

As mentioned before a large amount of tissue and fat forms a hump on top of the upper back. The peripheries are rather small compared to modern day elephants, the earlobes are on average smaller, and the tail is shorter. Trunks of woolly mammoths possessed a ventral and dorsal process, called. "fingers". *M. primigenius* was covered in a thick coat of shaggy fur with several different colour variations, including orange and black tints. The hair was not only of darker colouration, but several populations seemed to have included lighter haired mammoths (Plotnikov et al. 2015, Workman et al. 2011).

Ecology

M. primigenius serves as a prime example of a keystone species, even to the point of giving the ecosystem "mammoth" steppe its name. This mammoth dominated the landscape of the Upper Pleistocene. Being as cosmopolitan and far spread as it was, *M. primigenius* had to utilise the changes in mastication its evolved dentition and mandibles provided, due to the less ideal conditions of dry grasslands and a seasonally changing environment. The woolly mammoths diet consisted mainly of grasses in continental populations, however the mammoths of the far north were forced to eat everything that could be found such as twigs, bark and foliage of conifers, meaning woolly mammoth dentition still seemed to have allowed for mixed feeding. Results of research show that the teeth of *M. primigenius* have more and more wear damage caused by grasses, continuing the trend of focusing on grazing even within the species, reaching a peak by the end of Pleistocene during the last glaciation. Remains of digested sedge-grasses and small shrubs have been found in the excrement of mainland Asian M. primigenius. The high crowned teeth multiplied laminae and shorter jaw also points to a far more grazing oriented diet. Competing for the mammoths' sources of food were foregut grazers such as the steppe bison, *Bison priscus* (Álvarez-Lao et al. 2009, Guthrie 2001, Kirillova et al. 2015, Lister et al. 2005, Maglio 1973, Rivals et al. 2012, Virág et al. 2014).

Adult woolly mammoths did not possess any natural nonhuman predators. Reports of extant elephant adults being hunted by large felines do however exist, and the predators of Upper Pleistocene Eurasia did reach larger sizes than those of today (Valkenburgh et al. 2016).

Upper Pleistocene mammoths encountered human hunters. Signs of butchering, artwork, hunting injuries, fossil remains inside human residences, and maps of progressive human encroachment all support the fact that human species did interact with *M. primigenius*. Both *Homo sapiens* and *Homo neanderthalensis* are thought to have hunted woolly mammoths. Human species have often been attributed to have caused the extinction of large megafauna, but several other factors are thought to have contributed to the disappearance of these animals as well, such as climate change (Drucker et al. 2017, Halámková 2009, Meltzer 2020, Wojtal et al. 2019).

M. primigenius starts to disappear from Europe and northern America around the time when first signs of a warming episode of the Lower Holocene and the end of Pleistocene, and retreats into northern Asia where some population survive until very early Holocene. The last population of the woolly mammoth survived on the Wrangle Island but went extinct roughly 4000 years ago due to a lack of available food and genetic inbreeding (Arppe et al. 2019).

Mammuthus lamarmorai

Mammuthus lamarmorai was a Middle to Upper-Pleistocene pygmy mammoth from Sardinia. It was about 140 cm tall and could weigh up to 550 kg (Larramendi 2016). Formerly thought to have been a member of the genus *Palaeoloxodon*. However, the morphology of the elephant molars makes it fairly certain that it was a mammoth. The species is known from fragmentary finds. *M. lamarmorai* is thought to have been a descendant of *Mammuthus trogontherii*, which managed to swim to Sardinia from the Italian peninsula thanks to a climatic fluctuation lowering the sear levels around the Island. The mammoth was endemic to Sardinia and lived alongside other insular animals such as the deer *Praemegaceros sardu*s. *M. lamarmorai* survives on Sardinia up until around 57 Ka to 27 Ka before present (Palombo et al 2012).

Mammuthus creticus

Another pygmy mammoth confined to Pleistocene Mediterranean islands was *Mammuthus creticus*, which as the name implies evolved and lived on the island of Crete. *M. creticus* was one of the smallest mammoths, reaching up to 100 cm at the shoulder and weighing up to about 180 kg (Larramendi 2016). It was formerly assumed that all Mediterranean dwarf elephants were of single origin, but like *M. lamarmorai* it is now assumed to be a mammoth. This was due to aDNA evidence linking some remains of *M. creticus* to *Mammuthus*. *Mammuthus meridionalis* seems to have been the most likely ancestor of *M. creticus* as its hypsodonty index matches the morphology of *M. creticus* molars. This means that the ancestors of *M. creticus* colonized the island in-between 2.5 and 0.8 Ma. There is a possibility of earlier colonization but that could only be possible if *M. creticus* was a descendant of *M. rumanus* (Herridge & Lister 2012, Poulakakis et al. 2006)

Discussion

Early mammoth evolution and their migration into Europe from Africa is still not completely understood. Whilst the general outline of transition from *M. subplanifrons* to *M. meridionalis* can be seen through analysis of dental morphology, there is still some doubt concerning the placement of African mammoths within European mammoth phylogeny. Authors such as Lister (2007) had proposed that *M. africanavus* might have not been an ancestor of European mammoths. It could be possible that *M. subplanifrons* is evolved into *M. rumanus* directly. Material from Hadar (Ethiopia) might support the fact that *M. Africanavus* was a member of an extinct lineage with no European descendants as the material shows features intermediary between *M. subplanifrons* and *M. rumanus* but lacks some of the apomorphies of *M. africanavus*. Sadly, the material from Ethiopia remains unstudied and the remains of *M. africanavus* and *M. subplanifron*s are very fragmentary.

Another issue which is recently being solved thanks to isotopic data is the issue of mammoth migration. Whilst the ecology of mammoths is rather well known, it is still obscured by a couple of factors. The specifics of mammoth behaviour and migration has been inferred from extant elephants, this is however a fairly flawed as these animals do not inhabit environments like Pleistocene mammoths. This issue can be solved through isotopic analysis, thanks to the deposition of strontium isotopes within the dentition of mammoths, we can match the bodily values of strontium to soil strontium deposits. This process however assumes that the strontium concentration within the soil has not changed throughout time, which means that this method can be used only on Upper Pleistocene populations of *M. primigenius*.

The way in which migration, morphology and behaviour changed throughout the Quaternary will help explain the shifts and extinction of megafauna at its end, and even explain certain factors of today's faunal composition. The morphological data across the Quaternary could serve as an environmental indicator.

Conclusion

Mammoths serve as an emblematic feature of the Quaternary fauna. Not only were all individual species large key-stone mammals shaping their environments, but a genus with clear transitional features showcasing the changes in the environment. After migrating out of African. The lineage of *Mammuthus* changes its dental and cranial morphology to accommodate for the transition of relatively warm conditions, *M. subplanifrons* and *M. africanavus* found in African fed on a browsing diet, however eating more grass than herbivores of comparable size. *M. rumanus* migrates out of Africa into south-east Europe, living in temperate climates, thriving in deciduous semi-open forests which were common in Europe at the time, it was a browser capable of eating tougher vegetation than its contemporaries, with grass composing a substantial part of its diet. *M. meridionalis* succeeds *M. rumanus*, it was a mixed feeder, with certain populations showing larger grazing tendencies. Following the spread of large grassland ecosystems, *M. trogontherii* and *M. primigenius* reach peak dental morphology, with these two species being capable of obligate grazing whilst still occasionally browsing.

Mammoths go extinct at the end of the last glaciation. Likely due to a combination of over-hunting and climate change. Study of mammoth retreat and the factors which caused such a disappearance at the end of the Quaternary will certainly provide more information about the changes within Upper Pleistocene environments. Today we can study entire migration patterns of mammoths thanks to isotopic data. Using extant animals as comparative models, more information about megafaunal extinction will come to surface.

References

Adams M. M. (1807): XXIII. Some account of a journey to the frozen sea, and of the discovery of the remains of a mammoth. Translated from the French. *Geological Society, London, Special Publications Vol. 29(114), 141–153*. DOI: 10.1080/14786440708563715

Álvarez-Lao D. J., Kahlke R., García N. & Mol D. (2009): On the southernmost record of *Mammuthus primigenius* in Europe and its southern spread during the Late Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology Vol. 278(*1–4*), 2009, 57–70.* DOI: 10.1016/j.palaeo.2009.04.011

Andrews, C. W. (1901): Über das Vorkommen von Proboscidiern in untertertiären Ablagerungen Ägyptens. *Tageblatt des V Internationalen Zoologischen-Kongresses, Berlin Vol. 6, 4–5.*

Arppe, L., Karhu, J. A., Vartanyan S., Drucker D. G., Etu-Sihvola H. & Bocherens H. (2019): Thriving or surviving? The isotopic record of the Wrangel Island woolly mammoth population. *Quaternary Science Reviews, Vol. 222, 2019, 105884.* DOI: 10.1016/j.quascirev.2019.105884.

Arambourg C. (1952): Note preliminaire sur quelques elephants fossiles de Berbhrie. *Bulletin du Muséum national d'histoire naturelle Vol. 24(4), 407–418.*

Barrett P. 2008. A History of Antarctic Cenozoic Glaciation – View from the Margin. *Developments in Earth and Environmental Sciences Vol. 8, 33.* DOI: 10.1016/S1571-9197(08)00003

Bate D. M. S. (1907): On Elephant Remains from Crete, with Description of Elephas creticus, sp. n. *Proceedings of the Zoological Society of London (1907), 238–250.*

Bibi F., Kraatz B., Craig N., Beechde M., Schuster M. & Hill A. 2012. Early Evidence for Complex Social Structure in Proboscidea from a Late Miocene Trackway Site in the United Arab Emirates. *Biology Letters, Vol 8(4), 670–673.* DOI: 10.1098/rsbl.2011.1185

Blumenbach J. H. (1799): Handbuch der Naturgeschichte. *Edition 6, Göttingen, J. H. Dietrich.*

Boeskorov G., Tikhonov A., Shchelchkovac M., P. Ballardd J. & Mole D. (2020): Big tuskers: Maximum sizes of tusks in woolly mammoths - *Mammuthus primigenius* (Blumenbach) - from East Siberia. *Quaternary International Vol. 537, 2020, 88–96.* DOI: 10.1016/j.quaint.2019.12.023

Colleary C., Lamadrid H. M., O’Reilly S. S, Dolocan A. & Nesbitt S. J. (2021): Molecular preservation in mammoth bone and variation based on burial environment. *Scientific Reports Vol. 11, Article number: 2662 (2021).* DOI: 10.1038/s41598-021-81849-6

Brookes J. (1828): A catalogue of the Anatomical and Zoological Museum of Joshua Brookes, Esq. *London, Taylor R.*

Drucker D. G., Naito Y. I, Péan S., Prat S., Crépin L., Chikaraishi Y., Ohkouchi N., Puaud S., Lázničková-Galetová M., Patou-Mathis M., Yanevich A. & Bocherens H. (2017): Isotopic analyses suggest mammoth and plant in the diet of the oldest anatomically modern humans from far southeast Europe. *Scientific Reports Vol. 7, Article number: 6833 (2017).* DOI: 10.1038/s41598-017-07065-3

Cuvier G. (1825): Recherches sur les Ossimens Fossiles de Quadrupèdes, ou' l'on Rétablit les caractères de Plusieurs Espèces d'Animaux dont les Révolutions du Globe ont Détruit les Espèces. *Edition 3*.

Falconer H. (1857): On the Species of Mastodon and Elephant Occurring in the Fossil State in Great Britain. Part I. Mastodon. *Quarterly Journal of the Geological Society Vol. 13, 307–360.* DOI: 10.1144/GSL.JGS.1857.013.01-02.43

Ferretti M. P. (1999): *Mammuthus meridionalis* (Mammalia, Proboscidea, Elephantidae) from the 'Sabbie Gialle' of Oriolo (Cava La Salita, Faenza, Northern Italy) and other European late populations of southern mammoth. *Eclogae Geologicae Helvetiae Vol. 92, 503–515.*

Ferretti M. P. (2003): Structure and evolution of mammoth molar enamel. *Acta Palaeontologica Polonica Vol. 48(3), 383–396*.

Ferretti M. P. & Croitor R. V. (2001): Functional morphology and ecology of Villafranchian Proboscideans from Central Italy. *"The World of Elephants" - International Congress, Rome 2001, 103–108*.

Garutt V. E. & Dubinin V. B., (1951): On the skeleton of Taimyr mammoth. *Zoological Journal 30(1), 17–23*

Gheerbrant E. (2009): Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. *Proceedings of the National Academy of Sciences Vol. 106(26), 10717–10721*. DOI: 10.1073/pnas.0900251106

Gray, J. E. (1821): On the natural arrangement of vertebrate animals. *London Medical Repository Vol. 15(88), 296–310*.

Groenewald P. A., Sealy J., Stynder D. & Smith K. M. (2020): Dietary resource partitioning among three coeval proboscidean taxa (*Anancus capensis*, *Mammuthus subplanifrons*, *Loxodonta cookei*) from the South African Early Pliocene locality of Langebaanweg E Quarry. *Palaeogeography, Palaeoclimatology, Palaeoecology Vol. 543, 2020, 109606*. DOI: 10.1016/j.palaeo.2020.109606

Guthrie R. D (2001): Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews Vol. 20(1–3), 2001, 549–574.* DOI: 10.1016/S0277-3791(00)00099-8

Halámková L. (2009): Osteometric analysis and mammoth hunting strategies. Mammoth hunters of Southern Moravia. In: Oliva M. (ed.), Milovice: Site of the Mammoth people bellow the Pavlov hills. Antropos: *Studies in Anthropology, Paleoethnology, Paleontology, and Quaternary Geology Vol. 27, 108–117*.

Hay O. P. (1922): Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington Vol. 35, 97–101*.

Herridge V. L. & Lister A. M. (2012): Extreme insular dwarfism evolved in a mammoth. *Proceedings of the Royal Society B Vol. 279 (1741), 3193–3200.* DOI: 10.1098/rspb.2012.0671

Illiger J. K. W. (1811): Prodromus systematis mammalium et avium : additis terminis zoographicis utriusque classis, eorumque versione germanica. *Berolini, Sumptibus C. Salfeld, 1811, 301p*.

Kubo M. O. & Yamada E. (2014): The inter-relationship between dietary and environmental properties and tooth wear: comparisons of mesowear, molar wear rate, and hypsodonty index of extant Sika deer populations. *PLoS One Vol. 9(6*). DOI: 10.1371/journal.pone.0090745.

Kirillova I. V., Argant, J., Lapteva E., Korona O., Plicht J., Zinovyev E., Kotov A., Chernova O., Fadeeva E. O., Baturina O. A., Kabilov M., Shidlovskiy F. K., Zanina, O. G. & Severtsov, A. N. (2015): The diet and environment of mammoths in North-East Russia reconstructed from the contents of their feces. *Quaternary International Vol. 406(B), 2016, 147-161*. DOI: 10.1016/j.quaint.2015.11.002.

Konidaris G., Kostopoulos D. S. & Koufos G. D (2020): *Mammuthus meridionalis* (Nesti, 1825) from Apollonia-1 (Mygdonia Basin, Northern Greece) and its importance within the Early Pleistocene mammoth evolution in Europe. *Geodiversitas Vol 42(6), 69–91*. DOI: 10.5252/geodiversitas2020v42a6

Larramendi A. (2014): Skeleton of a Late Pleistocene steppe mammoth (*Mammuthus trogontherii*) from Zhalainuoer, Inner Mongolian Autonomous Region, China. *Paläontologische Zeitschrift Vol 89(2), 229–250 (2015).* DOI: 10.1007/s12542-014-0222-8

Larramendi A. (2016): Shoulder height, body mass, and shape of proboscideans. *Acta Palaeontologica Polonica 61(3), 537–574 (2016)*. DOI: 10.4202/app.00136.2014

Legrain E., Parrenin F. & Capron E. (2023): A gradual change is more likely to have caused the Mid-Pleistocene Transition than an abrupt event. *Communications Earth & Environment Vol. 4*, Article number: 90 (2023). DOI: 10.1038/s43247-023-00754-0

Liebrand D. & de Bakker A. T. M (2019): Bispectra of climate cycles show how ice ages are fuelled. *Climate of the Past Discussions Vol 15(6), 1959–1983*. DOI: 10.5194/cp-2019-43

Linnaeus C. (1758): Systema naturae, per regna tria naturae : secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. *Ed. 10. Vol. 1*.

Lister A. M. (2001): “Gradual” evolution and molar scaling in the evolution of the mammoth. *"The World of Elephants" - International Congress, Rome 2001, 648–651*.

Lister A. M. (2009): Late-glacial mammoth skeletons (*Mammuthus primigenius*) from Condover (Shropshire, UK): *Anatomy, pathology, taphonomy and chronological significance. Geological Journal Vol 44(4), 447–479*. DOI: 10.1002/gj.1162

Lister A. M. & Essen H. (2003): *Mammuthus rumanus* (Stefanescu), the earliest mammoth in Europe. *Advances in Palaeontology ‘Hen to Panta’, 47–52*. DOI: 10.13140/2.1.2677.4407

Lister A. M. & Bahn P. G. (2007): Mammoths: Giants of the Ice Age. The University of Michigan*, University of California Press, 2007*, *192p*. ISBN-13: 978-0520253193

Lister A. M., Sher A. V., Essen H. & Wei G. (2005): The pattern and process of mammoth evolution in Eurasia. *Quaternary International Vol 126–128, 2005, 49–64*. DOI: 10.1016/j.quaint.2004.04.014

Maglio V. J. (1973): Origin and Evolution of the Elephantidae. Philadelphia. *American Philosophical Society. 1973, Vol. 63(3)*, *149p*. DOI: 10.2307/1006229

Magri D. & Palombo M. R. (2013): Early to Middle Pleistocene dynamics of plant and mammal communities in South West Europe. *Quaternary International Vol 288, 2013, 63–72*. DOI: 10.1016/j.quaint.2012.02.028

Major F.C.J. (1883): Die Tyrrhenis: Studien über geographische Verbreitung von Tieren und Pflanzen im westlich Mittelmeergebiet. *Kosmos Vol. 13, 81–106.*

Makiyama J. (1924): Notes on a Fossil Elephant from Sahamma, Tôtômi. *Memoirs of the College of Science, Kyoto Imperial University Series B. Vol. 1(2), 255–264*.

Markov G. N (2012): *Mammuthus rumanus*, early mammoths, and migration out of Africa: Some interrelated problems. *Quaternary International Vol. 276–277, 2012, 23–26*. DOI: 10.1016/j.quaint.2011.05.041

Martin J., Pillans B. & Zalasiewicz J. A. (2021): Formal ratification of subseries for the Pleistocene Series of the Quaternary System. *Episodes Vol. 44(3), 241–247*. DOI: 10.18814/epiiugs/2020/020084

Mashchenko E. N., Protopopov, A. V., Plotnikov V. V. & Pavlov I. (2013). Specific features of the mammoth calf (*Mammuthus primigenius*) from the Khroma Rtver (Yakutia). *Biology Bulletin Vol. 40*. DOI: 10.1134/S1062359013070042.

Mashchenko E. N., Potapova O. R., Vershinina A., Shapiro B., Streletskaya I. D., Vasiliev A. A, Oblogov G. E, Kharlamova A. S, Potapov E., Plicht J., Tikhonov A. N., Serdyuk N. V. & Tarasenko K. K (2017): The Zhenya Mammoth (*Mammuthus primigenius* (Blum.)): Taphonomy, geology, age, morphology and ancient DNA of a 48,000 year old frozen mummy from western Taimyr, Russia. *Quaternary International Vol. 445, 2017, 104–134*. DOI: 10.1016/j.quaint.2017.06.055

Mashchenko E. N., Potapova O., Heintzman P. D. & Agenbroad L. D. (2021): Morphology, Individual Age, DNA and Sex of the Yuka Mammoth (*Mammuthus primigenius*) from Northern Yakutia, Russia. *Paleontological Journal Vol. 55, 1230–1259*. DOI: 10.1134/S003103012111006X

Maslin M. A. & Ridgwell A. J. (2005): Mid-Pleistocene revolution and the ‘eccentricity myth’. *Geological Society, London, Special Publications Vol. 247(1), 19–34.* DOI: 10.1144/GSL.SP.2005.247.01.02

Meltzer D. J. (2020): Overkill, glacial history, and the extinction of North America’s Ice Age megafauna. *Proceedings of the National Academy of Sciences Vol.117*. DOI: 10.1073/pnas.2015032117

Miller W., Drautz D. I, Ratan A., Pusey B., Qi J., Lesk A. M., Tomsho L. P, Packard M. D, Zhao F., Sher A., Tikhonov A., Raney B., Patterson N., Lindblad-Toh K., Lander E. S., Knight J. R., Irzyk G. P., Fredrikson K. M., Harkins T. T., Sheridan S., Pringle T. & Schuster S. C. (2008): Sequencing the nuclear genome of the extinct woolly mammoth. *Nature vol. 456, 387–390.* DOI: 10.1038/nature07446

Nesti F. (1825): Sulla nuova specie di elefante fossile del Valdarno. all'Illustrissimo Sig. Dott. Prof. Ottaviano Targioni Tozzetti (Lettere sopra alcune ossa fossili de Valdarno non per anco descritte). *Nuovo Giornale di Lettere Vol. 11(24), 95–216*.

Osborn H. F. (1918): A long-jawed mastodon skeleton from South Dakota and phylogeny of the Proboscidea. *Bulletin of the Geological Society of America Vol 29, 135–136*.

Osborn H. F. (1928): Mammoths and Man in the Transvaal. *Nature Vol. 121, 672–673*.

Osborn H. F. (1942): Proboscidea, Vol. 2: A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World; Stegodontoidea, Elephantoidea. *Vol. 2 (1942) 805–1676.* New York. *Published on the J. Pierpont Morgan Fund by the trustees of the American Museum of Natural History, 1936–1942*, *958p*. DOI: 10.5962/bhl.title.12097

Palkopoulou E., Lipson M., Mallick S., Nielsen S., Rohland N., Baleka S., Karpinski E., Ivancevic A. M., To T., Kortschak R. D., Raison J. M., Qu Z., Chin T., Alt K. W., Claesson S., Dalén L., MacPhee R. D. E., Meller H., Roca A, L., Ryder O. A., Heiman D., Young S., Breen M., Williams C., Aken B. L, Ruffier M., Karlsson E., Johnson J., Palma F. D., Alfoldi J., Adelson D. L., Mailund T., Munch K., Lindblad-Toh K., Hofreiter M., Poinare H. & Reich D. (2018): *A comprehensive genomic history of extinct and living elephants. Proceedings of the National Academy of Sciences Vol. 115(11)*. DOI: 10.1073/pnas.172055411

Palombo M. R., Ferretti M. P., Pillola G. L. & Chiappini L. (2012): A reappraisal of the dwarfed mammoth *Mammuthus lamarmorai* (Major, 1883) from Gonnesa (south-western Sardinia, Italy). *Quaternary International Vol. 255, 2012, 158–170*. DOI: 10.1016/j.quaint.2011.05.037

Pawłowska K., Greenfield H. & Czubla P. (2014): ‘Steppe’ mammoth (*Mammuthus trogontherii*) remains in their geological and cultural context from Be1chatów (Poland): A consideration of human exploitation in the Middle Pleistocene. *Quaternary International Vol. 326–327, 2014, 448–468*. DOI: 10.1016/j.quaint.2013.08.047

Péan S. & Patou-Mathis M. (2003): Taphonomy of mammoth sites. *Deinsea 9 Vol. 1, 331–346*.

Pisias N. G. & Moore T. C., Jr. (1980): The evolution of Pleistocene climate: A time series approach. Earth and *Planetary Science Letters Vol. 52, 450–458*. DOI: 10.1016/0012-821X(81)90197-7

Plotnikov V. V., Mashchenko E. N., Pavlov I. S., Protopopov A. V., Boeskorov G. G., & Petrova E. A. (2015): New Data on Trunk Morphology in the Woolly Mammoth, *Mammuthus primigenius* (Blumenbach). *Paleontological Journal Vol. 49, 200–210*. DOI: 10.1134/S0031030115020070

Pohlig H. (1885): Über eine Hipparionen-fauna von Maragha in Nord-Persien, über fossile Elephantenreste Kaukasiens und Persiens und über die die Resultate einer Monographie der fossilen Elephanten Deutschlands und Italiens. *Zeitschrift der Deutschen Geologischen Gesellschaft 37(4)*, 1022–1027.

Poulakakis N., Parmakelis A., Lymberakis P., Mylonas M., Zouros E., Reese D. S., Glaberman S. & Caccone A. (2006): Ancient DNA forces reconsideration of evolutionary history of Mediterranean pygmy elephantids. *Biology Letters Vol. 2, 451–454*. DOI: 10.1098/rsbl.2006.0467

Rabinovich R. & Lister A. M. (2017): The earliest elephants out of Africa: Taxonomy and taphonomy of proboscidean remains from Bethlehem. *Quaternary International Vol. 445, 2017, 23–42*. DOI: 10.1016/j.quaint.2016.07.010

Rook L. & Martínez-Navarro B. (2010): Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International Vol. 219(*1–2*), 2010, 134–144*. DOI: 10.1016/j.quaint.2010.01.007

Rossi M. A., Agostini S., Palombo M. R., Angelini I., Caramiello S., Filippo C., Ghezzo E., Marano, F., Molin G., Reggiani P., Sangati C., Santello, L., Socrate G. & Vinciguerra, E. (2017): *Mammuthus meridionalis* from Madonna della Strada (Scoppito, L'Aquila): Diagnostics and restoration. *Bollettino della Societa Paleontologica Italiana Vol. 56(3), 359–373*. DOI: 10.4435/BSPI.2017.31.

Rivals F., Semprebon G. & Lister A. (2012): An examination of dietary diversity patterns in Pleistocene proboscideans (*Mammuthus, Palaeoloxodon*, and *Mammut*) from Europe and North America as revealed by dental microwear. *Quaternary International Vol. 255, 2012, 188–195*. DOI: 10.1016/j.quaint.2011.05.036

Rivals F., Mol D., Lacombat F., Lister A. M. & Semprebon G. M. (2015): Resource partitioning and niche separation between mammoths (*Mammuthus rumanus* and *Mammuthus meridionalis*) and gomphotheres (*Anancus arvernensis*) in the Early Pleistocene of Europe. *Quaternary International Vol. 379, 2015, 164–170*. DOI: 10.1016/j.quaint.2014.12.031

Shoshani J. & Tassy P. (1996): The Proboscidea: Evolution and Palaeoecology of Elephants and Their Relatives. *Oxford,* New York, Tokyo. *Oxford University Press, 502p*. ISBN-13: 978-0198546528

Shoshani J., Sanders W.J. & Tassy P. (2001): Elephants and other Proboscideans: a summary of recent findings and new taxonomic suggestions. *"The World of Elephants" - International Congress, Rome 2001, 676–679*. DOI: 10.1016/j.quaint.2004.04.011

Shoshani J., Ferretti M.P., Lister A.M., Agenbroad L. D., Saegusa H., Mol D. & Takahashi K. (2007): Relationships within the Elephantinae using hyoid characters. *Quaternary International Vol. 169–170, 2007, 174–185*. DOI: 10.1016/j.quaint.2007.02.003

Smith G. J. & DeSantis L.R.G. (2018): Dietary ecology of Pleistocene mammoths and mastodons as inferred from dental microwear textures. *Palaeogeography, Palaeoclimatology, Palaeoecology Vol. 492, 2018, 10–25*. DOI: 10.1016/j.palaeo.2017.11.024

Ştefănescu S. (1924): Sur la Presence de l'Éléphas planifrons et de trois mutations de l'Éléphas antiquus dans les couches géologiques de Roumanie. *Comptes Rendus des séances de l'Académie des Sciences de Paris Vol. 179, 1418–1419*.

Stock C. & E. L. Furlong (1928): The Pleistocene elephants of Santa Rosa Island, California. *Science Vol. 68, 140–141*.

Strani F., DeMiguel D., Bellucci L. & Sardella R. (2018): Dietary response of early Pleistocene ungulate communities to the climate oscillations of the Gelasian/Calabrian transition in Central Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology Vol. 499, 2018, 102–111*. DOI: 10.1016/j.palaeo.2018.03.021

Szabó P., Kovács J., Kocsis L., Vennemann T., Domingo L., Újvári G., Halmai Á., Pirkhoffer E. & Codrea V. (2022): Pliocene - Early Pleistocene continental climate and vegetation in Europe based on stable isotope compositions of mammal tooth enamel. *Quaternary Science Reviews Vol. 288*, 2022, 107572. DOI: 10.1016/j.quascirev.2022.107572

Tabuce R., Asher R.J. & Lehmann T. (2008): Afrotherian mammals: a review of current data. *Mammalia Vol. 72, 2–14*. DOI: 10.1515/MAMM.2008.004

Tabuce R., Sarr R., Adnet S., Lebrun R., Lihoreau F., Martin J. E., Sambou B., Thiam M. & Hautier L. (2020): Filling a gap in the proboscidean fossil record: a new genus from the Lutetian of Senegal. *Journal of Paleontology Vol. 94(3), 580–588*. DOI: 10.1017/jpa.2019.98

Tassy P. (1988): THE CLASSIFICATION OF PROBOSCIDEA: HOW MANY CLADISTIC CLASSIFICATIONS? *Cladistics Vol. 4(1), 43–57*. DOI: 10.1111/j.1096-0031.1988.tb00467.x

Tütken T., Furrer H. & Vennemann T.W. (2007): Stable isotope compositions of mammoth teeth from Niederweningen, Switzerland: Implications for the Late Pleistocene climate, environment, and diet. *Quaternary International Vol. 164–165, 2007, 139–150*. DOI: 10.1016/j.quaint.2006.09.004

Valkenburgh B.V., Hayward M.V., Ripple W.J., Meloro C. & Roth V.L. (2016): The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences Vol. 113(4), 862–867*. DOI: 10.1073/pnas.1502554112

Vasiljevic D., Markovic S., Hose T., Smalley I., & O'Hara-Dhand K., Basarin B., Vujicic M. & Lukic T. (2011). Loess towards (GEO) tourism - proposed application on loess in vojvodina region (North Serbia). *Acta geographica Slovenica Vol. 51(2). 390–406*. DOI: 10.3986/AGS51305.

Virág A., Kocsis L, Gasparik M. & Vasile Ş. (2014): Palaeodietary reconstruction of fossil proboscideans from Hungary and Romania. *Inernational Conference on Mammoths and Their Relatives, Grevena Special Vol. 102, 215–216*.

Wojtal P., Haynes G., Klimowicz J., Sobczyk K., Tarasiuk J., Wronski S. & Wilczynski J. (2019): The earliest direct evidence of mammoth hunting in Central Europe - The Krakow Spadzista site (Poland). *Quaternary Science Reviews Vol. 213, 2019, 162–166*. DOI: 10.1016/j.quascirev.2019.04.004

Wooller M.J., Bataille C., Druckenmiller P., Erickson G.M., Groves P., Haubenstock N., Howe T.,Irrgeher J., Mann D., Moon K., Potter B.A., Prohaska T., Rasic J., Reuther J., Shapiro B., Spaleta K.J. & Willis A.D. (2021): Lifetime mobility of an Arctic woolly mammoth. *Science Vol. 373, 806–808*. DOI: 10.1126/science.abg1134

Workman C., Dalen L., Vartanyan S., Shapiro B., Kosintsev P., Sher A., Gotherstrom A. & Barnes I. (2011): Population-level genotyping of coat colour polymorphism in woolly mammoth (*Mammuthus primigenius*). *Quaternary Science Reviews Vol. 30(17–18), 2011, 2304–2308*. DOI: 10.1016/j.quascirev.2010.08.020

Anonymous (1827). *Zoology Journal Vol. 3, 140*