

MIOCENE PALEOENVIRONMENTAL RECONSTITUTION OF CHELAS (PORTUGAL) USING STABLE ISOTOPES FROM THE ENAMEL OF MOLARS FROM A PROBOSCIDEAN AND ASSOCIATED PALYNOMORPHS

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MASTER IN PALEONTOLOGY

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*“Changes comes like a little wind that ruffles the curtains at dawn, and it comes like
the stealthy perfume of wildflowers hidden in the grass ”.*

John Steinbeck

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"To be nobody-but-yourself, in a world which is doing its best, night and day, to make you everybody else, means to fight the hardest battle which any human being can fight; and never stop fighting."

E. E. Cummings

ABSTRACT

Paleoclimate reconstruction is essential for understanding the Earth's climate system, its dynamics, and the drivers of climate change. By examining past climate variability, it provides critical context for interpreting present-day climate trends and identifying key factors that shaped past climatic shifts. In this study, we reconstitute the palaeoenvironment of the Middle Miocene fossil sites of Quinta da Farinheira and Charneca (Chelas Valley and Lumiar, Lisbon, MN5, 13.7–16.0 Ma) using a multi-proxy approach. This includes biogeochemical analysis of stable isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) from proboscidean molar enamel and a paleobotanical investigation of site sediments to analyze local flora. These analyses are complemented by a systematic review of proboscideans from the area, housed at the Geological Museum of Lisbon, alongside a detailed description of previously undescribed fossils stored at NOVA University of Lisbon (UNL). These fossils include eleven molars, a vertebra, and an occipital cranial bone from large proboscideans.

Proboscidean records from the Miocene in Portugal, such as *Gomphotherium* sp., *Deinotherium* sp., and *Tetralophodon* sp., are numerous. Our findings indicate that most of the materials studied belong to *Gomphotherium angustidens*, with one exception, specimen FCT-DCT 4945 belongs to *Amebelodon* sp. *G. angustidens*, a species widespread in Europe during the Miocene. The combination of proxies suggests that the Middle Miocene climate in Chelas was subtropical and temperate, with mean annual temperatures (MAT) around 20°C. This aligns with the Mid-Miocene Climatic Optimum (MMCO), occurring between 17 and 15 Ma, a period marked by elevated global temperatures and atmospheric CO₂ levels. These findings provide valuable insight into how climate changes impact mammal faunas.

Keywords: Proboscidea, Middle Miocene, Paleoenvironment, Palynomorphs, Stable Isotopes, Mid-Miocene Climatic Optimum.

CONTENTS

1. INTRODUCTION	1
1.1. Geographical, geological, and chronological settings	2
1.2. Continental Paleoclimatic Analysis	4
1.2.1. Climatic settings: The Mid-Miocene Climate Optimum (MMCO)	4
1.2.2. Isotopic Climate Reconstruction: The Utility of Mammal tooth Enamel in Paleoenvironment Studies	6
1.2.3. Isotopic Abundance and Standard Notation: Understanding δ Values and Fractionation Factors	6
1.2.4. Isotopic Temperature and Precipitation Dynamics Reflected in $\delta^{18}\text{O}$ of Meteoric	7
1.2.5. Carbon Isotopic Composition and Diet Analysis	8
1.3. The Gomphotheriidae: state of the art	10
1.3.1. The Origins and Migration of <i>Gomphotherium</i> : A journey from Africa to Eurasia	10
1.3.2. Dental Structure and Evolutionary Adaptations of <i>Gomphotherium</i>	11
1.3.3. Systematics of <i>Gomphotherium</i>	12
1.3.4. <i>Gomphotherium</i> in Portugal and Nomenclature	13
2. MATERIALS AND METHODS	16
2.1. Materials	16
2.1.1. Fossil Materials	16
2.1.1.2. Comparison Material	17
2.1.1.3. Key Reference Materials	18
2.2. Methods	18
2.2.1. Systematics	18
2.1.2. Palynomorphs Materials	20
2.1.2.1. Sediments Collection	20
2.1.2.2. Field Work	21
2.1.2.3. Laboratory Procedures	23
2.2.3. Material for Isotopic Analysis: Gomphotheriidae teeth	25
2.2.4. Biochemistry Methods	25
2.2.4.1. Sample Preparation	25
2.2.4.2. $\delta^{18}\text{O}$ Analysis Methodology	27
2.2.4.3. $\delta^{13}\text{C}$ Analysis Methodology	29

3. RESULTS	31
3.1. Systematic Paleontology.....	31
3.1.1. Anatomical Description... ..	32
3.1.1.1. Upper Dentition.....	32
3.1.1.2. Lower Dentition.....	35
3.1.1.3. Cranial Skeleton.....	38
3.1.1.4. Postcranial Remains.....	39
3.1.2. Anatomical Comparison.....	41
3.1.2.1. Dentition... ..	41
3.1.2.2. Cranial Skeleton.....	46
3.1.2.3. Postcranial Remains	46
3.1.3. Biometrical Comparison.....	48
3.2. Results of Palynomorphs Analysis	52
3.3. Results of Biochemical Analysis.....	53
3.3.1. $\delta^{18}\text{O}$ and Mean Annual Temperatures	55
3.3.2 $\delta^{13}\text{C}$ VDPDB results and Paleoenvironment... ..	58
4. DISCUSSION	61
4.1. <i>Gomphotherium angustidens</i>: Updating the Systematics of the Mid-Miocene Proboscideans from Portugal.....	61
4.2. Palynomorph and $\delta^{13}\text{C}$: Vegetation Reconstruction.....	64
4.3. The $\delta^{18}\text{O}$ Climate and Temperature Estimations.....	65
5. CONCLUSION	66
REFERENCES.....	67
APPENDIX A.....	75
APPENDIX B.....	84

LIST OF FIGURES

Figure 1 – Map of Lisbon area.....	3
Figure 2 – Mid-Miocene Climate Optimum.....	5
Figure 3 –Oxygen Isotope Fractionation... ..	7
Figure 4 – Scheme of Isotope Fractionation	8
Figure 5 – Representation of C3 and C4 pathways.....	9
Figure 6 – Phylogeny of Proboscidea	11
Figure 7 – Morphological diversity of <i>Gomphotherium</i> genus.....	12
Figure 8 – Dental and Postcranial specimens to be describe.....	16
Figure 9 – Geological Museum specimens for comparison.....	18
Figure 10 – Scheme of dental nomenclature	20
Figure 11 – Teeth for sediments analysis.....	21
Figure 12 – Material for sediments analysis	21
Figure 13 – Coordinates of sites for Palynomorphs sampling.....	22
Figure 14 – Sediments sites.....	22
Figure 15 – Material for laboratory procedures.....	24
Figure 16 – Slides preparation... ..	24
Figure 17 – Material sent for Isotopic analysis	25
Figure 18 – Cutting the teeth for sampling	27
Figure 19 – Carbonates samples	27
Figure 20 – FCT-DCT 5362 description.....	33
Figure 21 – FCT-DCT 5359 description.....	33
Figure 22 – FCT-DCT 5364 description... ..	34
Figure 23 – FCT-DCT 5360 description... ..	34
Figure 24 – FCT-DCT 5358 description... ..	35
Figure 25 – FCT-DCT 4944 description... ..	35
Figure 26 – FCT-DCT 4942 description... ..	36
Figure 27 – FCT-DCT 5357 description... ..	36
Figure 28 – FCT-DCT 5361 description... ..	37
Figure 29 – FCT-DCT 5363 description... ..	37
Figure 30 – FCT-DCT 4943 description... ..	38
Figure 31 – FCT-DCT 5356 description... ..	39
Figure 32 – FCT-DCT 5366 description... ..	40
Figure 33 – FCT-DCT 4945 description... ..	41
Figure 34 – Museum specimens’ comparison.....	42
Figure 35 – Upper molars (M1) comparison... ..	42
Figure 36 – Upper molars (M2) comparison... ..	43
Figure 37 – Lower molars (m2) comparison.....	44
Figure 38 – Upper molars (M3) comparison... ..	45
Figure 39 – Lower molars (m3) comparison.....	45
Figure 40 – Cranial comparison... ..	46
Figure 41 – Postcranial comparison.....	47
Figure 42 – Scatterplot (M1) biometrical comparison... ..	48

Figure 43 – Scatterplot (M2) biometrical comparison.....	49
Figure 44 – Scatterplot (M3) biometrical comparison.....	50
Figure 45 – Scatterplot (m1) biometrical comparison.....	50
Figure 46 – Scatterplot (m2) biometrical comparison.....	51
Figure 47 – Scatterplot (m3) biometrical comparison.....	52
Figure 48 – Biochemistry values for FCT-DCT 4943.....	53
Figure 49 – Biochemistry values for FCT-DCT 4944.....	54
Figure 50 – Biochemistry values for FCT-DCT 4945.....	55
Figure 51 – Scheme of tooth grown to differentiate temperature	56
Figure 52 – <i>G. angustidens</i> diagnoses.....	62
Figure 53 – <i>G. subtapiroideum</i> diagnoses	62
Figure 54 – <i>G. steinheimense</i> diagnoses	63
Figure 55 – <i>G. sylvaticum</i> diagnoses.....	64
Figure 56 – Portugal Miocene climate fluctuations	65

LIST OF TABLES

Table 1 — Gomphotheriidae in Portugal	13
Table 2 — Classification of wear level in dental remains	19
Table 3 — Dental morphology of Gomphotheriidae.....	19
Table 4 — MAT estimated by 3 different equations.....	56
Table 5 — Carbon Isotopic results based on Domingos et al., 2012.....	58

GLOSSARY

Sieving

To separate particles or materials based on size. It involves passing a sample through a series of mesh screens with progressively smaller openings to isolate different size fractions.

Oxidation

Chemical process in which a substance loses electrons, typically to oxygen, resulting in an increase in its oxidation state.

ACRONYMS

Gn	Global Network of Isotopes in Precipitation
HCl	Hydrochloric acid
HF	Hydrofluoric acid
IUPAC	International Union of Pure and Applied Chemistry
Ma	Millions of years
MAT	Mean Annual Temperature
MCO	Miocene Climatic Optimum
MMC	Middle Miocene Cooling
MN	Neogene Mammals (lithostratigraphic zones)
MNHN	Muséum National d'Histoire Naturelle
r.M	Right upper first molar
r.m1	Right lower first molar
l.m2	Left lower second molar
l.M3	Left upper third molar
Dex	Right (tooth position)
Sin	Left (tooth position)
SMOW	Standard Mean Ocean Water
VPDB	Vienna PeeDee Belemnite

SYMBOLS

$\delta^{13}\text{C}$ Carbon isotope component of the carbonates.

$\delta^{18}\text{Oc}$ Oxygen isotope component of the carbonates.

INTRODUCTION

The Miocene epoch (23 – 5 Ma) represents a pivotal period for the study of the interaction between climatic changes and large mammals (megafauna). During this period, a significant migration of mammals occurred from Africa to Eurasia as a result of tectonic events that periodically disrupted the Paratethys barrier (Agustí & Antón, 2002). This event, designated as the “Proboscidean Datum Event” (Tassy, 1990), resulted in an increase of fauna and flora in Eurasia, with notable contributions from large mammalian species, such as the gomphothere *Gomphotherium angustidens* Cuvier 1817 and the mammutid *Zygodolophodon turicensis* Vacek, 1877 (Agustí & Antón, 2002). In Portugal, the first proboscidean record was discovered in Lisbon and described as *Tetrabelodon angustidens* Zbyszewski, 1949. Further revisions were conducted by Bergounioux et al., (1953); Mazo & Made, (2012).

The Miocene is also associated with significant changes in the global climate. The warmer periods during the Early and Middle Miocene had profound effects on vegetation, wildlife, and ecological dynamics. An understanding of how past climate changes influenced ecosystems can assist in the prediction and management of the impacts of ongoing and future climate change on biodiversity and ecosystem loss (Behrensmeyer et al., 1992). Tools such stable-isotope analysis of proboscidean enamel and the analysis of palynomorphs are fundamental for studying species dynamics, vegetation composition and the structure of the terrestrial landscape in space and time (Traverse, 2007).

Stable isotope analysis, particularly of carbon and oxygen isotopes, provides valuable insights into the paleoclimate of a particular region. The isotopic composition of enamel in extinct animals reflects the water they drank and the food they consumed. The bioapatite oxygen isotopic composition of precipitation, influenced by temperature and source (oceanic vs. continental) (De Winter et al., 2016). The carbon isotopic composition of the bioapatite, which informs the diet, is also of critical importance for the reconstruction of past

environmental conditions as different plants have distinct carbon isotope ratios, due to their different photosynthetic C3 and C4 pathways (Fry, 2006; Koch, 2007; De Winter et al., 2016). The analysis of carbon isotopes in enamel allows for the assessment of changes in vegetation types and their abundance over time (Fry, 2006). Mammal tooth enamel, due to its high resistance, is an ideal material for paleoenvironmental reconstructions. Furthermore, palynomorph analysis (pollen grains and spores) provides information on changes in vegetation types, ecosystem composition and vegetation dynamics over time (Halbritter et al., 2018).

In this study, previously undescribed gomphothere remains from the Middle Miocene (MN5, 16.0–13.7 Ma) of the Quinta da Farinheira and Charneca sites (Chelas Valley and Lumiar, Lisbon) were analysed. These remains are housed at the Department of Earth Sciences of NOVA School of Science and Technology.

The study is divided into two parts: (1) The description and comparison of the university's fossil specimens to accurately identify the proboscidean species, and (2) the laboratory analysis of (i) isotopes in the enamel of the molars, conducted in collaboration with laboratories in Spain and Brussels, along with the examination of (ii) palynomorphs in the sediment around the molars for paleoenvironmental reconstruction.

The principal objective of this research is to identify the species of the fossils through detailed description and comparison, to ascertain their characteristics and phylogenetic relationships, and to analyze isotopes in the enamel and associated palynomorphs in order to answer the question: How were past climate conditions and vegetation patterns in continental Lisbon during the Middle Miocene, a time of warmer conditions?.

1.1. Geographical, geological, chronological settings

Since the 1940's, the main authors of Portuguese Miocene geological and paleontological publications were Georges Zbyszewski, Miguel Telles Antunes, João Pais, J. C. Berkeley-Cotter, Pierre Mein, among others. The most frequently employed biostratigraphy for the Neogene of Europe is the MN units, or Neogene Mammal units, ranging from the oldest (MN 1) to the youngest (MN 17). They were introduced by Mein (1975) and updated several times (eg. Mein, 1990; De Bruijn et al., 1992; Mazo & Van der Made, 2012). The remains from this study come from the Middle Miocene (MN5, 13.7–16.0 Ma) of the Quinta da Farinheira and

Charneca sites within the Lower Tagus Basin (Chelas Valley and Lumiar, Lisbon, Figure 1). The Lower Tagus Basin flows through Lisbon and has played a significant role by shaping the geology of the region, depositing alluvial sediments, such as sands, silts, clays, along the floodplain (Pais, 2010). The Lisbon Formation (Lisbon Fm.) is a prominent geological unit in the region, composed of clay and sandy sediments. Those sediments were, primarily, formed in marine and coastal environments (Pais et al., 2010). The Lisbon Fm. includes a diverse range of environments, such as estuaries, lagoons, and shallow marine settings. It comprises sedimentary deposits from the Cenozoic, spanning approximately 66 to 2.6 Ma (Vieira et al., 2009).



Figure 1. Map of the area of Lisbon, specifically encompassing the fossil sites from the Middle Miocene (MN5, 16.0–13.7 Ma) at Quinta da Farinheira and Charneca within the Lower Tagus Basin (Chelas Valley and Lumiar, Lisbon). These sites are integral to the study as they provide valuable vertebrate fossils for analysis. The map scale is set to 1 km, allowing for precise localization and an accurate representation of the spatial distribution of these important fossil sites. A. Chelas site. B. Three sites from Chelas where was collected samples for palynology.

Chelas's formations during Miocene, defined by Cotter (1956), are composed by sands, sandstone, clay, and limestone. The unit of Chelas is Vb, belonging to the MN5 and corresponding with the Langhian stage (~15.9-16.1 Ma) (Cotter, 1956; Antunes & Ginsburg,

2003). There are both continental and marine records at Chelas, which can be explained by the transgressions and regressions of the sea.

As evidenced by for the known botanical and palynological from the Miocene of the Lower Tagus Basin (23 - 5.3 Ma), the region was home to a diverse array of flora, including representatives from the Pinaceae, Malvaceae, Sapotaceae, Engelhardia, Arecaceae, Castanea/Castanopsis, Engelhardia, Magnolia, Sapotaceae, Symplocos, these plant communities provided an attractive habitat for the appearance and growth of fauna, including proboscideans, which are the subject of this study (Vieira et al., 2009).

1.2. Continental Paleoclimatic Analysis

1.2.1 Climatic Settings: The Mid-Miocene Climate Optimum MMCO

During the Miocene, Eurasia went through some significantly tectonic movements that resulted in the rifting of East Africa and the union of the African-Arabian plate with Eurasia (Behrensmeyer et al. 1992), the union of the continents of Africa and Eurasia caused interruption and contraction of the Tethys Sea, the Paratethys barrier, which isolated Western Europe from the exchange of flora and fauna, was periodically disrupted, allowing the migration of animals (Agustí & Antón. 2002). This union enabled more exchanges of flora and fauna between Africa and Eurasia creating a large increase of fauna and flora that was maintained even with the warm climate during the Miocene Climate Optimum (Behrensmeyer, et al. 1992).

The isotopic records ($\delta^{18}\text{O}$), indicate that from the latter part of the Oligocene (27 Ma) the Earth was covered by ice sheets. After a brief but intense glacial period (lasting 200 ka) at the Oligocene-Miocene boundary (23 Ma), known as the Mi-1 event (Zachos et al., 2001), the Early Miocene saw a warming trend that reduced the extent of Antarctic ice. From that moment until the Middle Miocene (15 Ma) global ice volume remained low and bottom water temperatures trended slightly higher. This warm phase peaked in the late Middle Miocene (17 to 15 Ma) and was followed by a gradual cooling and re-establishment of a major icesheet in Antarctica.

The Mid-Miocene Climatic Optimum or Miocene Climate Optimum (MMCO or MCO) represents the warmest interval since the Eocene (Zachos et al., 2001; Zachos et al., 2008; Scheiner et al., 2023, Figure 2). In this context, the climate in European mid-latitudes was mainly subtropical as inferred from isotopic data values (Miller et al., 1991; Zachos et al., 2001).

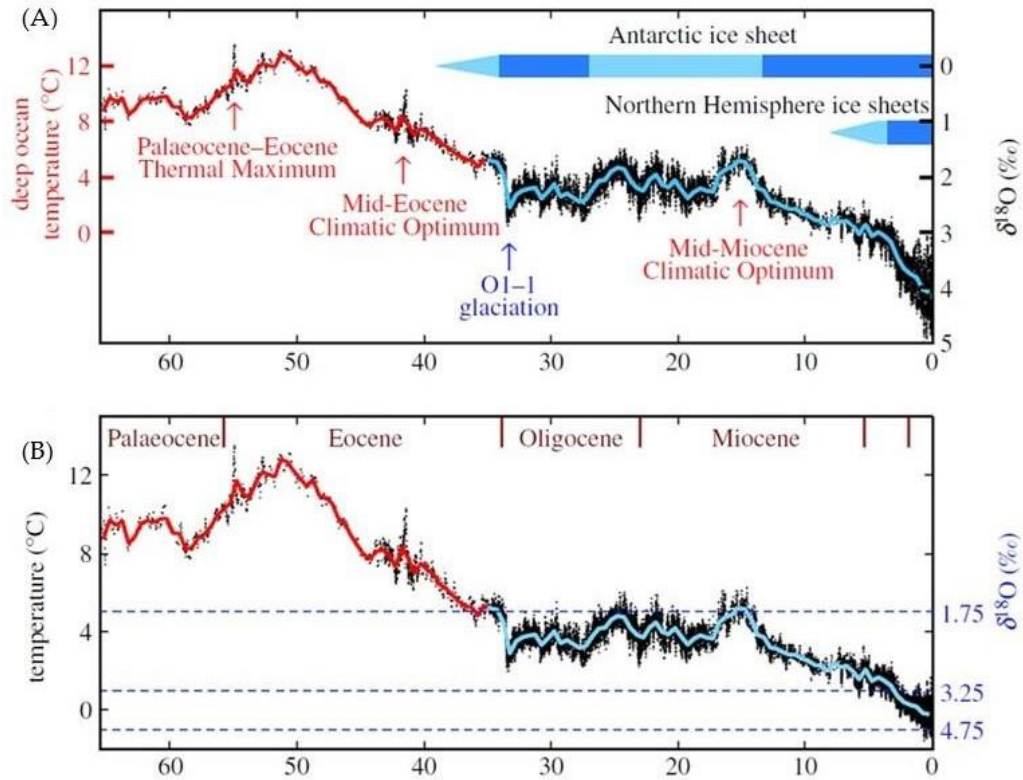


Figure 2. Mid-Miocene Climatic Optimum. (A) Global deep ocean $\delta^{18}\text{O}$ from Zachos et al. and (B) estimated deep ocean temperature. Black data points are five-point running means of the original temporal resolution; red and blue curves have a 500 kyr resolution (Zachos et al., 2001).

During the Miocene, Portugal experienced several marine regressions and transgressions, as evidenced by the diverse marine and terrestrial fossil records stored in various museums, including the Geological Museum of Lisbon, which was visited and consulted for this study. The Miocene climate in Portugal underwent several fluctuations, significantly impacting both flora and fauna. Previous studies indicate that, during Va2 (Lower Miocene stratigraphic unit) times in the Lower Tagus Basin, warm tropical to subtropical and humid conditions prevailed. However, by Vb (Middle Miocene stratigraphic unit) times, palaeobotanical evidence suggests a shift to much drier conditions, although the climate remained subtropical (Antunes & Ginsburg, 2003).

1.2.2 Isotopic Climate Reconstruction: The Utility of Mammal Tooth Enamel in Paleoenvironmental Studies

Mammal tooth enamel serves as a valuable tool in the realm of paleoenvironmental studies due to its exceptional resistance to diagenesis, the process by which organic materials transform into fossils. Comprised primarily of bioapatite $\text{Ca}_{10}(\text{PO}_4, \text{CO}_3)_6(\text{OH}, \text{F})$, mineral rich in calcium phosphate, tooth enamel preserves remarkably well over geological time scales (Zachos et al., 2001). This durability allows scientists to extract and analyze oxygen and carbon isotopic data embedded within the enamel matrix. Through isotopic analysis, researchers can reconstruct past environmental conditions with a high degree of accuracy (De Winter et al., 2016; Koch, 1998). These records offer insights into factors such as temperature, precipitation, and vegetation structure, providing a window into the Earth's climatic history. Furthermore, the sub annual resolution provided by tooth enamel records enables researchers to discern seasonal variations in environmental parameters, offering a nuanced understanding of past ecosystems (De Winter et al., 2016). Overall, the utility of mammal tooth enamel in paleoenvironmental studies lies in its ability to act as a reliable and informative archive of past environmental conditions, facilitating the reconstruction of Earth's paleoclimate.

1.2.3 Isotopic Abundance and Standard Notation: Understanding δ Values and Fractionation Factors

Isotopic abundances are reported as the deviation in parts per thousand (‰) in the isotopic ratio of a standard, using the notation $\pm$, where $\delta X = [(R\text{-Sample} / \text{Subtract}) - 1] \times 10^3$. R-Sample and Subtract are the ratios of the highest and lowest mass isotopes in the sample and standard, respectively (Koch, 1998). The commonly used standards for $^{13}\text{C}/^{12}\text{C}$, and $^{18}\text{O}/^{16}\text{O}$ ratios are marine carbonate, PeeDee Belemnite (PDB) and Standard Mean Ocean Water (SMOW), respectively. Positive δ values indicate enrichment in the higher mass isotope relative to the standard, while negative δ values indicate impoverishment. Isotopic fractionation between two substances a and b is described using either a difference value (Δ), where $\Delta X_{a-b} = \delta X_a - \delta X_b$, or a fractionation factor (α), where $\alpha_{a-b} = (\delta X_a + 1000) / (\delta X_b + 1000)$. The two fractionation measures are related by $\ln \alpha_{a-b} \approx \Delta X_{a-b}$ (Hoefs, 1997; Koch, 1998).

1.2.4 Isotopic Temperature and Precipitation Dynamics Reflected in $\delta^{18}\text{O}$ of Meteoric Water

The isotopic composition of oxygen-18 ($\delta^{18}\text{O}$) in meteoric water serves as a valuable proxy for understanding temperature and precipitation dynamics. The relationship between Mean Annual Temperature (MAT) and oxygen isotopic ratios in enamel is rooted in the principle of isotopic fractionation, whereby the distribution of isotopes within a compound is influenced by environmental conditions. Specifically, the oxygen isotopic composition of enamel reflects the isotopic composition of ingested water during tooth formation, which in turn is influenced by temperature. Warmer temperatures generally lead to higher rates of evaporation, resulting in increased enrichment of the heavier oxygen isotope ($\delta^{18}\text{O}$) in the remaining water (Figure 3). Consequently, organisms living in warmer climates tend to incorporate more $\delta^{18}\text{O}$ into their tissues, including tooth enamel, compared to those in cooler climates. This relationship is often expressed as a linear correlation between the $\delta^{18}\text{O}$ values of enamel and mean annual temperature, where higher $\delta^{18}\text{O}$ values correspond to higher temperatures.

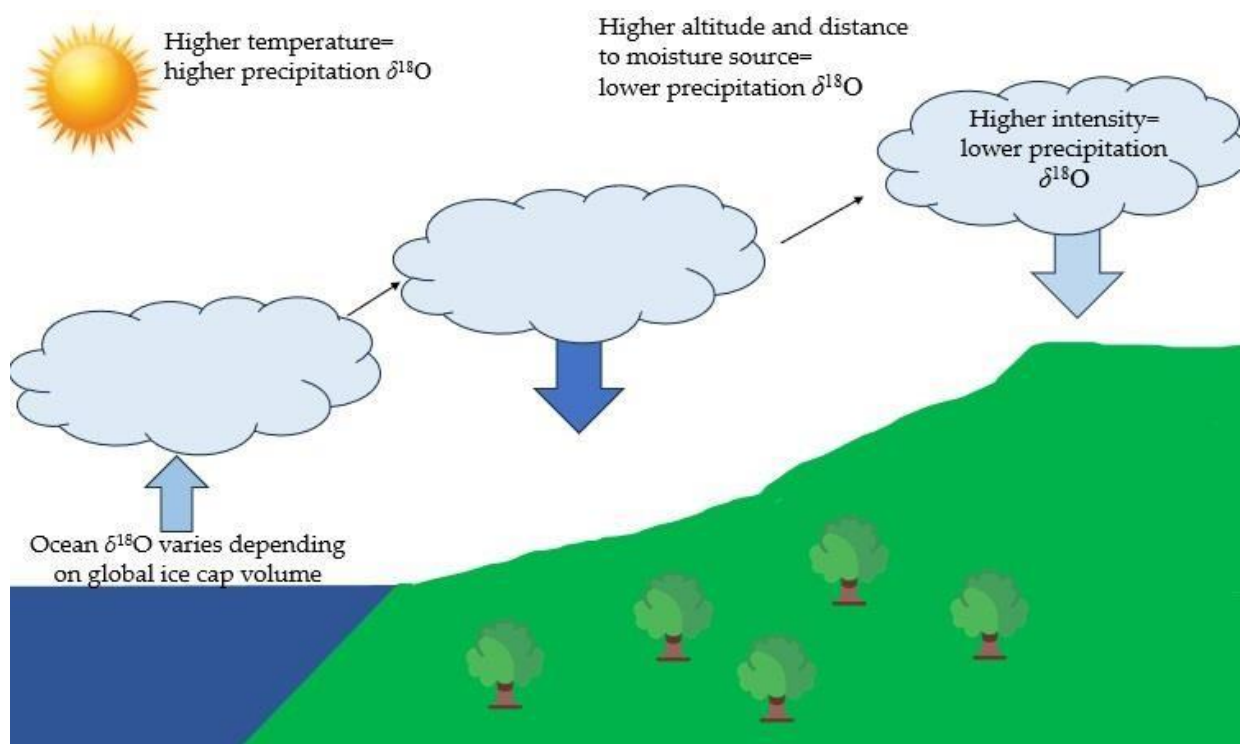


Figure 3. Representation of factors causing oxygen isotope fractionation of atmospheric and leaf water (light water: low $\delta^{18}\text{O}$, heavy water: high $\delta^{18}\text{O}$, following Janssen, 2017).

In temperate regions like Portugal, Mean Annual Temperatures (MAT) and mean annual $\delta^{18}\text{O}$ values of meteoric water show a strong positive correlation. The ratio between MAT and $\delta^{18}\text{O}$ at sites with MAT between 0° and 20°C is $\sim 6.0\text{‰}$ per degree Celsius ($r > 0.8$) (Rozanski et al., 1993). The water in plants represents a large fraction of the water ingested by some terrestrial animals. The $\delta^{18}\text{O}$ value of plant water is similar to that of surface water, except for leaf water, which is enriched in $\delta^{18}\text{O}$ due to evapotranspiration (Figure 4). The enrichment is greater in very hot and dry conditions (Koch, 1998).

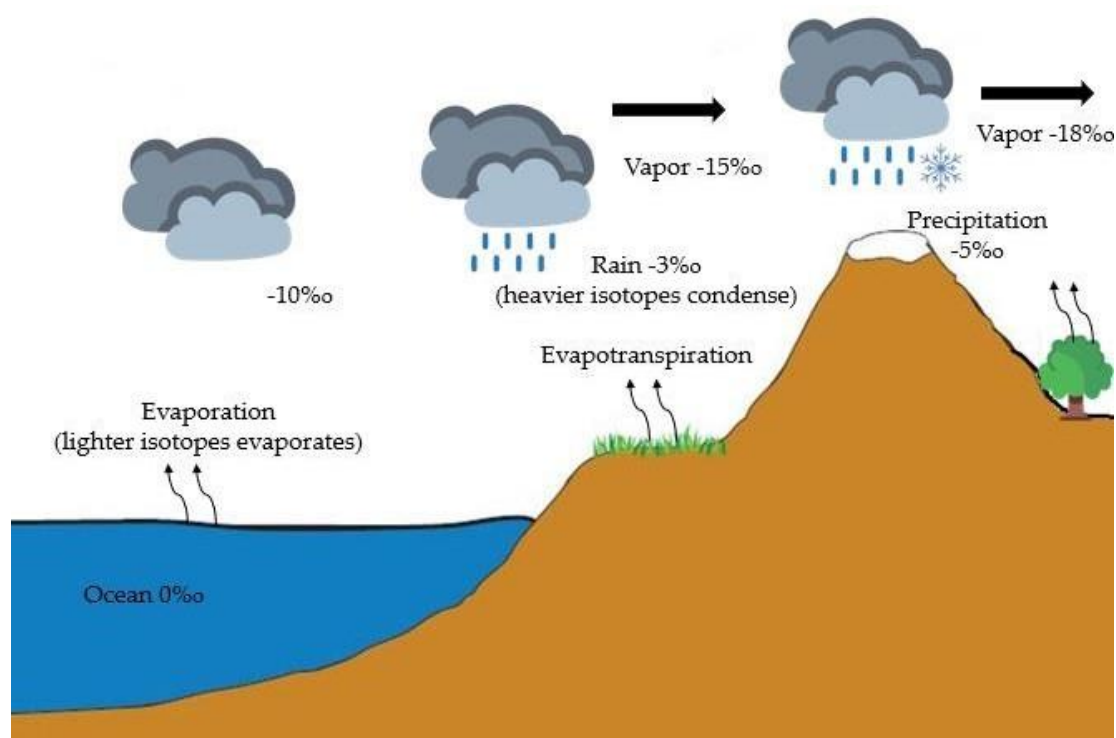


Figure 4. A schematic diagram of the isotope fractionation with the effects of evaporation and precipitation, following Kumar, 2013.

1.2.5 Carbon Isotopic Composition and Diet Analysis

The analysis of carbon isotopes in enamel offers a valuable approach to understanding the dietary preferences and ecological adaptations of ancient terrestrial animals. This method exploits the distinctive carbon isotopic signatures exhibited by different plant types, namely C_3 and C_4 photosynthesis pathways (Figure 5), in order to infer the dietary composition and foraging behaviour of animals (Traverse, 2007). C_3 plants, including trees, shrubs, and many cool-season grasses, employ the C_3 photosynthetic pathway, which incorporates carbon dioxide (CO_2) into organic compounds via the Calvin cycle. Typically, these plants exhibit $\delta^{13}\text{C}$ values ranging from -35‰ to -22‰ . In contrast, C_4 plants, such as warm-season grasses and

certain agricultural crops, including maize and sugarcane, employ the C4 photosynthetic pathway. This pathway initially fixes CO₂ into a four-carbon compound before entering the Calvin cycle. C4 plants exhibit $\delta^{13}\text{C}$ values that range from -16‰ to -9‰ (Koch, 1998; Domingo et al., 2012).

When animals consume plants as part of their diet, the carbon isotopic composition of the ingested vegetation is recorded in their tissues, including enamel. Animals that predominantly consume C3 plants will exhibit enamel with lower $\delta^{13}\text{C}$ values, reflecting the isotopic signature of their plant-based diet. Conversely, animals that consume a diet rich in C4 plants will display enamel with higher $\delta^{13}\text{C}$ values (Fry, 2006; Koch, 1998; Domingo et al., 2012).

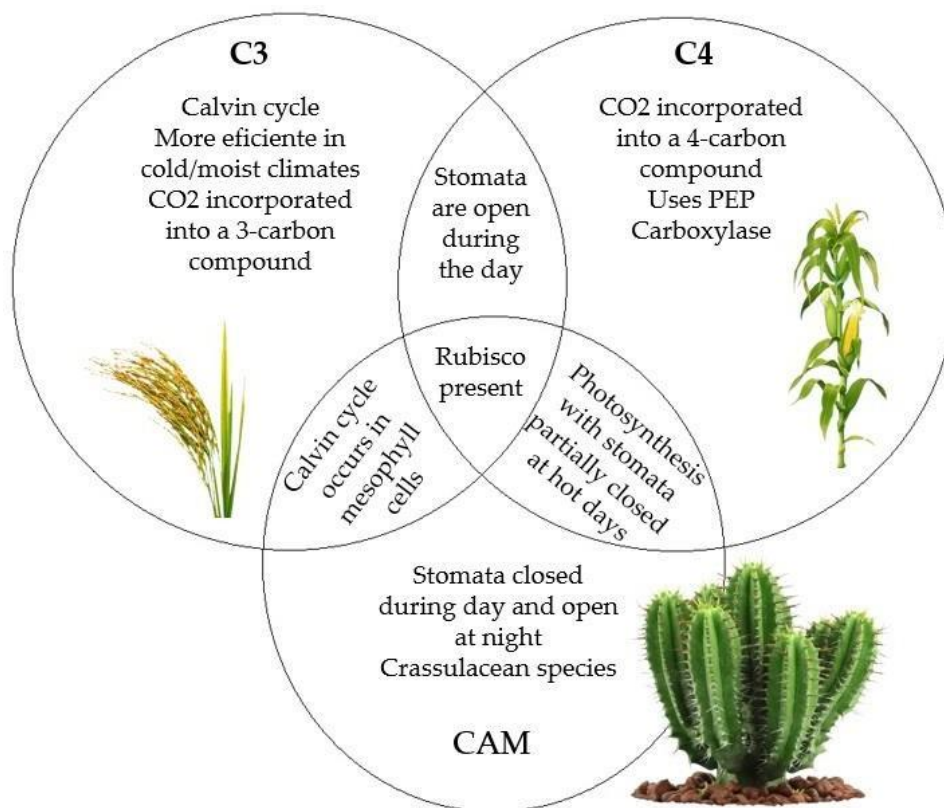


Figure 5. Representation of C3, C4 and CAM pathways.

By analyzing the $\delta^{13}\text{C}$ values preserved in enamel, researchers can reconstruct the dietary habits of ancient animals and infer the types of plants they consumed. This information, in turn, offers insights into past vegetation types and the ecological conditions of ancient ecosystems. For instance, the prevalence of animals with enamel enriched in C4-derived carbon suggests the dominance of C4 vegetation in the environment (Fry, 2006). Conversely,

animals with depleted $\delta^{13}\text{C}$ values in their enamel indicate a diet primarily consisting of C3 plants (De Winter et al., 2016; Koch, 1998; Domingo et al., 2012).

Furthermore, variations in the $\delta^{13}\text{C}$ values of enamel within and among populations can provide additional insights into dietary specialization, seasonal variations in resource availability, and ecological adaptations. By examining isotopic patterns across different individuals and species, researchers can elucidate the intricate interplay between environmental factors, dietary choices, and evolutionary pressures that have shaped the ecology of past ecosystems (De Winter et al., 2016; Koch, 1998; Domingo et al., 2012).

1.3. The Gomphotheriidae: state of the art

Gomphotheriidae is a family within the order Proboscidea, comprising prehistoric elephant-like mammals known as gomphotheres characterized by a number of distinctive features, including tusks and shovel-shaped lower incisor teeth (Shoshani & Tassy, 1996). These animals existed during the Miocene and Pliocene epochs, with some species surviving into the Pleistocene (Gohlich, 1999).

Gomphotheriidae is considered a paraphyletic stem group of Proboscidea, representing an evolutionary precursor to modern elephants. Gomphotheres were very diverse in terms of species and geographic distribution. They were found across various regions of the world during the Miocene, with fossils discovered in North America, South America, Europe, Africa, and Asia. This global distribution suggests their ability to adapt to diverse environments and ecological niches (Agustí & Antón, 2002).

1.3.1 The Origins and Migration of *Gomphotherium*: A Journey from Africa to Eurasia

The hypothesis is that the genus *Gomphotherium* originated in Africa during the late Oligocene-Early Miocene period. The earliest known fossils of *Gomphotherium*, dating back to the Early Miocene, have been discovered in Africa (Tassy, 1990). Approximately 19 Ma ago, *Gomphotherium* migrated to Eurasia via the *Gomphotherium* landbridge, where it underwent a rapid diversification, reaching its peak diversity during the Early-Middle Miocene (Agustí & Antón, 2002).

It has been postulated that *Gomphotherium* served as the ancestor of later gomphotheres genera, including the "tetralophodont gomphotheres," such as *Tetralophodon*, which may have given rise to stegodontids and elephantids (Tobien, 1973). The final European species of *Gomphotherium* became extinct approximately 10 Ma at the beginning of the Late Miocene, while the final North American species vanished from the continent around 5 Ma at the onset of the Pliocene (Mazo & Van der Made, 2012).

1.3.2 Dental Structure and Evolutionary Adaptations of *Gomphotherium*

Diagnostic features of *Gomphotherium* include the presence of upper and lower tusks, bunodont cheek teeth and molars with at least three lophs/lophids ("trilophodont"), a simple trefoil wear pattern, rare accessory cusps in the valleys, and anterior and posterior central conules mostly present on the pretrites and posttrites, without anancoidy, being illustrated (Figure 6). They are characterized by a long skull, and straight elongated mandible (Agustí & Antón, 2002).

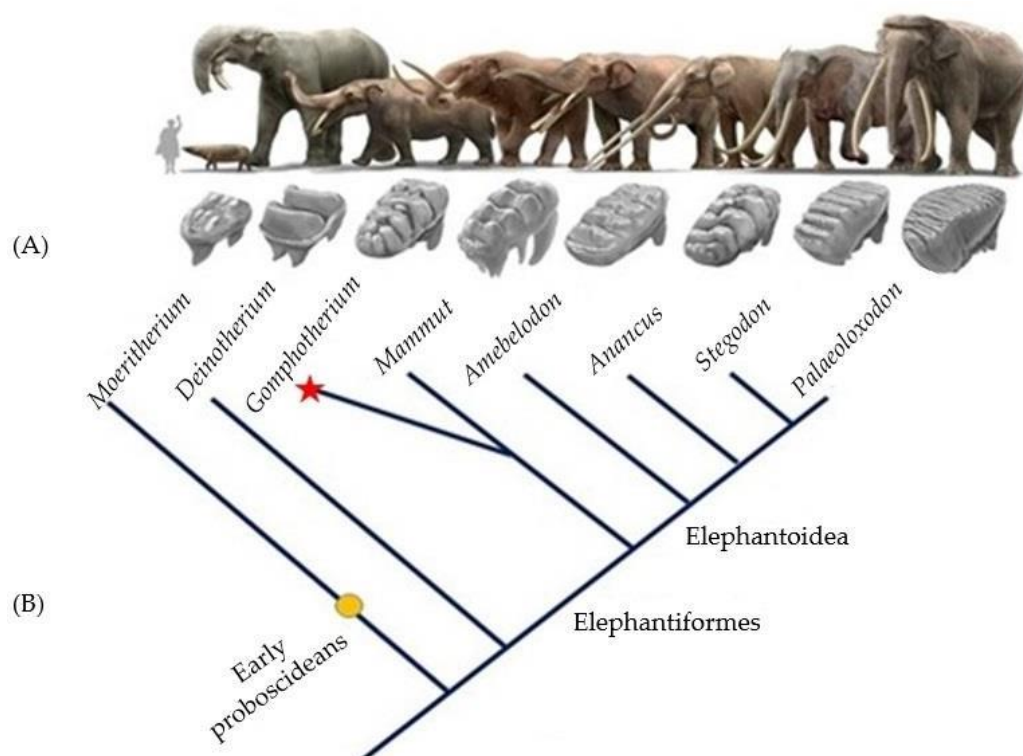


Figure 6. (a) Life reconstruction of the most representative genera of the order Proboscidea, with their respective upper m3 (molars not to scale); (b) Internal phylogeny of Proboscidea (adapted from Shoshani, 1998; Cozzuol et al., 2012; Cantalapiedra et al., 2021).

As mentioned above, their molars are composed of loph(id)s. Each loph is filled with dentin and surrounded by cementum on their roots. During the tooth formation the enamel grows from the anterior portion of the crown to the posterior portion loph-by-loph and rootward until it reaches the junction between crown and root. Proboscideans have cycles of tooth eruption throughout their lives, and old teeth are replaced by new teeth that grow in from the back of the mouth and move forward to push out the old ones, until the third/last molar (Lee et al., 2012).

1.3.3 Systematics of *Gomphotherium*

Gomphotherium was first described by Burmeister in 1837. Posteriorly in 1857, Falconer differentiated Mastodonts -in which he included *Gomphotherium* by the systematics of the molars, dividing them into Trilophodonts and Tetralophodonts according with the number of loph(s) and lophids dos molars, three and four respectively (Tobien, 1973). Later was described by Shoshani & Tassy (1996) that morphologically *Gomphotherium* is a genus with more than 12 species considered valid, while proposed four phylogenetic groups of *Gomphotherium* (Wang et al. 2017, Figure 7).

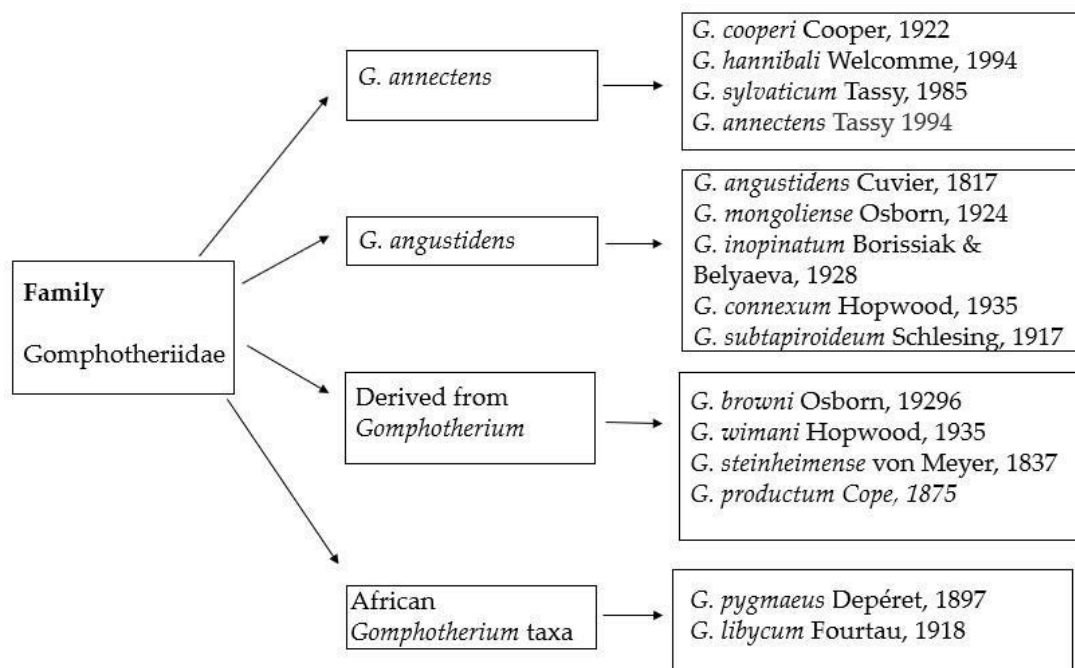


Figure 7. Species diversity within the genus *Gomphotherium*, which includes more than 12 valid species. It also depicts the four phylogenetic groups proposed for *Gomphotherium*, highlighting their evolutionary relationships and distinctions (Shoshani & Tassy, 1996; Wang et al., 2017).

1.3.4 *Gomphotherium* in Portugal and its Nomenclature

The sedimentary record of Lisbon is correlated with the first arrivals of *Gomphotherium* and *Deinotherium* in Europe (Mazo & Van der Made, 2012). There is an abundance of proboscidean material from the Miocene of Portugal described in various studies by Antunes and Zbyszewski during the 20th century most of them being recorded in Lisbon (see Table 1).

Table 1. Comprehensive list of Gomphoteriidae identified from the Miocene deposits in Lisbon.

Family	Genus/Species	Locations	References
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Mammutidae	<i>Zygodolophodon pyrenaicus</i> Mayet, 1908	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Serridentinus</i> Osborn, 1923	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Zygodolophodon</i> Vacek, 1877	Lisbon	Zbyszewski,

			1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Serridentinus</i> Osborn, 1923	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Gomphotheriidae	<i>Gomphotherium</i> syn. <i>Trilophodon</i> Falconer & Cautley, 1846	Lisbon	Zbyszewski, 1949
Mammutidae	<i>Zygodolophodon</i> Vacek, 1943	Lisbon	Zbyszewski, 1949
Gomphotheriidae	Indet.	Santarém	Antunes & Mein, 1977
Gomphotheriidae	Indet.	Santarém	Antunes & Mein, 1977
Gomphotheriidae	<i>Gomphotherium angustidens</i> Burmeister, 1937	Leiria	Antunes & Mein, 1981

In Portugal, this genus of proboscideans received many names during these past years, and there are a lot of materials still ascribed as *Serridentinus lusitanicus* and *Trilophodon olisiponensis* (Bergounioux et al., 1953; Ginsburg & Antunes, 1966. However, all these taxons are no longer valid, and this recent review was strongly needed. In the literature *Gomphotherium* had already been named *Mastodon*, *Trilophodon* and *Serridentinus*:

- *Mastodon angustidens* Cuvier, 1817 according with The International Commission on Zoological Nomenclature *Mastodon* is a synonym of *Mammut* Blumenbach, 1799 (Tobien, 1973).

- *Trilophodon* Falconer, 1857, *Trilophodon olisiponensis* Zbyszewski, 1949 it is a junior synonym of *Gomphotherium angustidens* (Shoshani & Tassy, 1996; Gohlich, 1999; Tassy, 2013).
- *Serridentinus* Osborn, 1923 in Portugal, some specimens were identified originally as *Serridentinus lusitanicus* because of its complex molar morphology but Tobien, 1972 included that genus in *Gomphotherium*. The “serridentinoid” morphotype of *Gomphotherium*, with many additional conelets, is abundant in MN5, where it appears along with typical *G. angustidens* (Mazo & Made, 2012).

MATERIALS AND METHODS

2.1 Materials

2.1.1 Fossil Materials

The materials examined in this study consist of eleven isolated cheek teeth, one vertebra and one occipital bone (Figure 8) of adult's individuals. These specimens are housed within the Department of Earth Sciences of FCT-NOVA (Caparica, Portugal). Although collected decades ago they have not been previously described. The majority of the proboscidean specimens selected for analysis originated from Chelas and Charneca, sites located within the Vb subdivision, corresponding to the Middle Miocene epoch (~15.9-16.1 Ma, MN5), to compare those specimens the fossil proboscidean materials from Geological Museum of Lisbon were consulted as well as the known literature specially by Wang et al., 2017 (Figure 9). For the stable isotope analysis, sediments from the enamel of two distinct cheek teeth specimens (FCT – DCT 4945 and FCT – DCT 4944) were collected, while the palynomorph analysis was conducted on sediments from the layers of Chelas (see Figure 14).

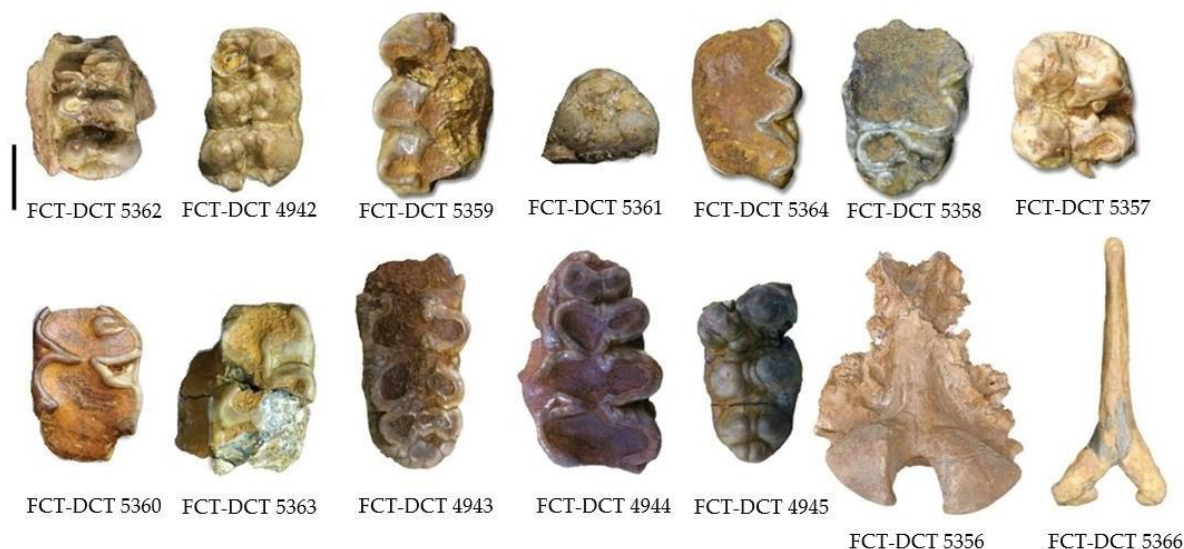


Figure 8. Dental and postcranial specimens of Gomphotheriidae described. These specimens are housed at the

2.1.1.2 Comparison Materials

The majority of the material chosen for comparison in this study is curated by the Geological Museum of Lisbon (Lisbon, Portugal) (Figure 9). This institution was selected due to its comprehensive collection of proboscidean material from the same geological age and area under investigation, which ensured both appropriateness and availability. The museum houses several proboscidean specimens and to facilitate precise identification and comparison, the most worn specimens were discarded. Notably, a significant portion of these teeth belongs to the genus *Gomphotherium*, making it highly useful for the comparative analysis.

Additional specimens utilized in this research were sourced from various scholarly papers on Eurasian proboscideans. These include influential works such as Tobien (1973), Tassy (2013, 2014), Göhlich (2010), Wang et al. (2017), among others. These publications provided a diverse array of proboscidean specimens, enriching the comparative framework and ensuring a broad, comprehensive analysis of the teeth. The integration of this literature allowed for a more robust and thorough examination of the material, contributing significantly to the study's overall findings and conclusions. The foundational diagnosis selected for this study was developed by Wang et al. (2017). According to their research, it is possible to identify species within the *Gomphotherium* genus by examining specific dental characteristics such as the shape of their molars, the presence of dental accessories, and particularly the spacing between interlophs and interlophids. Wang et al. (2017) emphasized that most *Gomphotherium* species typically possess low-crowned molars. This morphological criterion is crucial for distinguishing between species within the genus and serves as the main analytical basis for this study.



Figure 9. Geological Museum of Lisbon selected teeth for genus and species comparison. *Amebelodon* sp. (10648); *G. angustidens* (10612); *Zygolophodon* sp. (10651); *Tetralophodon* sp. (10640); *Serridentinus lusitanicus* (10625; 7912; 7951); *Trilophodon olisiponensis* (7970). Scale bar 50mm.

2.1.1.3 Key Reference Materials

It was consulted the reference literature on proboscideans to obtain data for comparative analysis such as Bergounioux et al. (1953), Antunes & Mazo (1983), Mazo & Van der Made (2012), Wang et al., (2017), Gohlich (1999; 2010) among others for *Gomphotherium*'s morphology and its spread in Europe, the dental etymology used was Tassy (1990) and Wang et al. (2017), the pattern of the level of wear by Simpson & Paula-Couto (1957), for the occipital bone and the vertebra, it was, respectively, follow by Van der Merwe et al. (1995) and Ferretti (2010). The skull and mandible of the African elephant (*Loxodonta africana*). For the palynomorphs literature it was consulted Traverse (2007), Halbritter et al. (2018), Barrón et al. (2010) and the stable isotopes Fry (2006), De Groot (2004) and others.

2.2. Methods

2.2.1 Systematics

Thirteen gomphotheres remains were described and compared based on the nomenclature

on (Tassy, 1990; 2013; Wang et al., 2017) (Figure 10), all measurements were taken by using calipers (mm) and all the pictures are in ventral view, the level of wear were based according to Simpson & Paula-Couto (1957) as it shows in the Table 2.

Table 2. Classification of wear levels in *Gomphotherium* remains, based on the criteria established by Simpson & Paula-Couto (1957).

Level of wear	Stage
0	Tooth formed but not erupted
0+	Erupted but unworn
1	Wear on anterior lophids only
2	Light wear on all lophids
3	Extensive wear but pattern still clear
4	Severe wear, pattern partly or wholly obliterated

To clarify the description of the remains, an identification scheme was drawn up for the nomenclature of dental morphology (Table 3; Figure 10).

Table 3. Dental morphology following (Tassy, 1990; 2013), Wang et al., 2017).

Acronymus	Meaning
Ca	Anterior cingulum
CuP	Main cusp
CP	Posterior cusp
CL	Labial cingulum
CLi	Lingual cingulum
CA	Anterior cusp

M	Mesoconelet
M/M	Medial mesoconelet

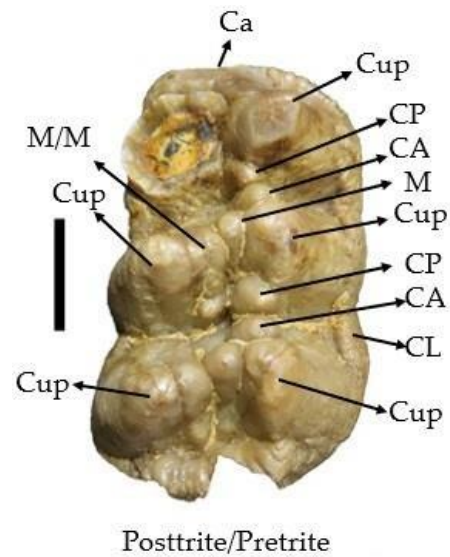


Figure 10. Dental morphology and nomenclature of Gomphothere molars following Tassy, (1990; 2013), and Wang et al. (2017).

2.1.2 Palynology Materials

2.1.2.1 Sediments collection

The sediments were collected at Chelas, place where the teeth (FCT-DCT 4944; FCT-DCT 4943) utilized for the isotopic analysis were labelled as found (Figure 11), two pickaxes, gloves and plasticbags were used to collect the sediment at the site (Figure 12).

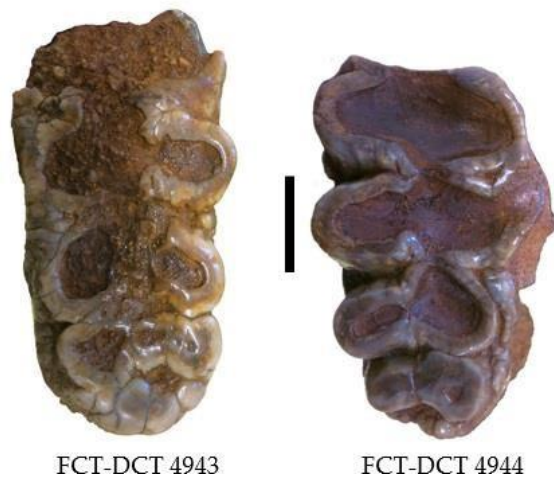


Figure 11. Teeth used to analyze the surrounding sediment matrix. Scale bar: 50mm.



Figure 12. Material used for collecting sediments from the layers of Chelas region.

2.1.2.2. Field Work

The main objective of the sampling phase, in addition to collecting the sediment, is to record the geological characteristics of the site. The samples were collected in three different sites

(Figure 13) and organized into three bags, properly labelled, according to the place where they were collected (Figure 14).

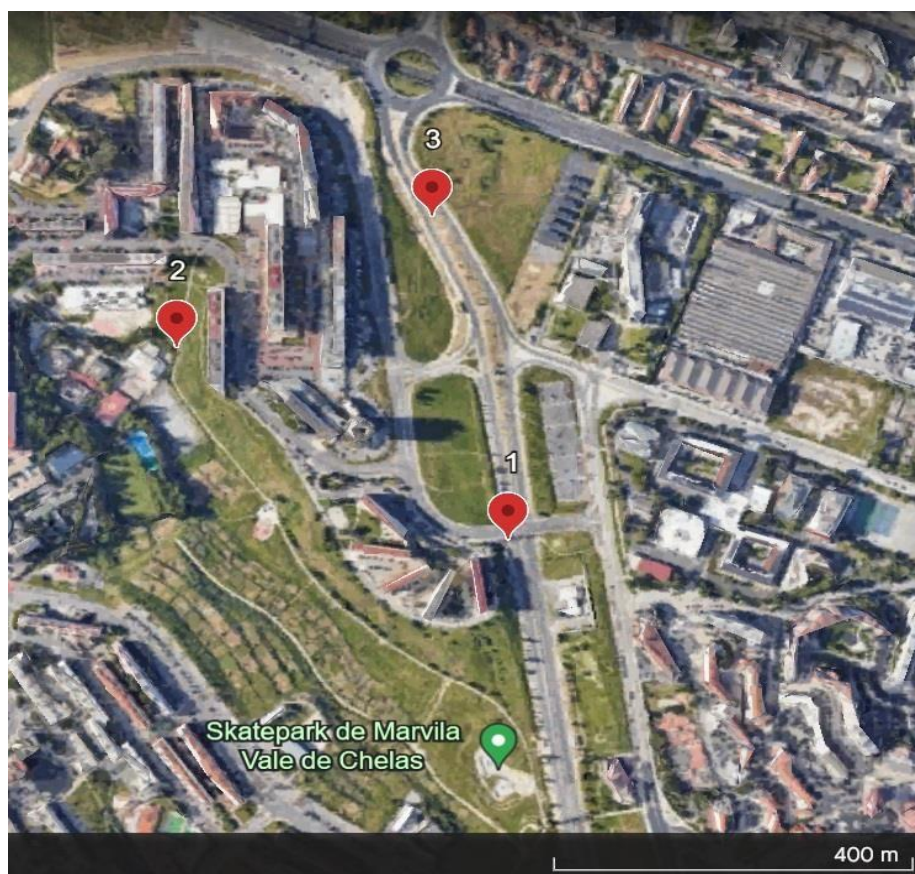


Figure 13. Sites of the palynomorphs sampling. Sample 1: $38^{\circ}45'17.9''\text{N}$ $9^{\circ}07'10.5''\text{W}$ (in front of the gas station); Sample 2: $38^{\circ}45'28.9''\text{N}$ $9^{\circ}07'25.6''\text{W}$ (Chelas Valley); Sample 3: $38^{\circ}45'38.0''\text{N}$ $9^{\circ}07'16.2''\text{W}$ Av. Santo Contestável.

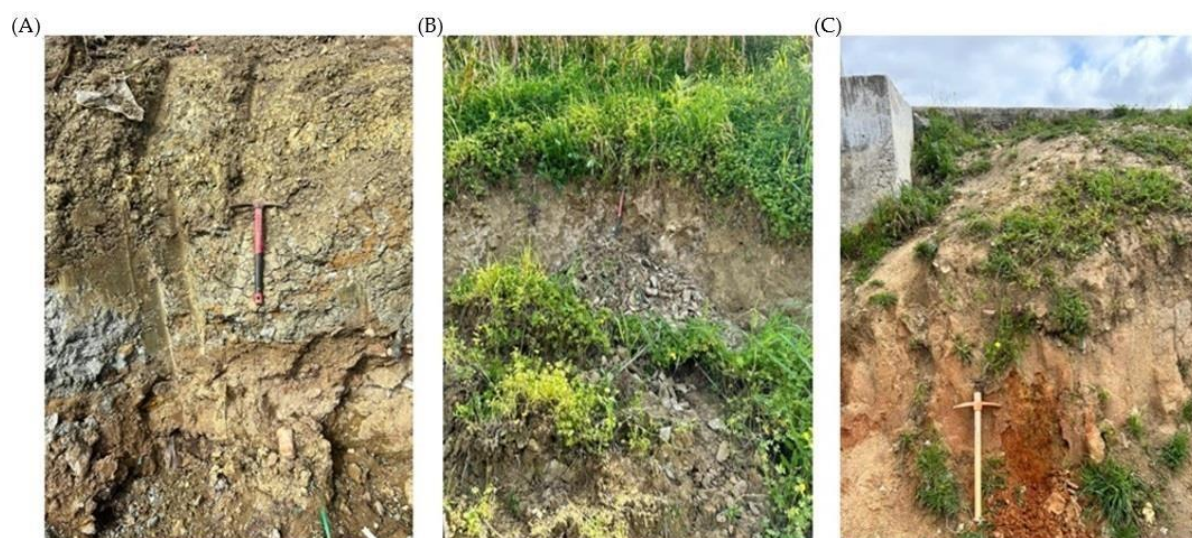


Figure 14. Sediments sites. A. First section $38^{\circ}45'17.9''\text{N}$ $9^{\circ}07'10.5''\text{W}$ (in front of the gas station); B. $38^{\circ}45'28.9''\text{N}$ $9^{\circ}07'25.6''\text{W}$ (Chelas Valley); C. $38^{\circ}45'38.0''\text{N}$ $9^{\circ}07'16.2''\text{W}$ Av. Santo Contestável.

2.1.2.3 Laboratory procedures

The laboratory phase has the main goal of separating the palynomorphs from the sediment, commercialized acids such as HCl (37%) and HF (51-55%) were used to detach the palynomorphs from the sediment. Acid digestion is a common method used to detach palynomorphs from the enamel surface or sediments. Distilled water is the most recommended because it doesn't contain minerals. All laboratory preparation was conducted in the Paleontological laboratory of the Earth Sciences Department of NOVA - FCT. The laboratory procedures were based on Castro, 2006 and they were conducted in the following order:

1. **Carbonate elimination (HCl attack):** the first step was using the HCl to eliminate the carbonates, during 1 or 2 hours (Figure 15).
 - 1.1. **Washing the samples with distilled water:** after the HCl attack it was used distilled water to remove the chlorides formed, it was left to decant for 4 hours (time for palynomorphs to settle at the bottom) Then, the content was carefully discarded since palynomorphs tend to stay at the bottom.
2. **Silicate elimination (HF attack):** it as used to eliminate silica, was applied to half of the cup for four hours (placing it in the agitator, which agitates (90 rpm) and at a hot temperature (90°C) to speed up the elimination of silicates).
 - 2.1. **Washing the samples with distilled water:** after the HF attack it was used the distilled water again to help the removal of silica, it was left to decant for 4 hours.
3. **Fluorides solubles and sulphides elimination:** again, it was used the HCl attack and then the distilled water decantation for four hours. Before sieving, sodium hexametaphosphate (CALGON™) is added to remove the clays. Then distilled water is used again.
4. **Sieving:** after all the acids and washing phases, it was sieved the residues of 15 and 125 µm and stored in tubes, properly labelled, along with distilled water and two drops of HCl to prevent fungi contamination (Figure 15b).

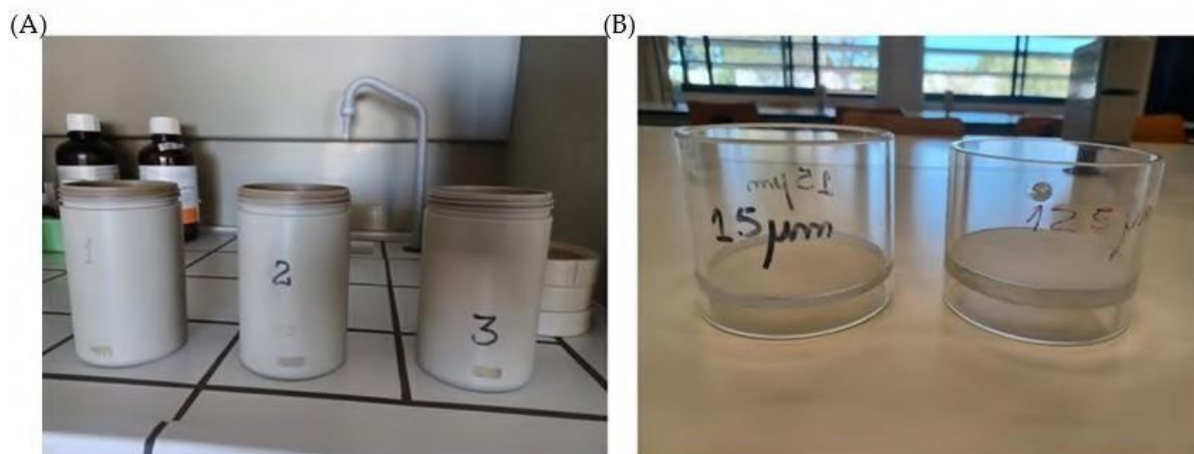


Figure 15. Teflon cups to eliminate carbonates and silicates (A); Sieving the residues (B).

5. **Thin blade mounting with residues:** the slides were cleaned with toilet paper soaked in alcohol to remove any grease. After cleaning the slide, it is placed on a hotplate, the residue is homogenized and collected with a disposable pipette (enough to fill the slide), then left for a few hours to dry, following which two drops of glycerine gelatine (to prevent fungi contamination) is placed on top of the residue (Figure 16).

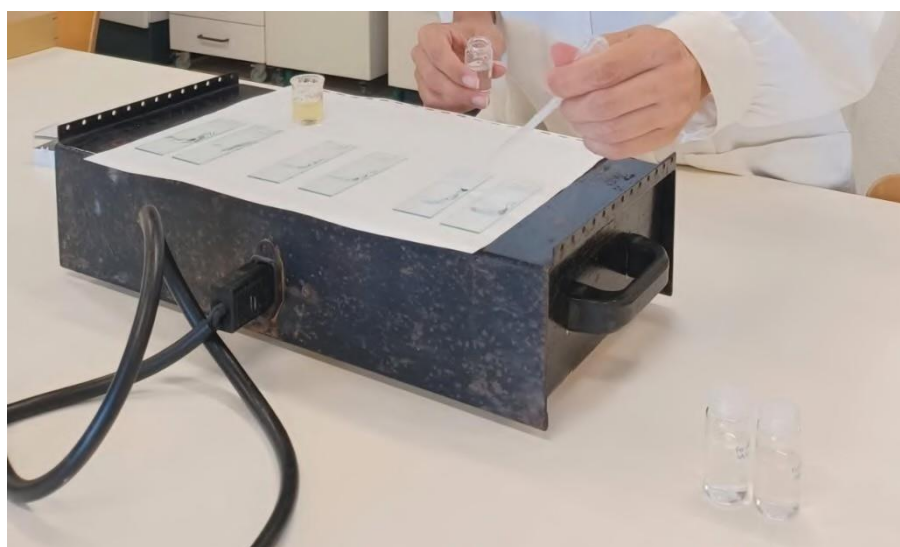


Figure 16. Slides preparing.

6. **Microscopic analysis:** After the slide is ready it was able to examine the palynomorphs through optical microscopy, with objective lenses of 20x and 40x, for Palynology - Leica DM 2500 LED stand, with a digital camera - Flexacam C3), they can be identified based on their morphological characteristics, such as size, shape, surface ornamentation, and other diagnostic features.

2.2.3 Material for Isotopic Analysis: Gomphotheriidae Teeth

Gomphotherium molars were selected for this analysis due to their abundance in Miocene deposits in Portugal and their availability (Figure 17). The molars of proboscideans exhibit a dental characteristic where teeth are continuously replaced throughout the animal's life (Lee et al., 2012). Elephant molars are horizontally positioned in the jaw, and new teeth gradually move forward to replace the worn-out ones. This process ensures that elephants maintain functional teeth for efficient mastication, essential for their herbivorous diet (Lee et al., 2012). The replacement rate varies among individual elephants and can be influenced by factors such as diet, genetics, and wear patterns. Therefore, the measured oxygen isotopic composition is average at different times of the animal's life, since the earlier part is relatively older than the later part (Metcalf & Longstaffe, 2012).

Two measurements were taken from each sample and averaged when analysing the oxygen isotopic composition (Lee et al., 2012). Oxygen and carbon in the enamel carbonates of *Gomphotherium* molars were analysed ($\delta^{18}\text{O}_c$, $\delta^{13}\text{C}$). The procedure was performed under the supervision of Dr. Aurora María Grandal D'Anglade at the Instituto Universitario de Xeoloxía, Universidad da Coruña (Coruña, Spain) and with the assistance of MSc. Darío Estraviz-López.

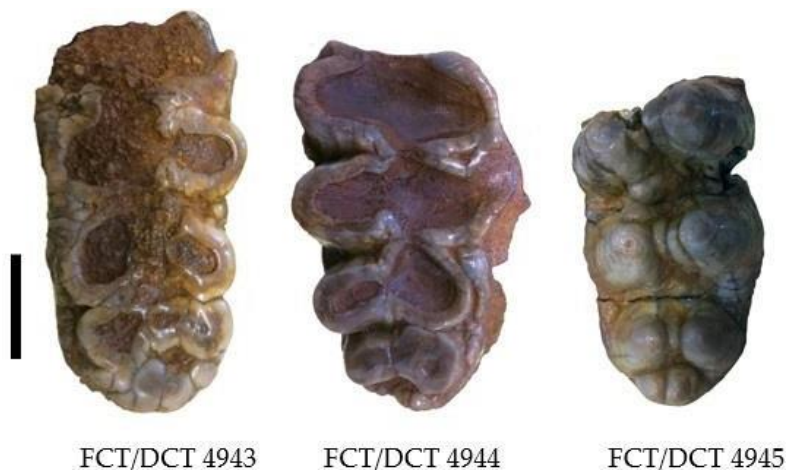


Figure 17. Teeth selected for isotopic analysis. Scale bar 50mm.

2.2.4 Biogeochemistry Methods

2.2.4.1 Sample Preparation

Before any destructive method was employed, it was obtained the 3D image of each specimen through photogrammetry, and also molded them with silicone as a safeguard. At the NOVA FCT, the enamel samples were drilled using a hand-held dental drill from the cross sections through the molars for stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analyses of the structurally bound carbonate in the tooth bioapatite, which were performed at Universidad da Coruña (A Coruña, Spain) (Figure 18). Bioapatite samples were drilled from multiple parallel cusps and various heights along the cusps within the molars to quantify inter-tooth variability in isotopic composition, approximately, 1 mg of enamel powder was used for stable isotope analyses, no pre-treatment was carried out since the samples were obtained from clean cross sections through the molars and were highly unlikely to have been in contact with diagenetic fluids, considering the diagenetic history of the sample site. Therefore, the risk of introducing diagenetic carbonate fractions in the samples (Figure 19) was sufficiently low to motivate the choice of not using pre-treatment techniques, which have been demonstrated to affect the original isotopic composition of enamel in some cases. The samples of ± 1 mg of bioapatite was reacted for 10 minutes with phosphoric acid ($\text{H}_3\text{PO}_4 \cdot \text{H}_2\text{O}$) at 70°C . The produced CO_2 then will be led into the mass spectrometer using a dual inlet device, in a carbonate preparation device (GasBench II, by ThermoFinnigan) to produce CO_2 , which is purified using a series of condensation traps before being led into an isotope-ratio mass spectrometer (MAT253, by ThermoFinnigan) through a dual inlet interface. Stable isotope ratios were calculated from the ratios of CO_2 masses 44, 45 and 46 analysed by the mass spectrometer and converted to delta values with reference to the international Vienna Pee Dee Belemnite (‰VPDB) scale using the standards NBS19, NBS18, CO-8 and LSVEC (IAEA, Vienna, Austria). Stable isotope results were determined to be reproducible with a standard deviation lesser than 0,2 ‰ based on repeated measurements of Carrara marble powder. This method was followed after de Winter et al., 2016.



Figure 18. Cutting the tooth (FCT – DCT 4945) for preparation of carbonates.

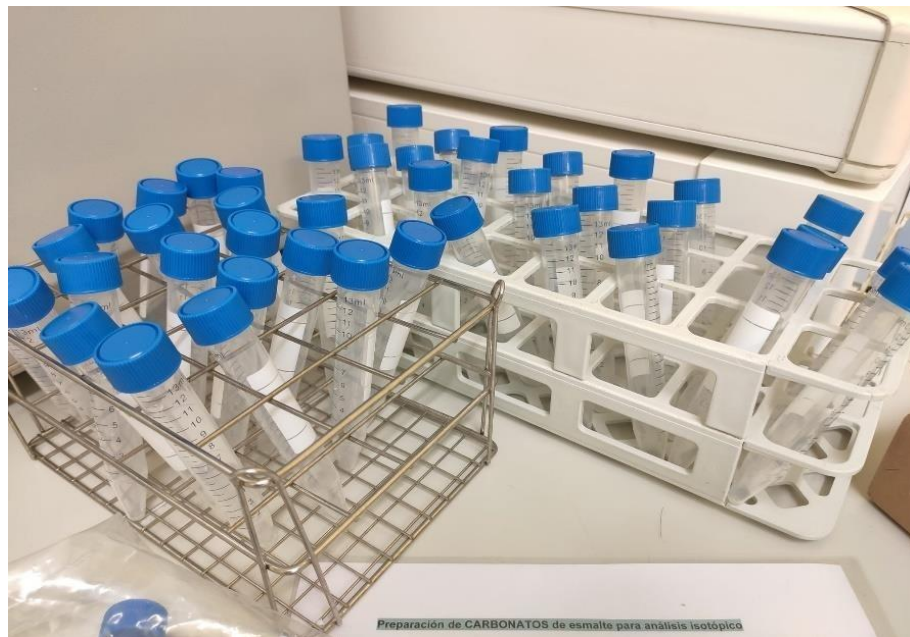


Figure 19. Samples of carbonate from the enamel of FCT – DCT 4945.

2.2.4.2 $\delta^{18}\text{O}$ Analysis Methodology

Once we obtained $\delta^{18}\text{O}_{\text{VPDB}}$ data we proceeded to convert it to $\delta^{18}\text{O}_{\text{VSMOW}}$ scale using the following equation (Coplen et al., 1983; Brand et al., 2014).

$$\delta^{18}\text{O}_{\text{VSMOW}} = 0,97001/29,99 + \delta^{18}\text{O}_{\text{VPDB}}$$

This correlation was established by the 37th IUPAC General Assembly in Lisbon (1993) and

the Commission recommended guidelines for reporting $\delta(^{18}\text{O})$ measurements. The full recommendation appears in Reporting of stable hydrogen, carbon, and oxygen isotopic abundances by Coplen (1994). Today, three concurrent delta scales are in use: one for water (VSMOW), one for carbonates (VPDB), and one for oxygen gas (Air-O₂). The relations of the scales are well-established; however, they are not fixed permanently. Rather, with new studies or technological advances, these relations might be refined in the future.

After this step, we can correlate mean annual temperatures (MAT) and the $\delta^{18}\text{O}$ of meteoric water to estimate palaeotemperatures (°C). Sheppard (1986) considered that the isotopic compositions of hydrogen and oxygen in meteoric waters of the past were governed by relationships similar to those today, assuming that the compositions of the Earth's water deposit, and average annual surface temperatures were not drastically different from those today. However, the correlation between MAT and $\delta^{18}\text{O}$ cannot be explained by a single process but reflects a complex series of processes that fractionate oxygen isotopes in water, including evaporation, transport (with water loss due to precipitation) and condensation and partial equilibrium of atmospheric water at each site. These complications led Domingo et al. (2012) to resolve the uncertainties related to these factors using three additional calibration equations:

The first equation, proposed by Yurtsever & Gat, 1981, uses data from selected weather stations across the globe and thus from all existing biomes and climate regimes, is as shown below:

$$\text{MAT (}^{\circ}\text{C)} = (\delta^{18}\text{O}_w \text{ (VSMOW)} + 11.9) / 0.338 \quad (1)$$

The second equation is formulated using the "Global Network of Isotopes in Precipitation" (GNIP) database (available at <http://nds121.iaea.org/wiser/>) and includes MAT and $\delta^{18}\text{O}_w$ data for the prevailing/predominant biomes II, II/III and III, as well as the rarer biomes I and V (Supplementary Data 7) (Hernández Fernández et al., 2003; 2006). Using this approximation, they calculated the following linear regression ($\pm\text{SD}$):

$$\text{MAT (}^{\circ}\text{C)} = \delta^{18}\text{O}_w + 8.7 (\pm 0.96) / (0.202 (\pm 0.04)) \quad (R^2 = 0.3) \quad (2)$$

With the intention of comparing with the approximation carried out by other authors we have

used current data of the MAT and $\delta^{18}\text{O}_w$ of the GNIP of the region of Madrid between 1971 and 2006 because it belongs to the same period of time and the same basin (Lower Tagus) which Domingo et al., (2012) obtained the following equation ($\pm\text{SD}$):

$$\text{MAT } (^{\circ}\text{C}) = (\delta^{18}\text{O}_w (\text{VSMOW}) + 11.2(\pm 0.62)) / (0.376(\pm 0.04)) \quad (R^2 = 0.9) \quad (3)$$

2.2.4.3 $\delta^{13}\text{C}$ Analysis Methodology

The $\delta^{13}\text{C}$ values of the enamel of herbivore teeth record the $\delta^{13}\text{C}$ values of the plants they consumed ($\delta^{13}\text{C}$ diet), terrestrial environments, it is the photosynthetic pathway used by plants that exerts the dominant control over their $\delta^{13}\text{C}$ values (Koch, 1998; Hayes, 2001; Ríos, 2013). As mentioned in the introduction, but just to remind the reader, C3 or Calvin-Benson photosynthetic pathway is the most common and occurs in all trees, most bushes and herbs and some grasses. Here, CO_2 is fixed as a three-carbon sugar by the enzyme RUBP (Ribulose-1,5-bisphosphate) carboxylase (Koch, 1998). Plants following this pathway exhibit strong discrimination against ^{13}C during CO_2 fixation, contributing to tissues with $\delta^{13}\text{C}$ values of about -27‰ (VPDB) on average (ranging from -36 to -22‰) (Domingo et al., 2012). The most negative $\delta^{13}\text{C}$ values in this range (-36 to -30‰) reflect closed-canopy forest conditions due to ^{13}C depleted CO_2 recycling and low irradiance. Higher values (-25 to -22‰) correspond to C3 plants from high irradiance, arid or water-stressed environments (Domingo et al., 2012). C4 photosynthesis (Hatch-Slack photosynthetic pathway) occurs in some sedges and grasses in areas with a warm growing season and some dicots adapted to arid conditions. C4 plants discriminate less against ^{13}C during carbon fixation (resulting from extremely efficient CO_2 fixation, offering mean $\delta^{13}\text{C}$ values of -13‰ (in a range between -17‰ and -9‰) (Domingo et al., 2012), more similar to those of the atmosphere (Koch, 1998).

Using the expected ranges of $\delta^{13}\text{C}$ for C3 and C4 plants and the typical fractionation of +14. 1‰ from Cerling & Harris (1999), we can estimate the expected $\delta^{13}\text{C}$ values for organisms feeding strictly on C3 plants in different habitats: closed canopy, -22 to -16‰; mesic (moderate moisture input, good moisture balance); forest, -16 to -11‰; open and arid C3, -11 to -8‰ and for organisms feeding strictly on C4 plants (-3‰ to +5‰). Enamel $\delta^{13}\text{C}$ values ranging from -8‰ to -3‰ represent mixed C3-C4 diets. However, when considering

fossil taxa, variations in the $\delta^{13}\text{C}$ value of atmospheric CO_2 (the plant's carbon source) need to be taken into account, including anthropogenic modification due to the burning of fossil fuels, which has reduced the $\delta^{13}\text{C}$ values of atmospheric CO_2 from -6.5 to -8‰ since the Industrial Revolution (Ríos, 2013).

Results

3.1. Systematic Paleontology

Proboscidea Illiger, 1811

Gomphotheriidae Hay, 1922

Gomphotherium Burmeister, 1837

Gomphotherium angustidens Cuvier, 1817

Type Species: *Gomphotherium angustidens* Cuvier, 1817

Etymology: *Gompho-*: from the Greek word "gomphos" (γόμφος), meaning "peg" or "bolt." This likely refers to the appearance of its molars, which were characterized by cone-like or peg-shaped projections. *-therium*: From the Greek word "thērion" (θηρίον), meaning "beast." *Angusti-*: From the Latin word "angustus," meaning "narrow." *-dens*: From the Latin word "dens," meaning "tooth."

Lectotype: right m2 Si -1, stored at the MNHN (Paris, France).

Type Locality: Simorre, France (Tassy & Gohlich, 2011).

Age: Middle Miocene.

Synonyms: *Trilophodont angustidens* Cuvier, 1817, *Serridentinus* Osborn, 1923, *Mastodon angustidens* Zbyszewski, 1949.

General remarks: *Gomphotherium* molar is characterized by its robust structure and distinctive morphology. Typically, these molars are large and exhibit an oval or rectangular shape (Gohlich,

2010). They possess multiple lophs (ridges) or lophids (ridge-like structures) that run transversely across the chewing surface. A standard *Gomphotherium* molar has three to four prominent lophs, often referred to as trilophodont or tetralophodont depending on the number of ridges present. The molars display a bunodont pattern, meaning the cusps are rounded and bulbous (Agustí & Antón, 2002). The wear pattern on the chewing surface is generally simple and trefoil-shaped, indicating the teeth's adaptation to a diet of coarse vegetation. The enamel extends from the crown down to the roots, typically showing different stages of wear that provide insights into the animal's age and dietary habits (Shoshani & Tassy, 1996).

Anterior and posterior cingula (raised, shelf-like structures) are well-developed and encircle the base of the crown. The pretrites (the anterior parts of the lophs) and posttrites (the posterior parts of the lophs) are distinct, with the pretrites often showing more wear than the posttrites. Central conules (small, secondary cusps) are primarily present on the pretrites, adding to the complexity of the tooth's surface (Tassy, 1990; 2014). Accessory cusps are rare, but when present, they are located in the valleys between the lophs. The lingual cingulum (the raised edge on the side facing the tongue) can be well-defined. The molars are usually found with sedimentary grains adhered to them, indicating their fossilization process (Lee et al., 2012). Overall, *Gomphotherium* molars are highly diagnostic due to their unique combination of lophs, cingula, and wear patterns, making them crucial for identifying and understanding this extinct proboscidean's feeding behavior and ecological niche.

3.1.1 Anatomical Description

3.1.1.1 Upper Dentition

FCT-DCT 5362 (Figure 20) is a left upper M1. The specimen has an oval shape. It features three lophs and a well-developed, preserved distal cingulum. The pretrite shows greater wear than the posttrites, and the mesoconelet on both the pretrite and postrite is clearly visible. The lingual cingulum is also noticeable. The anterior cusp is broken. The tooth exhibits a level one wear pattern, indicating that wear is present only on the anterior lophids.



Figure 20. FCT-DCT 5362, M1 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5359 (Figure 21) is an upper left M2. It has an oval shape and has, practically, the same size as FCT-DCT 4942 (lower m2). It has the pretrite completely worn, indicating the four level of wear, which means that is severe wear, pattern partly or wholly obliterated. It has three lophs, and we can see the postrites. There are anterior and posterior cingula present. The tooth has 3 exposed roots.



Figure 21. FCT – DCT 5359 M2 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5364 (Figure 22) identified from Quinta da Farinheira - Chelas) is a left upper M2 With a level four of wear, the pretrite is almost completely worn. The three posttrite lophids are still

visible, although they are also worn. The labial and anterior cingula can be seen as well. Two of its roots are exposed.



Figure 22. FCT – DCT 5364, M2 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5360 (Figure 23) is a right upper. It has a four level of wear. The posterior cingula can be seen slightly as well as two lophs.



Figure 23. FCT – DCT 5360, M2 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5358 (Figure 24) is a left upper M3. With a level four of wear, the posterior cingulum can be seen. The tooth has three lophs, but the first loph is worn and cannot be distinguished. Although both the postrite and pretrite are severely worn, their posterior cusp and mesoconelet are still visible. This tooth also presents its roots.



Figure 24. FCT – DCT 5358, M3 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT- DCT 4944 (Figure 25) is a right upper M3 of an adult proboscidean, it has four lophs, it presents a level two of wear, rounded, as the pattern for upper molars from proboscideans, although the lophs are wear we can still see clearly the shape of then, it presents a distal, labial and lingual cingula and a small part of the antero cingula.



Figure 25. FCT -DCT 4944, M3 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

3.1.1.2 Lower Dentition

FCT – DCT 4942 (Figure 26), is well preserved right lower m2. The tooth is elongated antero-posteriorly, and it has three lophids/trilophodont. The first posttrite is broken and the wear stage is zero, although pretrite one has a slight wear. The second and third lophids are complete and have no wear. The second and third pretrites show the main cusp, the mesoconelet, the anterior and posterior central conules. The second and third posttrites show the main cusp, the mesoconelet and the posterior central conule. This tooth has anterior, lingual and posterior cingula which is (the posterior) fragmented at pretrite area.



Figure 26. FCT-DCT 4942, m2 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5357 (Figure 27) identified from Quinta da Charneca – Lumiar, is a left lower m2 but the anterior part is broken, the level of wear is 2, which means that it is light wear on all lophids. It shows the posterior cingula, the posterior cusp and mesoconelet of both sides (pretrite and postrite), the main cusp of the pretrite is a little worn than the others, there is some sedimentary grains around the tooth.



Figure 27. FCT – DCT 5357, m2 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5361 (Figure 28) specimen is only a fraction of a tooth, that seems to be left a lower m3. It has a zero level of wear, and it has a distal cingulum. Both the postrite and pretrite are present. There is also a posterior cusp and the mesoconelet.



Figure 28. FCT – DCT 5361 m3 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 5363 (Figure 29) is a left lower m3. Only one loph can be seen clearly, while the other is very broken. The tooth exhibits a level three of wear, indicating extensive wear but with the wear pattern still discernible.

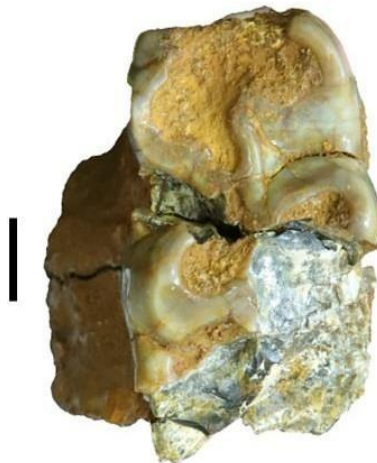


Figure 29. FCT – DCT 5363, m3 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

FCT – DCT 4943 (Figure 30) is a left lower m3 of an adult proboscidean. Is more elongated than m2's or m1's molars, a pattern typical of proboscideans lower molars. It has three lophids and a

broken part of a fourth lophid, it presents a distal/posterior, labial and lingual cingula, the level of wear is two. Due the level of wear it cannot be seen if the cusps and mesoconelets of the lophids.



Figure 30. FCT – DCT 4943, m3 of *Gomphotherium angustidens* in occlusal view. Scale bar: 50mm.

3.1.1.3 Cranial Skeleton

FCT- DCT 5356 (Figure 31) the posterior portion of a fragmented skull preserving occipital bone. In caudal view, there is a large foramen magnum, a circular opening at the base of the skull through which the spinal cord passes, connecting the brain to the spinal column. On both sides of the foramen magnum the two occipital condyles or *condyles occipitalis* are preserved. They are prominent, robust structures located at the base of the skull. These condyles are rounded and convex, providing a smooth surface for articulation with the atlas, the first cervical vertebra. The articulation points are well-defined and slightly oval in shape, facilitating a range of head movements such as nodding. The surface of the occipital condyles is smooth, reflecting their function in forming a stable and flexible joint with the atlas. FCT- DCT 5356 occipital condyles are relatively large, accommodating the substantial musculature and skeletal support necessary for the animal's massive head and elongated trunk. On ventral view there is also preserved the left external auditory meatus on the side of the skull is relatively large and oval-shaped, reflecting the need to accommodate substantial auditory

structures that support the animal's hearing capabilities.

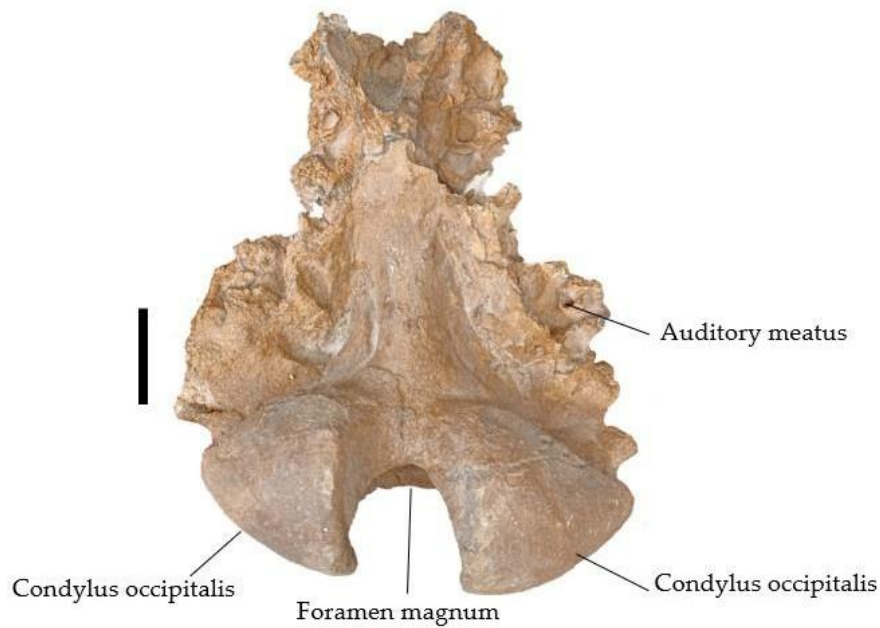


Figure 31. Occipital bone FCT- DCT 5356 of *Gomphotherium angustidens* in ventral view. Scale bar: 50mm.

3.1.1.4 Postcranial remains

FCT- DCT 5366 (Figure 32) is a dorsal spine from a fragmented thoracic vertebra, which is part of the thoracic region. It is a long and robust, reflecting the substantial size of these animals. It arises from the dorsal aspect of the neural arch. The spine's dimensions suggest its role in providing support and attachment points for muscles and ligaments essential for locomotion and posture.



Figure 32. FCT- DCT 5366, vertebra of *Gomphotherium angustidens*. Scale bar: 50mm.

Proboscidea Illiger, 1811

Gomphotheriidae Hay, 1922

Amebelodontinae Barbour, 1927

cf. *Amebelodon* Barbour, 1927

Type Species: *Amebelodon filholi* Frick, 1933

Etymology: *Amebe-*: Derived from the Greek word "amebos" (ἀμεβός), meaning "change" or "blunt." *-lodon*: From the Greek word "odon" (ὀδών), meaning "tooth." *filholi*: Named after Henri Filhol, a French paleontologist who contributed significantly to the study of prehistoric mammals. The species name is in honor of his work.

Locality: Sansan, France

Holotype: molar MNHN.F.SA2843 stored at the MNHN (Paris, France)

Age: Middle Miocene

Synonyms: *Serridentinus filholi* Frick, 1933

Remarks: *Archaeobelodon filholi* Frick, 1933 recorded during the early and Middle Miocene (MN 4a – MN 6) of western and central Europe (and Africa). Because the bunodont,

trilophodont cheek teeth of *A. filholi* are very similar to *G. angustidens*, they are often not distinguishable (Tassy, 2014). But *A. filholi* differs from *Gomphotherium* in the lower flattened tusks and in the upper tusks with a lateral enamel band without torsion (Gohlich, 2010).

FCT – DCT 4945 (Figure 33) it is a lower right m1. This specimen shows patterns of Amebelodontidae which is a family similar to Gomphotheriidae, but the crown of the tooth is more pointed than in *Gomphotherium* molars, which are flatter. This particular tooth also has three lophs with mesoconelets not very developed, another difference from the *Gomphotherium*.

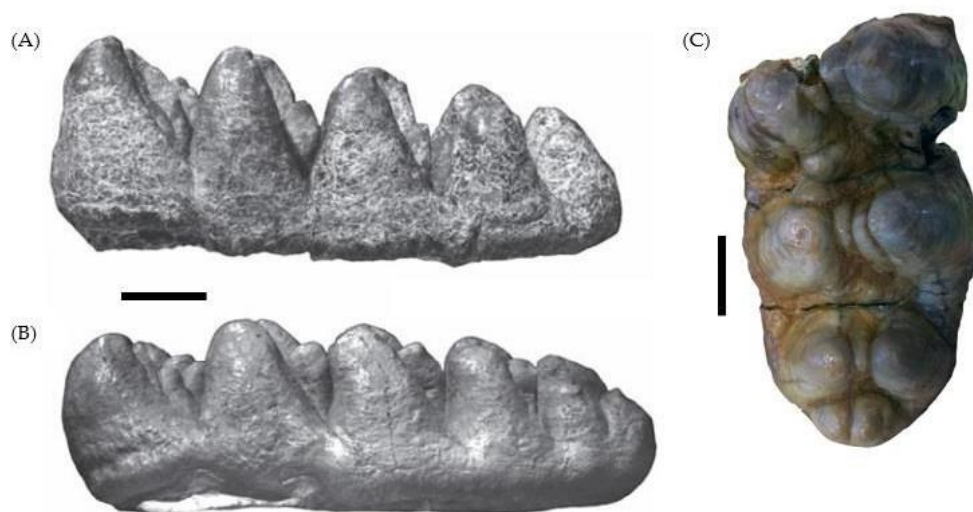


Figure 33. Comparison between *A. filholi* MNHN.F.SA2843 (A) and *G. angustidens* SEP249 (B) by Tassy, 2014, proboscidean tooth FCT-DCT 4945 (C). Scale bar: 50mm.

3.1.2 Anatomical Comparison

3.1.2.1 Dentition

The foundational diagnosis selected for this study was developed by Wang et al. (2017). According to their research, it is possible to identify species within the *Gomphotherium* genus by examining specific dental characteristics such as the shape of their molars, the presence of dental accessories, and particularly the spacing between interlophs and interlophids.

When analyzing Specimen "A" (Figure 34), we see that it exhibits a pattern resembling anancoid on the lophs, indicating that the lophs are more "twisted" and not fully developed compared to specimen "B," which displays the characteristic loph pattern of the *Gomphotherium*.

genus. On the other hand, specimen "C" displays the *Zygodolophodon* pattern, featuring crest-like lophs. Specimen "D" presents signs of anancoid patterns similar to specimen "A," as well as similarities to the loph patterns of *Gomphotherium*, albeit more complex, suggesting a possible classification within the *Tetralophodon* genus.

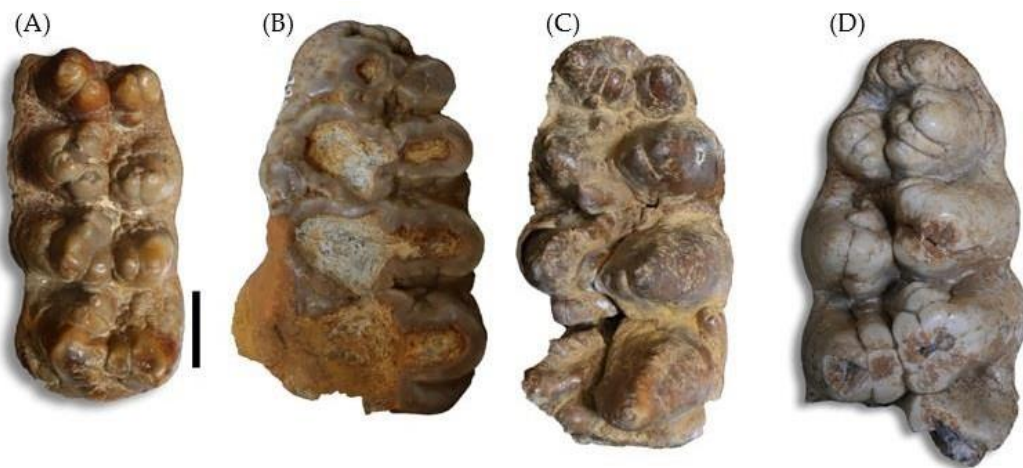


Figure 34. Occlusal view of cheek teeth from different genus housed at Geological Museum of Lisbon: A. *Amebelodon* sp. (10648); B. *G. angustidens* (10612); C. *Zygodolophodon* sp. (10651); D. *Tetralophodon* sp. (10640). Scale bar: 50mm.

The three specimens (Figure 35) exhibit the trilophodont bunodont pattern, characteristic of *Gomphotherium* species. However, what distinguishes them are subtle differences in their interloph spacing. Specimen A (FCT-DCT 5362) and B (GML10625) displays a wider space between interlophs, reminiscent of *G. angustidens*. Specimen C (identified as *G. subtapiroideum*) features a narrow interloph space shaped like a "V".

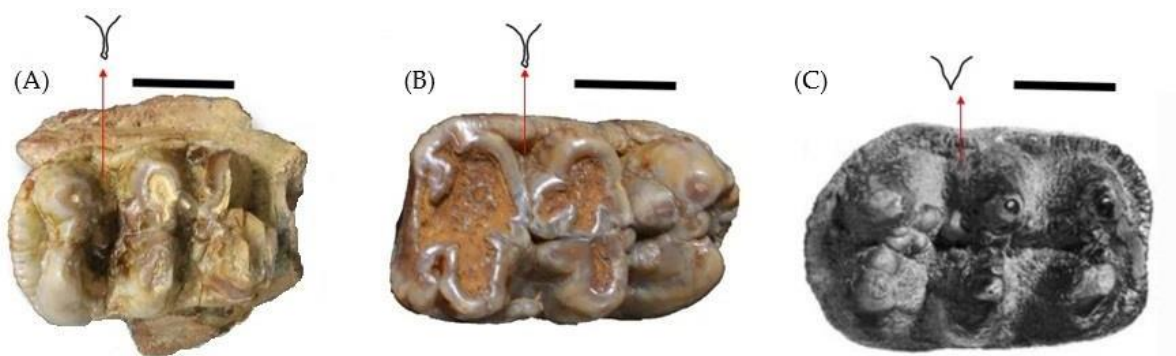


Figure 35. Occlusal view of uppers molars (M1) A. FCT-DCT 5362 (sin); B. GML10625 *Serridentinus lusitanicus*/*Gomphotherium* (dex) and C. 1959 II 440 *G. subtapiroideum* (dex) (Gohlich, 2010). Scale bar: 50mm.

The six specimens presented below (Figure 36) exhibit the characteristic "*Gomphotherium* pattern" of trilophodont bunodont. Specimens A (FCT-DCT 5359), B (FCT-DCT 5364), and C (FCT-DCT 5360) share a consistent pattern, featuring a narrower space between the interlophs, which is indicative of *G. angustidens*. In contrast, specimen D (GML7912) displays a wider interloph space, similar to specimen F (identified as *G. subtapiroideum*), while specimen E resembles the spacing pattern observed in *G. sylvaticum*.

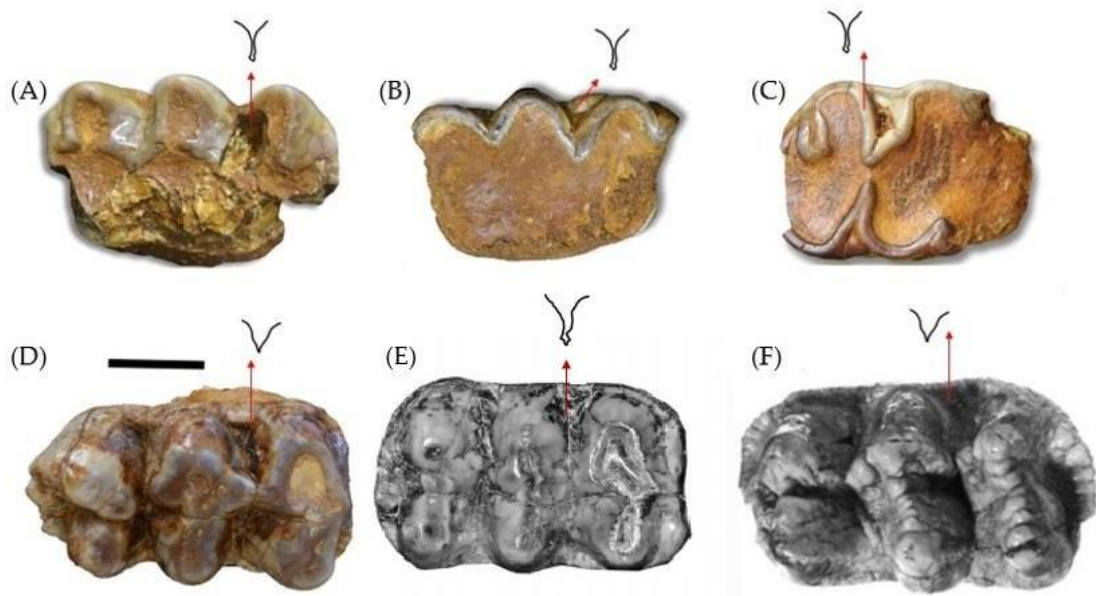


Figure 36. Occlusal view of upper molars (M2); A. FCT-DCT 5359 (sin); B. FCT-DCT 5364 (sin); C. FCT-DCT 5360 (dex); D. GML7912 *Trilophodon angustidens*/*Gomphotherium* (sin); E. *G. sylvaticum* (Tassy, 2014; Wang et al., 2017); F. 1959 II 11386 *G. subtapiroideum* (dex) (Gohlich, 2010).

The next specimens (Figure 37) A, B, and C, while exhibiting some variations, consistently display a broader pattern in the spacing between the interlophids, particularly notable in the lower molars. This characteristic aligns closely with the morphology observed in *G. angustidens*. In contrast, specimen D (identified as *G. praetypicum*) presents a narrower interlophid spacing. Notably, specimens E (recognized as *G. inopinatum*) and F (designated as *G. tassyi*) exhibit spacing patterns remarkably akin to those observed in *G. sylvaticum*. This resemblance is particularly evident in their upper molars, which bear striking similarities to the dental features of *G. sylvaticum*. These observations suggest a potential taxonomic affinity between *G. inopinatum*, *G. tassyi*, and *G.*

sylvaticum, warranting further investigation into their evolutionary relationships and morphological distinctions.

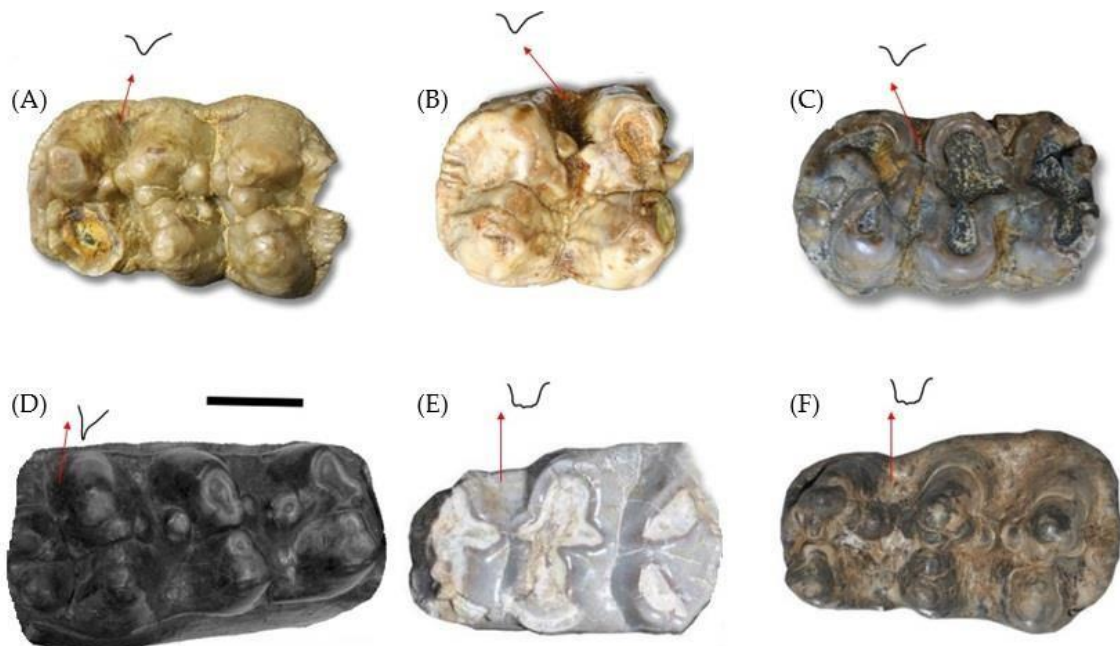


Figure 37. Occlusal view of lower molars (m2); A. FCT-DCT 4942 (dex); B. FCT-DCT 5357 (sin); C. GML 7951(sin); D. HNHN V 2007.96.2 *G. praetypicum* (sin) (Gasparik & Markov, 2009); E. IVPPV18700 *G. inopinatum* (dex) (Wang, 2014); F. HNV1948 *G. tassyi* (sin) (Wang et al., 2017).

In Figure 38, the cheek tooth crown pattern of *G. subtapiroideum* typically exhibits a slightly less bunodont morphology compared to *G. angustidens* (Gohlich, 2010). The first three specimens display a consistently narrower pattern characteristic of *G. angustidens*, while specimen "D" precisely mirrors the wider pattern previously observed in *G. subtapiroideum*.

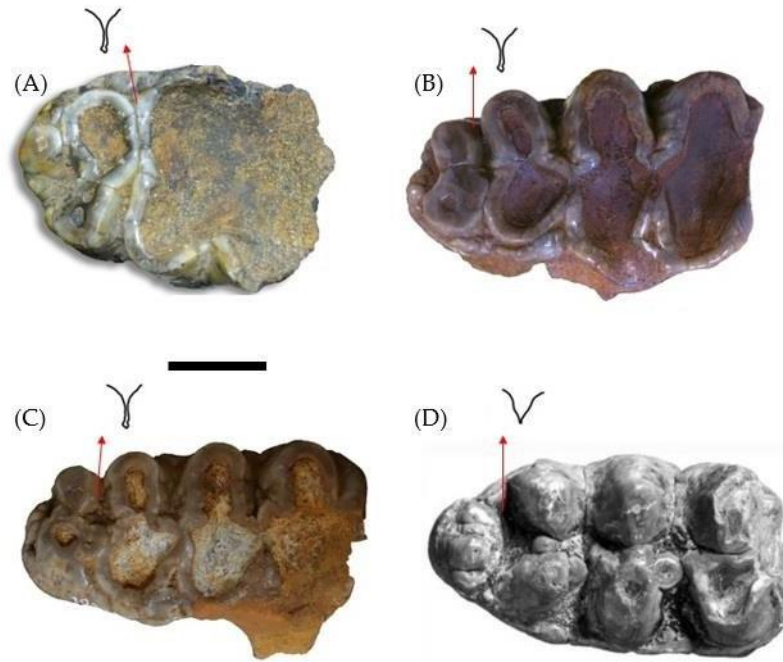


Figure 38. occlusal view of upper molars (M3); A. FCT-DCT 5358 (sin); B. FCT-DCT 4944 (dex); C. GML10612 (dex); D. 1959 II 4783 *G. subtapiroideum* (dex) (Gohlich, 2010).

Following this, specimens "A," "B," "C," and "D" (Figure 39) exhibit a consistent wider pattern between the interlophids, characteristic of the *G. angustidens* species. In contrast, specimen "E" displays a pattern akin to that of the lower m3, indicative of the *G. subtapiroideum* species. The specimen "F" shows features of *G. steinheimense*, their interlophids are much narrower than specimen "E".

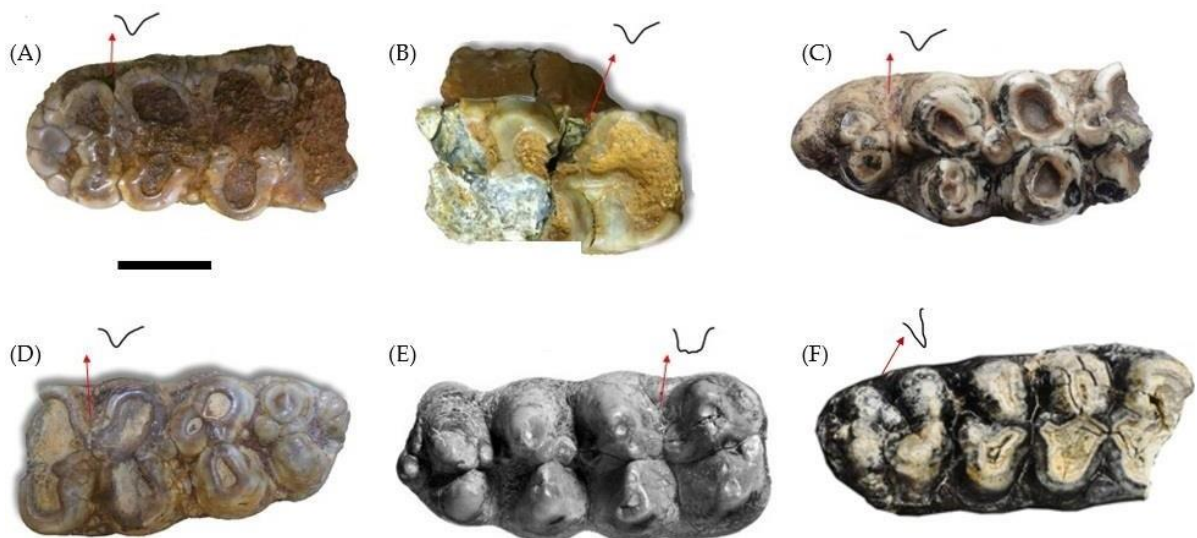


Figure 39. Occlusal view of lower molars (m3); A. FCT-DCT 4943 (sin); B. FCT-DCT 5363 (sin); C. NHMW 2013/0002/0001 *G. angustidens* (sin) (Gohlich, 2020); D. GML7970 (dex); E. 1959 II 11381 *G. subtapiroideum* (sin) (Gohlich, 2010); F. IVPP 23283 *G. steinheimense* (Wu et al., 2018).

3.1.2. Cranial Remains

The occipital bones of the three specimens pictured below (Figure 40) exhibit similar morphological features typical of the *Gomphotherium* genus. However, due to differences in preservation in the the collected parts, these features may not be readily apparent. The specimen under study here presents only the back portion of the skull, so we can compare it with the specimen analyzed in Tassy's (2013), as well as *G. tassyi*. All three specimens share rounded and prominent occipital condyles, and wide external auditory meatus, suggesting common morphological characteristics within the *Gomphotherium* genus. Further examination and comparative analysis of additional specimens may provide deeper insights into these shared features and their taxonomic significance.

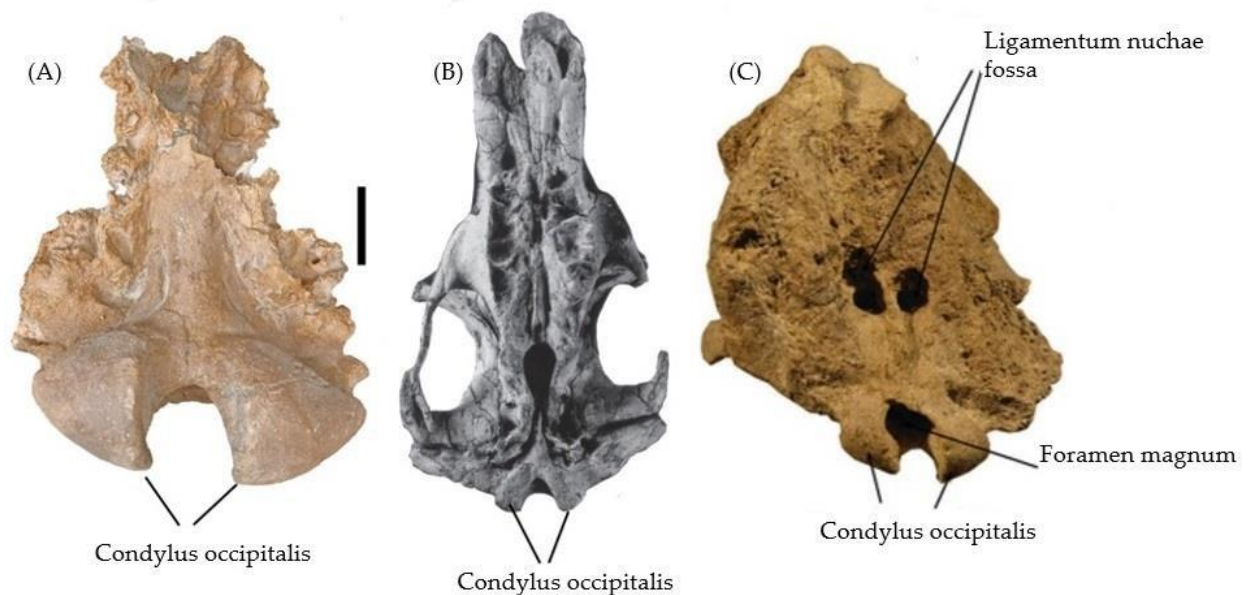


Figure 40. Ventral view of: A. FCT-DCT 5356; B. (MNHN.F. SEP185) *Gomphotherium angustidens* (Tassy, 2013); C. HMV 1824 *G. tassyi* (Wang et al., 2017). Scale bar 50mm.

3.1.2.3 Postcranial skeleton

Comparison with the thoracic vertebrae described in Ferretti's study (2011) reveals notable similarities, although this comparison can be challenging due to the limited parts available for examination in the FCT/DCT specimen, as previously mentioned. However, it can be inferred that the specimen represents a thoracic vertebra from a Gomphothere (Figure 41). In all thoracic vertebrae of *Haplomastodon chimborazi*, there is a consistent presence of backwardly bent spinous processes. This inclination becomes more pronounced in the anterior thoracics (T2 to T5). In comparison to *G. sylvaticum* and *G. productum*, the spinous processes of the anterior thoracics in *H. chimborazi* exhibits a greater degree of backward bending. This suggests that the head was held in a more elevated posture in the latter taxon (Ferretti, 2011).

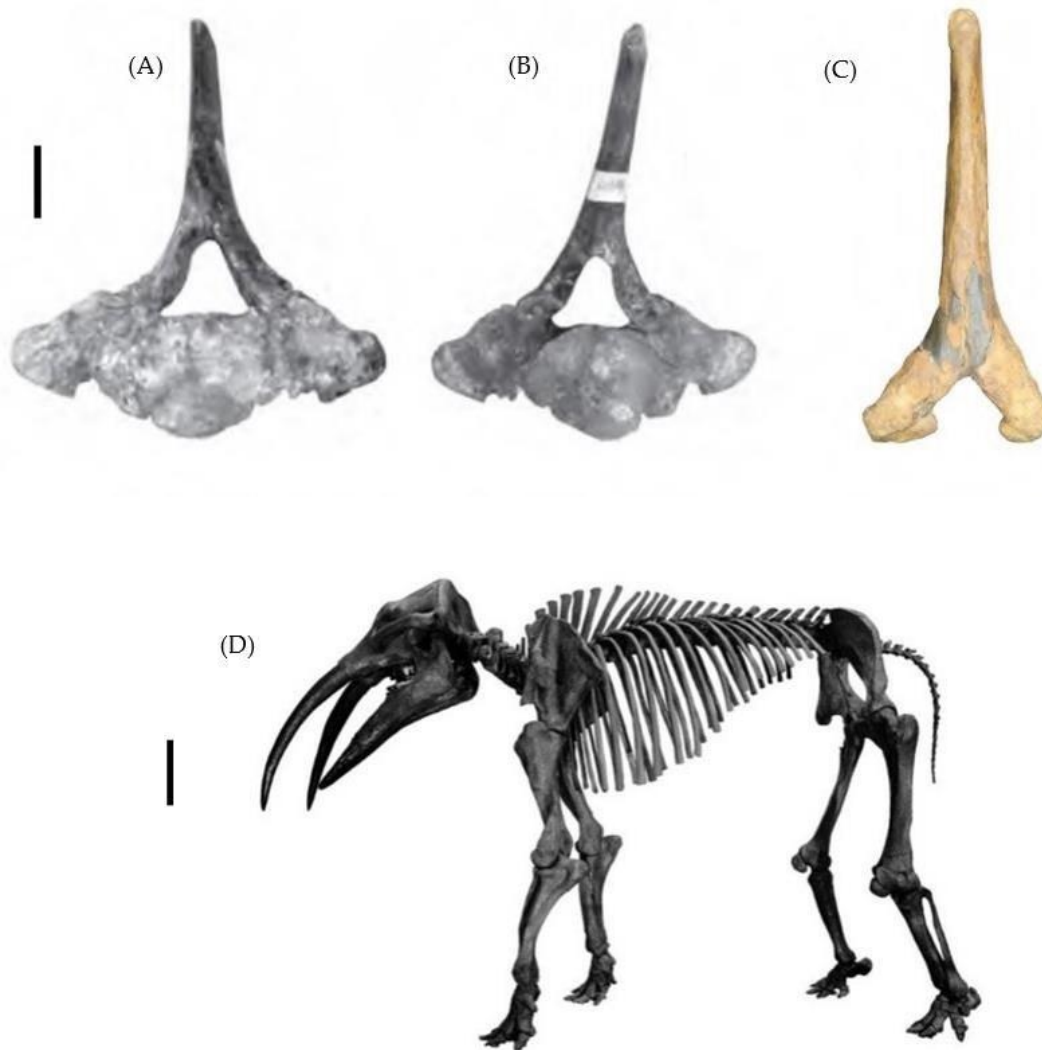


Figure 41. A, B. Oclusal and caudal view of thoracic vertebrae (T2) of *Haplomastodon chimborazi* (Ferretti, 2011); C. FCT-DCT 5366; D. Skeleton of *Gomphotherium aff. steinheimense* (Gohlich, 1999). Scale bar: 50mm.

3.1.3 Biometrical Comparisons

To provide a more detailed representation of our identification and findings, it is presented here some scatter plots that illustrate the similarities and differences among the species. Despite variations in tooth position, the width remains relatively consistent across the specimens studied, while differences in length emerge as a potential distinguishing factor between species. It is crucial to consider variations in tooth preservation, including the possibility of breakage, when interpreting these findings. The measurements for those scatterplots can be found in Appendix section (Appendix A).

The scatterplot of upper cheek teeth, M1, (Figure 42) presents similarities on almost all species of *Gomphotherium*, except the new specie described by Wang et al., 2017. Which can be a differentiation of this new specie, that can be result of several factors, like locality, dietary etc.

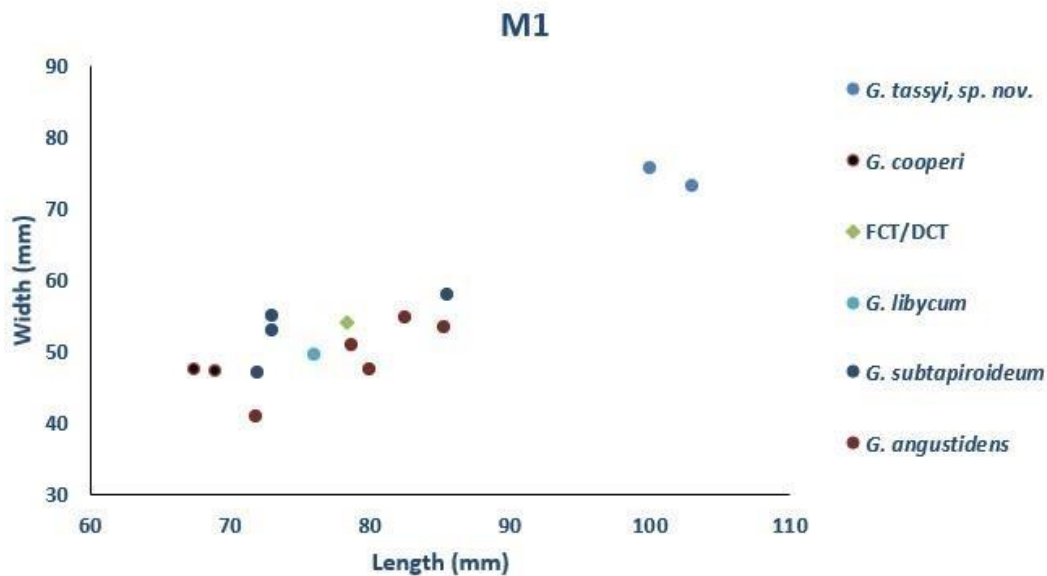


Figure 42. Comparison scatterplot of *Gomphotherium*'s upper cheek teeth (M1). Data. *G. tassyi* (Wang et al., 2017); *G. cooperi* (Wang & Yang, 2022); *Gomphotherium* sp. (FCT-DCT); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. angustidens* (Museu Geológico de Lisboa).

The scatterplot of upper cheek teeth, M2, (Figure 43) presents a more spread results but still consistent with the previous scatterplot, which still can be the result of several factors, but still shows a bigger gap with the new specie described by Wang et al. (2017).

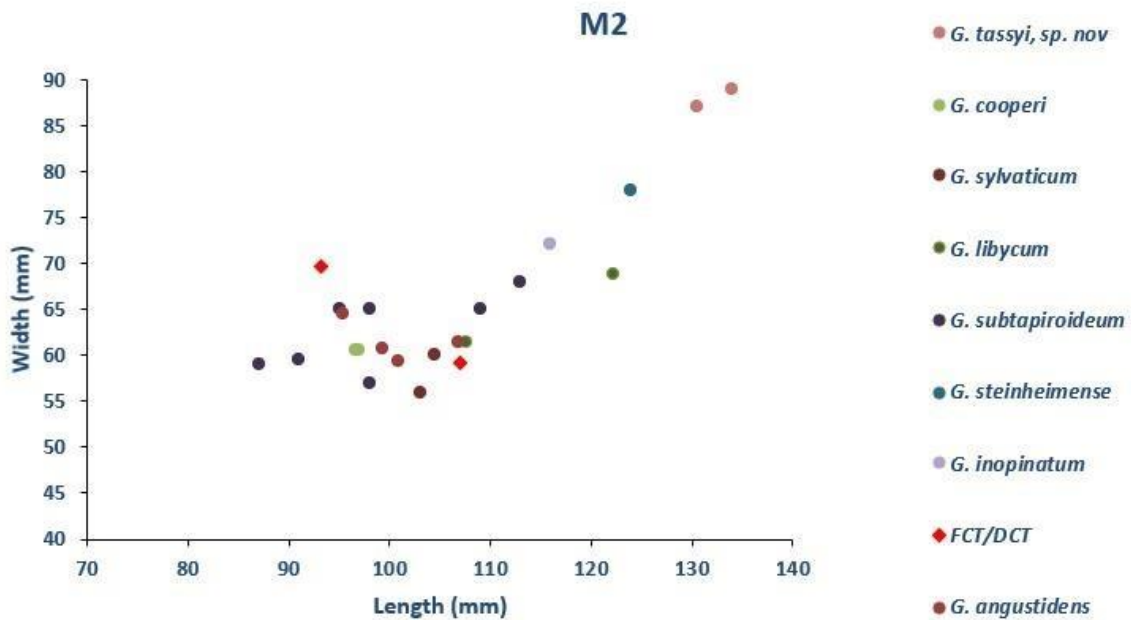


Figure 43. Comparison scatterplot of *Gomphotherium*'s upper cheek teeth (M2). Data. *G. tassyi* (Wang et al., 2017); *G. cooperi* (Li et al., 2022); *G. sylvaticum* (Tassy, 1977); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. steinheimense* (Gohlich, 1998); *G. inopinatum* (Borissiak & Belyaeva, 1928; Wang et al., 2015); *Gomphotherium* sp. (FCT-DCT); *G. angustidens* (Museu Geológico de Lisboa).

The scatterplot of upper cheek teeth, M3, (Figure 44) presents also a large difference on the results but the change here comes with the width and length of the specie described by Wang et al. (2017), which now shows a closer similarity with almost all the *Gomphotherium* species.

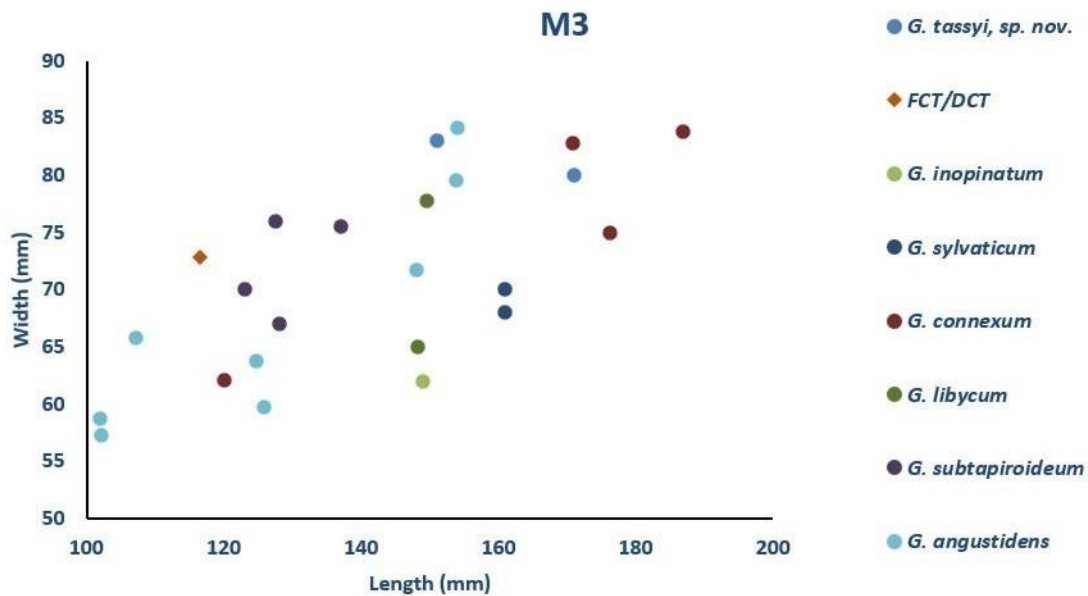


Figure 44. Comparison scatterplot of *Gomphotherium*'s upper cheek teeth (M3). Data. *G. tassyi* (Wang et al., 2017); *Gomphotherium* sp. (FCT-DCT); *G. inopinatum* (Borissiak & Belyaeva, 1928; Wang et al., 2015); *G. sylvaticum* (Tassy, 1977); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. angustidens* (Museu Geológico de Lisboa).

The scatterplot of lower cheek teeth, m1, (Figure 45) presents similarities on almost all species of *Gomphotherium*, except the species described by *Serridentinus mongoliensis*, which (again) can be a differentiation of this specie or just the result of several factors, like locality, dietary etc.

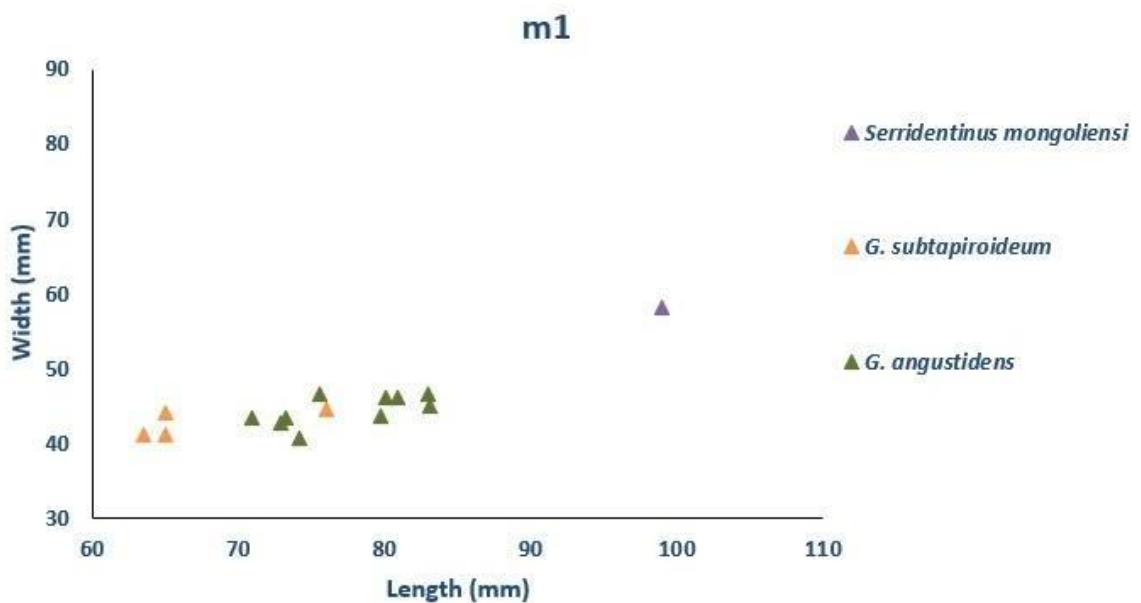


Figure 45. Comparison scatterplot of *Gomphotherium*'s lower cheek teeth (m1). Data. *Serridentinus mongoliensis* (Osborn,

1924; Wang et al., 2015); *G. subtapiroideum* (Gohlich, 2010); *G. angustidens* (Museu Geológico de Lisboa).

The scatterplot of upper cheek teeth, m2, (Figure 46) presents the most consistent similarities on all species of *Gomphotherium*, except two specimen, which can be related with the conservation status.

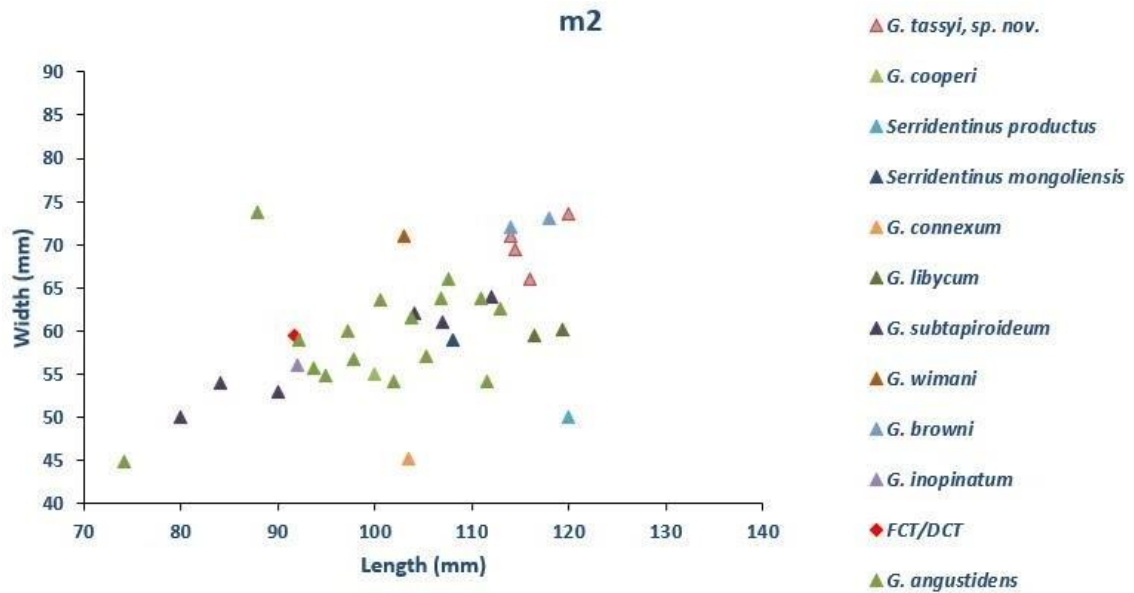


Figure 46. Comparison scatterplot of *Gomphotherium*'s lower cheek teeth (m2). Data. *G. tassyi, sp.* (Wang et al., 2017); *G. cooperi* (Osborn, 1932; Wang et al., 2015); *Serridentinus productus* (Frick & Rak, 1926); *Serridentinus mongoliensis* (Osborn, 1924; Wang et al., 2015); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. wimani* (Hopwood, 1935; Wang et al., 2015); *G. browni* (Osborn, 1926; Wang et al., 2015); *G. inopinatum* (Wang, 2014); *Gomphotherium sp.* (FCT-DCT); *G. angustidens* (Museu Geológico de Lisboa).

The scatterplot of lower cheek teeth, m3, (Figure 47) presents a large difference on the results but presents the same biometrical pattern with the upper M3, which can be a new diagnosis for the genus *Gomphotherium*, excluding those specimens that has broken parts.

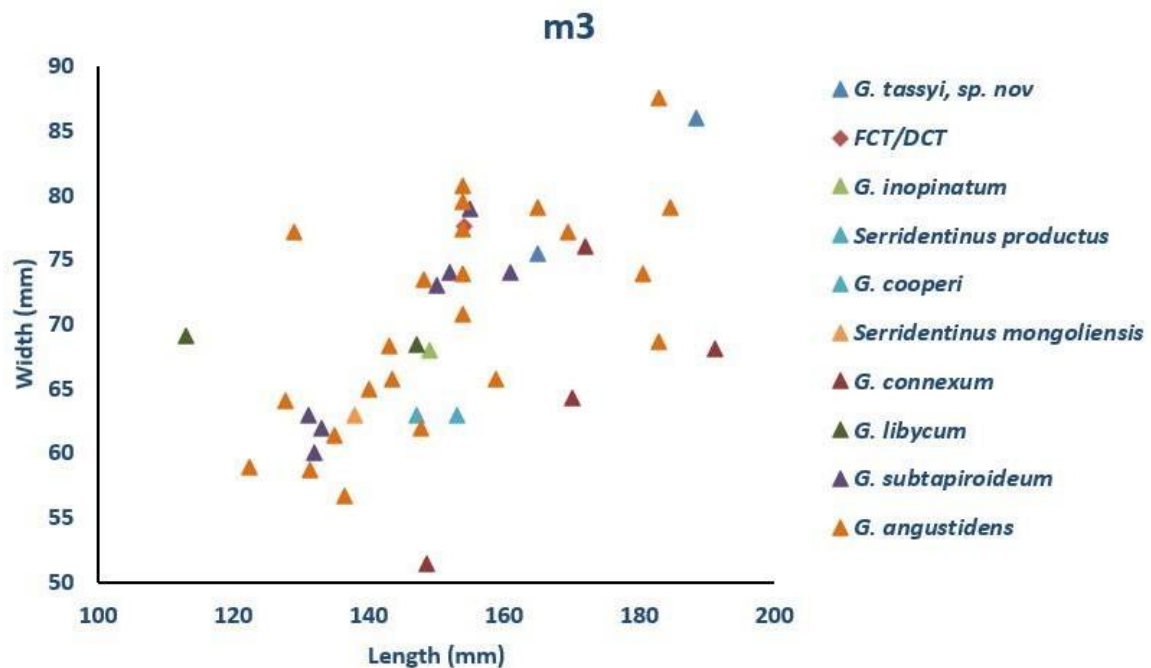


Figure 47. Comparison scatterplot of *Gomphotherium*'s lower cheek teeth (m3). Data: *G. tassyi.sp* (Wang et al., 2017); *Gomphotherium sp.* (FCT-DCT); *G. inopinatum* (Wang, 2014); *Serridentinus productus* (Frick & Rak, 1926); *G. cooperi* (Osborn, 1932; Wang et al., 2015); *Serridentinus mongoliensis* (Osborn, 1924; Wang et al., 2015); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. angustidens* (Museu Geológico de Lisboa).

The significance of the description and comparison conducted here lies in the validation of previous diagnoses for this particularly challenging taxon, facilitating the accurate identification of remains from Portugal. Given that the last identification was made decades ago, the ability to now recognize the taxon based on its distinct patterns is crucial. Notably, our findings shed light on the prevalence of *Gomphotherium angustidens* in Portugal, the necessity to update information from the collections curated the GML.

3.2. Results of Palynomorphs analysis

The research made with slides from the teeth remains and sediments from the site where some of teeth were found presented two specimens fossil pollen (which appears several times on different slides), the pollen seen in the slides are a bisaccate pollen, but unfortunately the pollen

found were all recent, which means they're not fossilised. It was difficult to collect sediments in Chelas and also from the dental remains, as the area has been altered too much due to urbanization and the sediment matrix around the teeth was very small. Sediment collection had to be superficial because of the foundations of the buildings, therefore, the pollen survey was not so conclusive, but the bibliographical research coincided with the isotopes, revealing similarities between vegetation and climate.

3.3. Results of the Biogeochemical Analysis

The isotopic data obtained from the molars of *Gomphotherium* offers valuable insights into the animal's feeding behaviors and the environmental conditions it experienced throughout its lifespan. The table provided in the Appendix section, labeled as (Appendix B), serves to summarize the oxygen isotopic composition of carbonates ($\delta^{18}\text{O}_\text{c}$) and the carbon isotopic composition of carbonates ($\delta^{13}\text{C}_\text{c}$). Additionally, the results of the isotopic analysis are visually presented in images 48-50.

Our results indicate $^{18}\text{O}_{\text{VPDB}} (\text{‰})$: values between -4,0 and -4,16 and $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ values between -9,95 and -10,09 in specimen FCT-DCT 4943 (Figure 48).

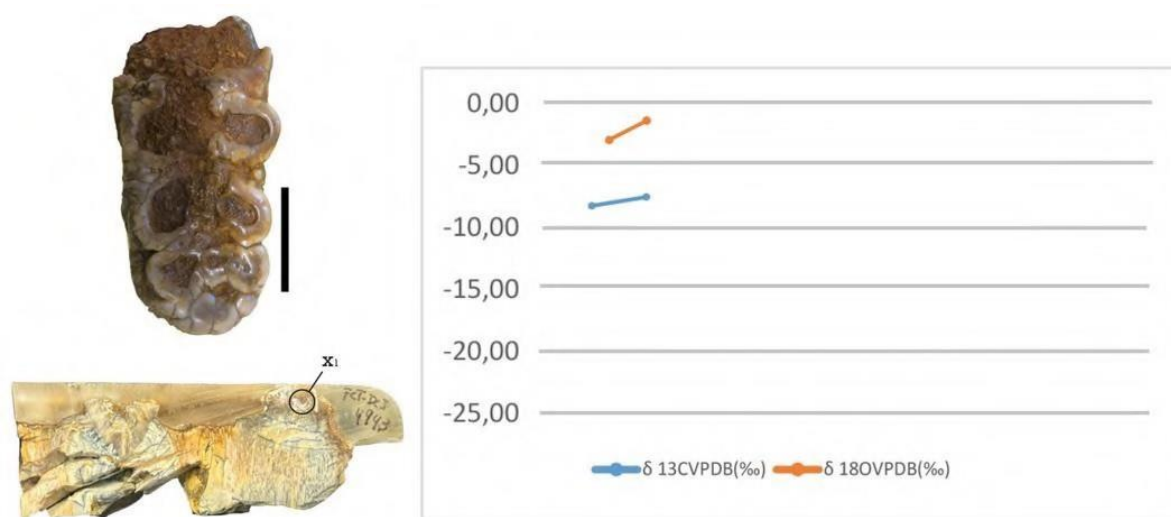


Figure 48. Isotopic values in specimen FCT-DCT 4943. A) Occlusal view of the tooth. B) Scatter plot showing the $^{18}\text{O}_{\text{VPDB}} (\text{‰})$ and $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ values of the specimen, C) Lateral view of a cut section of the specimen, indicating the location from which the enamel sample was taken for analysis.

Our results indicate $^{18}\text{O}_{\text{VPDB}} (\text{‰})$: values between -2,73 and -4,19 and $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ " values between -9,46 and -10,12 in specimen 4944 (Figure 49).

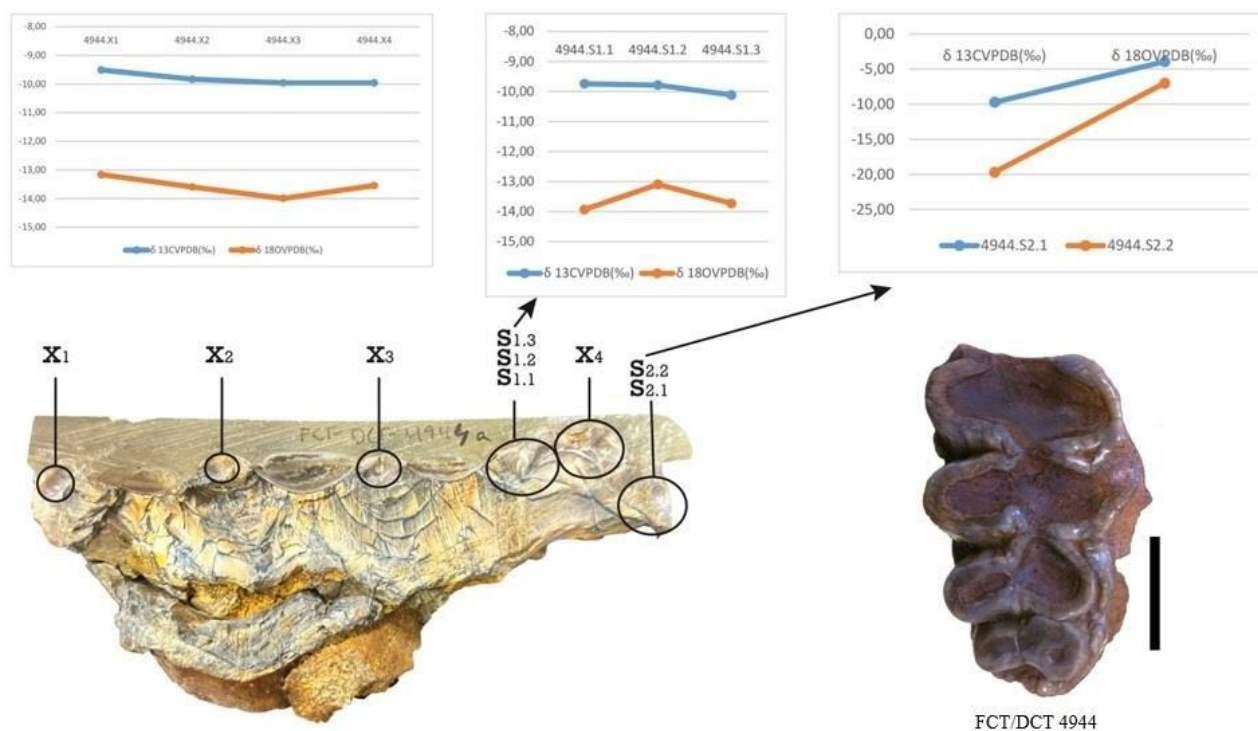
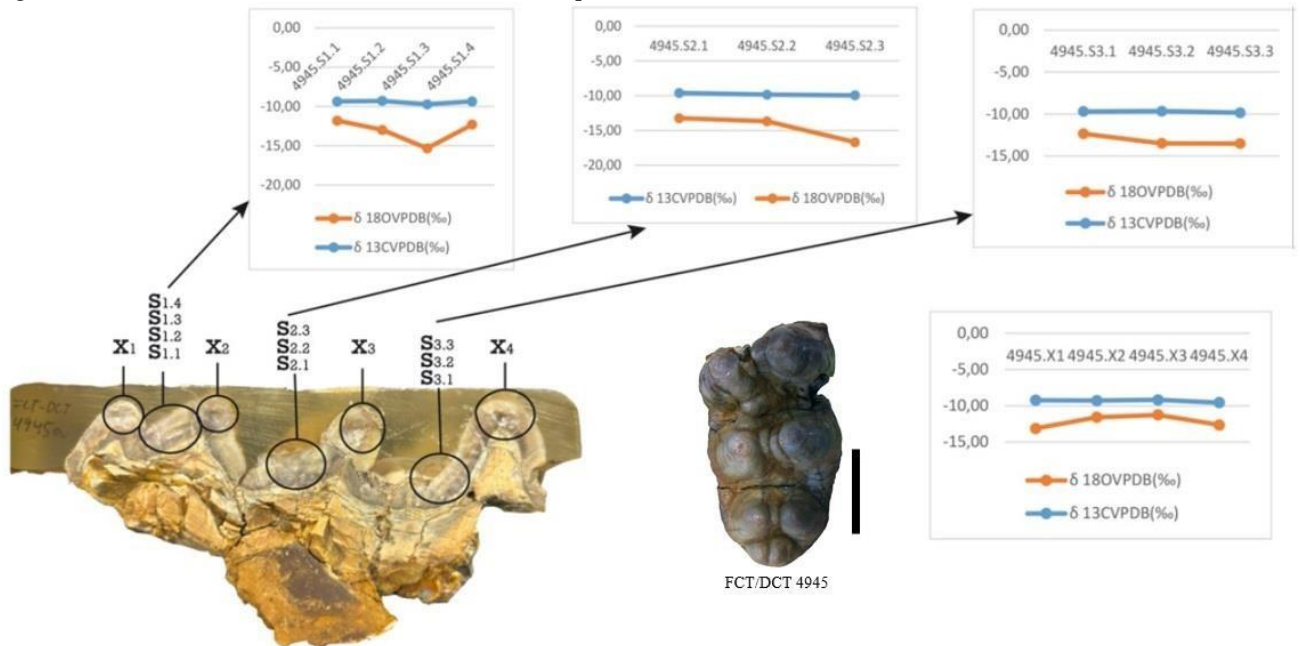


Figure 49. Isotopic values in specimen FCT-DCT 4944. A) Occlusal view of the tooth. B) Dispersal plot showing the $^{18}\text{O}_{\text{VPDB}} (\text{‰})$ and $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ " values of the specimen, C) Lateral view of a cut section of the specimen, indicating the location from which the enamel samples were taken for analysis.

Our results indicate $^{18}\text{O}_{\text{VPDB}} (\text{‰})$: values between -1,76 and -6,72 and $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ " values between -9,16 and -9,96 in specimen 4945 (Figure 50).

Figure 50. $\delta^{18}\text{O}_{\text{VPDB}} (\text{‰})$ ad $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ values in specimen FCT-DCT 4945. A) Occlusal view of the tooth. B)



Scatter plot showing the $\delta^{18}\text{O}_{\text{VPDB}} (\text{‰})$ ad $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ values of the specimen, C) Lateral view of a cut section of the specimen, indicating the location from which the enamel, sample was taken for analysis.

3.3.1 $\delta^{18}\text{O}$ and Mean Annual Temperatures

We have been able to estimate the Mean Annual Temperature (MAT) in degrees Celsius ($^{\circ}\text{C}$) derived from various equations (Table 4). The different equations used to estimate the MAT reflect the variability and potential range of temperatures inferred from the isotopic data. These results will be following the most refined equation of Domingo et al. (2012).

- Specimen FCT-DCT 4943 results indicate MAT ($^{\circ}\text{C}$) values between 18,02 $^{\circ}\text{C}$ and 18,44 $^{\circ}\text{C}$. These results indicate MAT ($^{\circ}\text{C}$) values between 18,02 $^{\circ}\text{C}$ and 18,44 $^{\circ}\text{C}$. We only had one valid data point for this specimen so we couldn't analyze any trend.
- Specimen FCT-DCT 4944 results indicate MAT ($^{\circ}\text{C}$) values between 17,93 $^{\circ}\text{C}$ and 21,82 $^{\circ}\text{C}$. These results indicate MAT ($^{\circ}\text{C}$) values between 17,9 $^{\circ}\text{C}$ and 21,82 $^{\circ}\text{C}$. This specimen $\delta^{18}\text{O}_{\text{t}}$ values oscillated from the sample point x4 (most modern) to sample point x1 (oldest). It can be seen how the $\delta^{18}\text{O}_{\text{c}}$ oscillates with time, starting with a - $\delta^{18}\text{O}_{\text{c}}$ 3.09‰ which drops to -4.03‰ and then rises again to -3.07‰. As for the samples

taken from lower enamel layers of the same tooth (4944.S1.1, 4944.S2.1) these show lower $\delta^{18}\text{O}_\text{c}$ values than those of the uppermost layers 4944.S1.2, 4944.S1.3, 4944.S2.2. This result presents us the seasonality changes during the lifetime of that animal.

- Specimen FCT-DCT 4945 results indicate MAT ($^{\circ}\text{C}$) values between 11,19 $^{\circ}\text{C}$ and 24,4 $^{\circ}\text{C}$. These results indicate MAT ($^{\circ}\text{C}$) values between 11,19 $^{\circ}\text{C}$ and 24,40 $^{\circ}\text{C}$ highest and lowest MAT recorded, for example, with Eq 3 (11.19 $^{\circ}\text{C}$ and 24.40 $^{\circ}\text{C}$). In this specimen the MAT recorded in the lower enamel layers is higher than in the upper layers. As for the register of the posterior x1 vs. the anterior x4 shows a slight increase in temperature followed by a slight decrease during the lifetime of the animal (Figure 51).

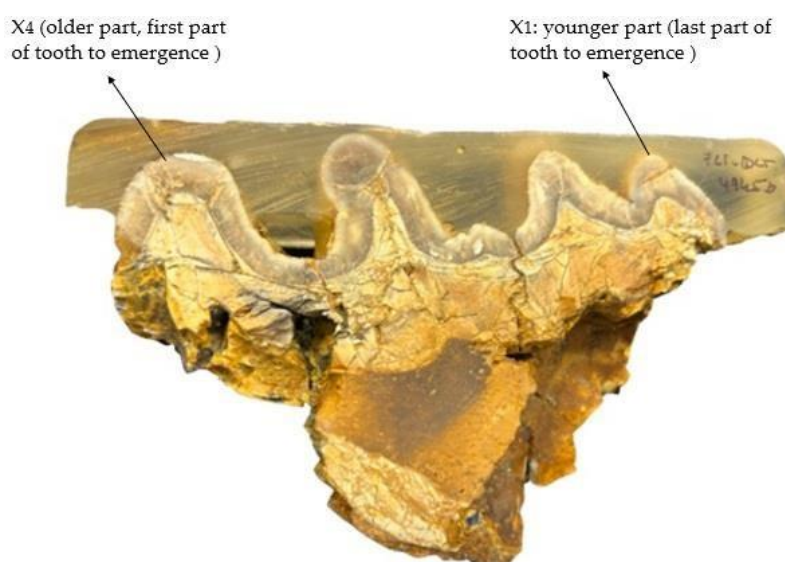


Figure 51. Scheme for tooth growing and differentiation of temperature.

Table 4. Mean annual temperatures ($^{\circ}\text{C}$, MAT) estimated by equations (1) to (3), calculated with the local $\delta^{18}\text{O}$ calculated by Eq. (1); determined with data from selected meteorological stations around the world and therefore from all existing biomes and climatic regimes by (Yurtsever & Gat, 1981); Eq. (2); formulated using the 'Global Network of Isotopes in Precipitation' (GNIP) database and including MAT and local $\delta^{18}\text{O}$ water data from the predominant biomes as well as the rarer biomes (Hernández Fernández et al., 2003; 2006) and Eq. (3); calculated with current MAT and local $\delta^{18}\text{O}$ water data from GNIP for the city of Madrid between 1971 and 2006 (Domingo et al., 2012). $\delta^{18}\text{O}_\text{SMOW}$ converted from $\delta^{18}\text{O}_\text{VPDB}$ values.

Sample	Nº SAI	δ $^{18}\text{O}_{\text{VPDB}}(\text{‰})$	δ $^{18}\text{O}_{\text{SMOW}}(\text{‰})$	MAT (°C)Yurtsever & Gat (1981)	MAT (°C) Hernández Fernández et al., 2003,2006	MAT (°C) Domingo et al., (2012)	
4943.X1	2022/30752	-4,00	-3,96	23,47652067	23,44091083	19,24219146	4943.X1
		-4,16	-4,12	23,00692393	22,65514994	18,82005396	
4944.S1.1	2022/30767	-4,19	-4,16	22,9110063	22,4946541	18,73383013	4944.S1.1
		-4,05	-4,02	23,3233189	23,18456331	19,10447284	
4944.S1.2	2022/30768	-3,30	-3,27	25,52875837	26,87485311	21,08702215	4944.S1.2
		-3,06	-3,03	26,24214576	28,06854093	21,72831188	
4944.S1.3	2022/30769	-3,40	-3,36	25,25699174	26,42011489	20,8427213	4944.S1.3
		-3,61	-3,57	24,63152884	25,37354826	20,28047007	
4944.S2.1	2022/30770	-3,93	-3,90	23,6736847	23,77081895	19,41942933	4944.S2.1
		-3,61	-3,58	24,62486789	25,36240271	20,27448231	
4944.S2.2	2022/30771	-3,09	-3,05	26,1748702	27,95597093	21,66783545	4944.S2.2
		-2,73	-2,69	27,23662511	29,73257073	22,62228534	
4944.X1	2022/30772	-3,09	-3,06	26,16021612	27,93145073	21,65466236	4944.X1
		-3,65	-3,62	24,49431334	25,14395004	20,1571221	
4944.X2	2022/30773	-3,76	-3,73	24,18043056	24,61874024	19,87496151	4944.X2
		-3,59	-3,56	24,67044488	25,43866519	20,31545311	
4944.X3	2022/30774	-3,70	-3,67	24,35820014	24,91619628	20,03476502	4944.X3
		-4,03	-4,00	23,37620357	23,27305351	19,15201279	
4944.X4	2022/30775	-3,07	-3,04	26,2218289	28,03454539	21,71004832	4944.X4
		-3,59	-3,55	24,69274807	25,4759844	20,33550226	
4945.S1.1	2022/30756	-2,45	-2,41	28,0639147	31,11684737	23,36596587	4945.S1.1
		-2,43	-2,39	28,1265276	31,22161549	23,42225087	
4945.S1.2	2022/30757	-3,63	-3,60	24,55359576	25,24314539	20,21041321	4945.S1.2
		-3,70	-3,66	24,36908754	24,9344138	20,0445521	
4945.S1.3	2022/30758	-5,61	-5,58	18,70062186	15,44955539	14,94896327	4945.S1.3
		-5,34	-5,31	19,49793718	16,78367707	15,66569885	
4945.S1.4	2022/30759	-2,68	-2,65	27,37850328	29,96997083	22,74982476	4945.S1.4
		-2,96	-2,93	26,54788322	28,58012143	22,00315034	
4945.S2.1	2022/30753	-3,62	-3,59	24,58490221	25,29552945	20,23855571	4945.S2.1
		-3,43	-3,40	25,14941745	26,24011435	20,74601888	
4945.S2.2	2022/30754	-3,83	-3,80	23,96676636	24,26122291	19,68289103	4945.S2.2
		-3,64	-3,61	24,52228931	25,19076133	20,18227071	
4945.S2.3	2022/30755	-6,72	-6,69	15,41078026	9,944770931	11,99160566	4945.S2.3
		-6,58	-6,54	15,84574008	10,67257499	12,38260678	
4945.S3.1	2022/30760	-2,65	-2,61	27,47175653	30,12600846	22,83365348	4945.S3.1
		-2,52	-2,48	27,85809144	30,77245004	23,1809439	
4945.S3.2	2022/30761	-3,34	-3,31	25,41530024	26,68500733	20,98503054	4945.S3.2
		-3,84	-3,80	23,95610884	24,24339004	19,67331061	
4945.S3.3	2022/30762	-3,20	-3,17	25,82272815	27,36674314	21,35128222	4945.S3.3
		-3,67	-3,64	24,44568843	25,06258757	20,1134114	
4945.X1	2022/30763	-3,90	-3,86	23,77892766	23,94691856	19,51403603	4945.X1
		-3,75	-3,72	24,21455357	24,67583717	19,90563593	

4945.X2	2022/30764	-2,30	-2,27	28,50087281	31,84799509	23,75876332	4945.X2
		-2,30	-2,26	28,50953204	31,8624843	23,76654742	
4945.X3	2022/30765	-1,76	-1,72	30,1084923	34,53797227	25,20391063	4945.X3
		-2,07	-2,04	29,18561813	32,99375707	24,37430566	
4945.X4	2022/30766	-3,08	-3,04	26,20151399	28,00055311	21,69178651	4945.X4
		-3,06	-3,02	26,25746594	28,09417568	21,74208375	

3.3.2 $\delta^{13}\text{C}_{\text{PDB}}$ results and paleoenvironment

The $\delta^{13}\text{C}$ analysis indicates a predominance of C3 vegetation in the Chelas flora, resembling a messic forest environment (Table 5), with values consistently hovering around -9‰, falling within the upper range typical of messic forests and close to that of mixed forests.

Table 5. Results of the paleoecological interpretations based on Domingo et al., (2012) where $\delta^{13}\text{C}$ in closed canopy forests would vary between -20 and -14‰, messic/forest between -14 and -9‰, open, arid C3 between -9 and -6‰, mixed C3-C4 between -6 and -1‰ and strict C4 feeders between -1‰ and +7‰. Color scaled showing higher values (slightly more arid).

Sample	N° SAI	$\delta^{13}\text{C}_{\text{VPDB}}(\text{‰})$	Domingo et al., 2012).
4943.X1	2022/30752	-9,95	messic/forest
		-10,09	messic/forest
4944.S1.1	2022/30767	-9,74	messic/forest
		-9,63	messic/forest
4944.S1.2	2022/30768	-9,69	messic/forest
		-9,79	messic/forest
4944.S1.3	2022/30769	-9,97	messic/forest
		-10,12	messic/forest
4944.S2.1	2022/30770	-9,70	messic/forest
		-9,72	messic/forest
4944.S2.2	2022/30771	-9,95	messic/forest
		-9,97	messic/forest
4944.X1	2022/30772	-9,51	messic/forest
		-9,46	messic/forest
4944.X2	2022/30773	-9,83	messic/forest
		-9,71	messic/forest
4944.X3	2022/30774	-9,96	messic/forest
		-9,91	messic/forest
4944.X4	2022/30775	-9,96	messic/forest
		-9,94	messic/forest
4945.S2.1	2022/30753	-9,61	messic/forest
		-9,59	messic/forest
4945.S2.2	2022/30754	-9,85	messic/forest

		-9,84	messic/forest
4945.S2.3	2022/30755	-9,96	messic/forest
		-9,94	messic/forest
4945.S1.1	2022/30756	-9,36	messic/forest
		-9,34	messic/forest
4945.S1.2	2022/30757	-9,30	messic/forest
		-9,29	messic/forest
4945.S1.3	2022/30758	-9,73	messic/forest
		-9,70	messic/forest
4945.S1.4	2022/30759	-9,32	messic/forest
		-9,37	messic/forest
4945.S3.1	2022/30760	-9,70	messic/forest
		-9,69	messic/forest
4945.S3.2	2022/30761	-9,63	messic/forest
		-9,66	messic/forest
4945.S3.3	2022/30762	-9,80	messic/forest
		-9,84	messic/forest
4945.X1	2022/30763	-9,19	messic/forest
		-9,23	messic/forest
4945.X2	2022/30764	-9,28	messic/forest
		-9,29	messic/forest
4945.X3	2022/30765	-9,19	messic/forest
		-9,16	messic/forest
4945.X4	2022/30766	-9,56	messic/forest
		-9,55	messic/forest

A C3 messic forest environment is characterized by a temperate climate with moderate and well-distributed rainfall throughout the year, supporting a diverse vegetation. These forests are typically dominated by C3 plants, which use the C3 carbon fixation pathway in photosynthesis, making them well-suited to cooler, wetter conditions compared to C4 and CAM plants. The forest canopy is often dense, providing a shaded understory where moisture levels remain relatively high (Percy & Ehleringer, 1984). This shading effect helps maintain a stable microclimate with less variation in temperature and humidity, fostering the growth of a variety of plant species, including broadleaf deciduous trees, shrubs, and a rich understory of herbaceous plants. Common tree species in these Mid Miocene Lisbon forests included oaks (*Quercus*), maples (*Acer*), beeches (*Fagus*), and elms (*Ulmus*), among others (Pais, 1986; Vieira et al., 2009).

The soil in a C3 messic forest is typically rich in organic matter, benefiting from the continuous input of leaf litter and other plant debris, which decompose and contribute to the nutrient cycle. This fertile soil supports a diverse array of flora and fauna, creating a complex

ecosystem with multiple trophic levels. Animal life in these forests is abundant and varied, with many species adapted to the relatively stable and moist conditions (Pearcy & Ehleringer, 1984). Mammals, birds, insects, and amphibians thrive in this kind of ecosystems, contributing to the dynamic ecological interactions within the forest.

Discussion

This study encompassed three major areas: morphological analysis and comparison, palynological analysis, and biochemistry analysis, to reconstruct the climate, vegetation, environment and landscape in which the study animal lived during the Middle Miocene in the Lisbon Area. With this study it was possible to understand the ecology of *Chelas* and *Charneca* and to detect the climatic scenario and fluctuations accompanying these mammals.

4.1 *Gomphotherium angustidens*: Updating the Systematics of the Middle Miocene Proboscideans from Portugal

The updated systematic identification of the proboscidean material is a critical step in refining our understanding of these specimens. Following the diagnosis of different species of *Gomphotherium* and comparing them, all dental remains studied here, belong to *G. angustidens*. Our morphological analysis aligns with previous studies, particularly those by Wang et al., (2017) and Göhlich et al., (2010), which provide species-specific diagnoses.

By organizing the diagnoses in this structured way, it becomes easier to compare and contrast the dental features of various *Gomphotherium* species. This approach enhances the clarity of our analysis and enables a more detailed exploration of both the variations and commonalities among species, allowing for a more comprehensive evaluation of the material under investigation. Following are the diagnoses of the key elements of the genus:

***G. angustidens*:** The upper molars of *G. angustidens* exhibit compressed interlophs, with the first entoflexus forming a clear "Y" shape. In the lower molars, the first ectoflexid takes on a "V" shape (Figure 52). In contrast to species with a higher degree of zygodonty, *G. angustidens*, which has a lower degree of zygodonty, shows posttrite half-lophids that are notably bulky and pear-

shaped. These posttrite half-lophids feature a constriction in the middle, effectively dividing them into two distinct parts: the main conelet and the mesoconelet. This particular dental morphology reflects adaptations that likely influence the species' dietary habits and ecological niche, emphasizing the diversity within the *Gomphotherium* genus.

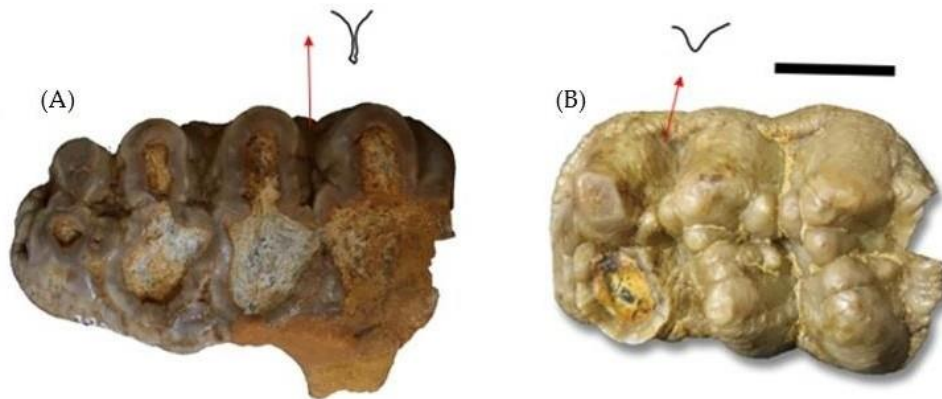


Figure 52. Specimen *G. angustidens* (GML 10612) interlophs (A) and (FCT-DCT 4942) interlophids (B) shape.

***G. subtapiroideum*:** The upper molars of this species feature wide anteroposterior interlophs, with the first entoflexus displaying a distinct "V" shape. In the lower molars, the first ectoflexid adopts a "U" shape. In taxa with a high degree of zygodonty, such as *G. subtapiroideum*, the posttrite half-lophids are anteroposteriorly compressed, forming an oval ring (Figure 53). This species exhibits a combination of bunodont and zygodont characteristics, a trait that has been recognized for some time (Schlesinger, 1917; Mazo, 1996; Göhlich, 2010). The cheek tooth crown pattern in *G. subtapiroideum* is generally slightly less bunodont compared to that of *G. angustidens* (Göhlich, 2010), highlighting subtle differences within the genus.

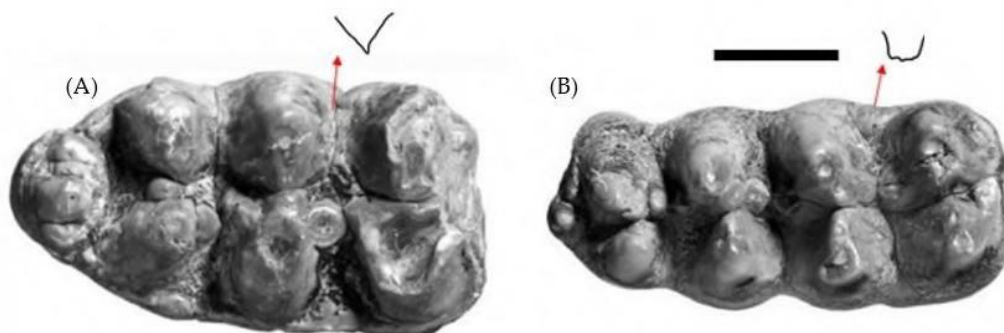


Figure 53. Speciment *G. subtapiroideum* (1959 II 4783) interlophs (A) and (1959 II 11381) interlophids (B) shape.

G. steinheimense: this taxon is distinguished by its larger molars compared to those of *G. angustidens* (Figure 54) with notable differences in the development and structure of the conules. These variations in dental morphology among different *Gomphotherium* species suggest distinct dietary preferences, which in turn indicate a low level of competition for food resources among them. According to a study by Calandra et al., (2008), *G. subtapiroideum* likely consumed more abrasive materials than *G. steinheimense*. This conclusion is drawn from the wear patterns and structure of the teeth, which reflect the types of vegetation and other dietary components each species primarily ingested. The interlophids space are very similar to *Gomphotherium angustidens* species, being difficult to differentiate these species just with the interloph/interlophid methods.



Figure 54. Specimen *G. steinheimense* interlophs shape, Wu et al., (2018).

G. sylvaticum: this taxon has been proposed by (Tassy, 1985; Gohlich, 1999) as the ancestral species to *G. steinheimense*, indicating a potential evolutionary lineage between these two taxa. One notable dental characteristic of *G. sylvaticum* is the shape of the interlophs in its upper molars, which are 'Y'-shaped and exhibit anteroposterior compression (Figure 55). In contrast, the interlophids in the lower molars of *G. sylvaticum* are 'U'-shaped, displaying an anteroposteriorly wide structure.

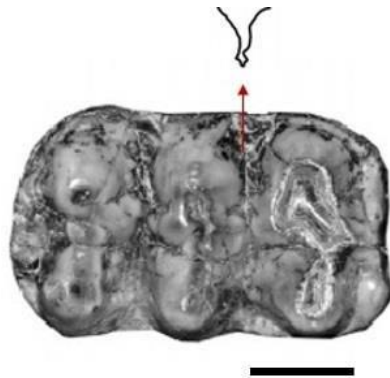


Figure 55. Specimen *G. sylvaticum* (MNHN 1787) interlophs shape, after Tassy, (2014); Wang et al., (2017).

4.2 Palynomorph and $\delta^{13}\text{C}$: Vegetation Reconstitution

Although the pollen analysis only presented contamination than fossils it was an important part of this study because it proves the impact of the pavement in the area, which makes a deeper search impossible. During Miocene in Portugal, the vegetation had abundance of certain pollen types, such as oak (*Quercus*), beech (*Fagus*), walnut (*Juglans*), and laurel (*Laurus*). Previous studies (Figure 56) have extensively documented Miocene pollen types, including those from a variety of tree species such as chestnut (*Castanea*), elm (*Ulmus*), and various herbaceous plants (Pais, 1986; Vieira et al., 2009; Pais, 2010). Throughout Langhian and Serravallian stages of the Miocene, inland forests flourished under warm temperate climate conditions, characterized by well-marked dry seasons. The development of these forests underscores the dynamic nature of climatic patterns during this period, providing valuable insights into the ecological landscape of ancient Portugal (Pais, 1986). By studying the composition and distribution of pollen types, researchers can gain a deeper understanding of the climatic fluctuations and environmental dynamics that shaped the Miocene landscape in this region.

Epoch		Units	Units Mein	Climate	Spores and Pollens	Vertebrate fossils
Mid Miocene	Serravalian	VIb	MN6	Humid and tropical, cooler than Langhian stage Inland forests	Sapotaceae, Quercus, Ulmus, Castanea...	
	Langhian	Vb	MN5	Subropical (warmer) and drier Forest galleries	Terminalia, Pinus, Magnolia	<i>Gomphotherium sp.</i>
Lower Miocene	Burdigalian	IVb	MN4b MN3b	Subtropical and temperate Forest and open spaces, rich vegetation; warm and humid climate	Bombax, Myrica, Quercus, Alnus, Sapotaceae...	First Mastodonts found
	Aquitanian			Tropical, warm and humid: allowing the development of dense forest		

Figure 56. Temperature and climate differences during the Miocene of Portugal, according to Pais, 1986; Vieira et al., 2009).

4.3 The $\delta^{18}\text{C}$ climate and Temperature Estimates

During the middle Miocene global climate transition approximately 15 Ma, global ice volume remained low, and bottom water temperatures exhibited a slight upward trend, interspersed with brief periods of glaciation. Throughout the studied time interval, temperature estimates, represented as Mean Annual Temperature (MAT) using Equations (1-3), range from 19.67°C (Eq 3) to 24.24°C (Eq 1). The results obtained from the $\delta^{18}\text{O}$ analysis indicate consistently warm MATs (°C) across all samples, with some minor fluctuations observed when examining different enamel sections, which indicates seasons changes. These findings align with our initial predictions and are consistent with existing knowledge regarding the paleoclimate of Lisbon derived from marine and pollen records (Vieira et al., 2009; Pais et al., 2010). The mammal continental records now provide further evidence of how this warm period manifested in Lisbon's climate was consistent with global conditions.

Conclusions

This study encompassed three major areas: morphological comparison, palynology and biochemistry, to reconstruct the climate, vegetation and environment in which the studied animal lived. With this study it was possible to understand the ecology of Chelas and to detect climatic fluctuations.

The differentiation studied here shows that the new dental remains has features of *Gomphotherium angustidens*, a ubiquitous taxon of the European fauna during the Miocene and widely described in Portugal. *Gomphotherium* remains a very diverse and controversial genus with several species, through the comparison made, it was easier to exclude some taxons, like *Deinotherium*, *Anancus* and *Zygodont*. The species differentiation was more difficult because of the patterns, which can be tricky considering age, tooth position and diet. This study shows that is possible to differentiate the species but also teaches us that Gomphotheres, clearly needs more studies that encompasses all the elements already mentioned. Most of the teeth remains were identified as *G. angustidens*, while the occipital bone and thoracic vertebrae were identified as *Gomphotherium* genus, possibly *G. angustidens* because of the record of this species in Lisbon. The isotopes essays reveal evidence for seasonal changes in temperatures (Winter/Summer) with oscillations of temperature (dryer/humid, warmer/colder) and the flora dominated by C3 vegetation. The pollen bibliographical research reveals a mosaic of forested and open environments, like woodlands.

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Appendix

App.1.2 Measurements (mm) of upper M1. **Data.** *G. tassyi* (Wang et al., 2017); *G. cooperi* (Liet al., 2022); *Gomphotherium* sp. (FCT-DCT); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>G. tassyi</i> (HMF 0028)	103	73,0
<i>G. tassyi</i> (HMF 0028)	100	75,5
<i>G. cooperi</i> (V25395)	67,4	47,43
<i>G. cooperi</i> (V25395)	68,92	47,34
<i>Gomphotherium</i> sp. (FCT-DCT 5362)	78,33	54,14
<i>G. libycum</i> (97-675)	76,0	49,5
<i>G. subtapiroideum</i> (1959 II 440)	85,5	58,0
<i>G. subtapiroideum</i> (1959 II 11351)	72,0	47,0
<i>G. subtapiroideum</i> (1959 II 11352)	73,0	55,0
<i>G. subtapiroideum</i> (1959 II 11353)	73,0	53,0
<i>Gomphotherium</i> sp. (Museum 10624)	78,71	50,85
<i>Gomphotherium</i> sp. (Museum 10625)	79,97	47,53
<i>Gomphotherium</i> sp. (Museum 10626)	71,81	40,92

<i>Gomphotherium</i> sp. (Museum 7875)	82,48	54,71
<i>Gomphotherium</i> sp. (Museum 7876)	85,28	53,44

App 1.2. Measurements (mm) of lower m1. **Data.** *Serridentinus mongoliense* (Osborn, 1924; Wang et al., 2015); *G. subpitaroideum* (Gohlich, 2010), and *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>Serridentinus mongoliense</i> (19152)	99,0	58,0
<i>G. subpitaroideum</i> (1959 II 439)	76,0	44,5
<i>G. subpitaroideum</i> (1959 II 453)	65,0	44,0
<i>G. subpitaroideum</i> (1959 II 42)	65,0	41,0
<i>G. subpitaroideum</i> (1959 II 11360)	63,5	41,0
<i>Gomphotherium</i> sp. (Museum 7952)	72,85	42,68
<i>Gomphotherium</i> sp. (Museum 7953)	73,21	43,43
<i>Gomphotherium</i> sp. (Museum 7954)	70,94	43,38
<i>Gomphotherium</i> sp. (Museum 7955)	80,88	46,12
<i>Gomphotherium</i> sp. (Museum 7956)	75,57	46,48
<i>Gomphotherium</i> sp. (Museum 7957)	80,12	45,97
<i>Gomphotherium</i> sp. (Museum 7958)	83,06	44,84
<i>Gomphotherium</i> sp. (Museum 7959)	82,93	46,48
<i>Gomphotherium</i> sp. (Museum 7960)	74,19	40,59
<i>Gomphotherium</i> sp. (Museum 10618)	46,84	45,72
<i>Gomphotherium</i> sp. (Museum 10617)	79,70	43,51

App 1.3. Measurements (mm) of upper M2. **Data.** *G. tassyi* (Wang et al, 2017); *G. cooperi* (Li et al., 2022); *G. sylvaticum* (Tassy, 1977); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. inopinatum* (Borissiak & Belyaeva, 1928; Wang et al., 2015); *G. steinheimense* (Gohlich, 1998); *Gomphotherium* sp. (FCT-DCT); *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>G. tassyi</i> (HMV 0028)	130,5	87,0
<i>G. tassyi</i> (HMV 0028)	134,5	89,0
<i>G. cooperi</i> (V25395)	96,98	60,63
<i>G. cooperi</i> (V25395)	96,55	60,58
<i>G. sylvaticum</i>	103,0	56,0
<i>G. sylvaticum</i>	105,0	60,0
<i>G. libycum</i> (DPC 6442)	122,2	68,9
<i>G. libycum</i> (97-655)	107,6	61,4
<i>G. subtapiroideum</i> (1959 II 438)	109,0	65,0
<i>G. subtapiroideum</i> (1959 II 384)	87,0	59,0
<i>G. subtapiroideum</i> (1959 II 11364)	95,0	65,0
<i>G. subtapiroideum</i> (1959 II 11365)	98,0	57,0
<i>G. subtapiroideum</i> (1959 II 11366)	98,0	65,0
<i>G. subtapiroideum</i> (1959 II 11367)	91,0	59,5
<i>G. subtapiroideum</i> (1959 II 11368)	113,0	68,0
<i>G. inopinatum</i>	116,0	72,0
<i>G. steinheimense</i>	124,0	78,0
<i>Gomphotherium</i> sp. (FCT-DCT 5359)	106,96	59,2
<i>Gomphotherium</i> sp. (FCT-DCT 5364)	93,19	69,70

<i>Gomphotherium</i> sp. (Museu 10623)	99,25	60,78
<i>Gomphotherium</i> sp. (Museu 7887)	95,34	64,59
<i>Gomphotherium</i> sp. (Museu 7911)	106,89	61,45
<i>Gomphotherium</i> sp. (Museu 7912)	100,90	59,35

App 1.4. Measurements (mm) of lower m2. **Data.** *G. tassyi* (Wang et al., 2017); *G. cooperi* (Osborn, 1932; Wang et al., 2015); *Serridentinus productus* (Frick & Rak, 1926); *Serridentinus mongoliensis* (Osborn, 1924; Wang et al., 2015); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders, 2002); *G. subtapiroideum* (Gohlich, 2010); *G. wimani* (Hopwood, 1935; Wang et al., 2015); *G. browni* (Osborn, 1926; Wang et al., 2015); *G. inopinatum* (Wang, 2014); *Gomphotherium* sp. (NOVA/FCT); *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>G. tassyi</i> (HNV 1807)	114,5	69,5
<i>G. tassyi</i> (HNV 1940)	114,0	71,0
<i>G. tassyi</i> (HNV 1948)	120,0	73,0
<i>G. tassyi</i> (HNV 1824)	116,0	66,0
<i>G. cooperi</i> (M 12181)	100,0	55,0
<i>Serridentinus productus</i> (AM21111)	120,0	50,38
<i>Serridentinus mongoliensis</i> (19152)	108,0	59,0
<i>G. connexum</i> (RV35015)	103,49	45,13
<i>G. libycum</i> (DPC 12926)	116,4	59,4
<i>G. libycum</i> (DPC 4581)	119,4	60,2
<i>G. subtapiroideum</i> (1959 II 384)	84,0	54,0

<i>G. subtapiroideum</i> (1959 II 11360)	90,0	53,0
<i>G. subtapiroideum</i> (1959 II 11362)	80,0	50,0
<i>G. subtapiroideum</i> (1959 II 11376)	104,0	62,0
<i>G. subtapiroideum</i> (1959 II 11377)	107,0	61,0
<i>G. subtapiroideum</i> (1959 II 11378)	112,0	64,0
<i>G. wimani</i>	103,0	71,0
<i>G. browni</i>	114,0	72,0
<i>G. browni</i>	118,0	73,0
<i>G. inopinatum</i> (IVPPV18700)	92,0	56,0
<i>Gomphotherium</i> sp. (FCT-DCT 4942)	91,75	59,43
<i>Gomphotherium</i> sp. (Museu 10619)	111,55	54,16
<i>Gomphotherium</i> sp. (Museu 10622)	103,70	61,50
<i>Gomphotherium</i> sp. (Museu 10631)	74,09	44,80
<i>Gomphotherium</i> sp. (Museu 10646)	87,92	73,81
<i>Gomphotherium</i> sp. (Museu 10647)	100,58	63,55
<i>Gomphotherium</i> sp. (Museu 7946)	97,82	56,69
<i>Gomphotherium</i> sp. (Museu 7947)	93,73	55,63
<i>Gomphotherium</i> sp. (Museu 7948)	92,12	58,98
<i>Gomphotherium</i> sp. (Museu 7949)	105,22	57,09
<i>Gomphotherium</i> sp. (Museu 7951)	97,14	59,98
<i>Gomphotherium</i> sp. (Museu 7976)	94,84	54,89
<i>Gomphotherium</i> sp. (Museu 7977)	102,0	54,05
<i>Gomphotherium</i> sp. (Museu 7883)	107,65	65,92

<i>Gomphotherium</i> sp. (Museu 7884)	112,9	62,64
<i>Gomphotherium</i> sp. (Museu 7885)	110,89	63,81
<i>Gomphotherium</i> sp. (Museu 7886)	106,84	63,72

App 1.5. Measurements (mm) of upper M3. **Data.** *G. tassyi* (Wang et al., 2017); *Gomphotherium* sp. (FCT-DCT); *G. inopinatum* (Borissiak & Belyaeva, 1928; Wang et al., 2015); *G. sylvaticum* (Tassy, 1977); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>G. tassyi</i> (HNV 1949)	151,0	83,0
<i>G. tassyi</i> (HNV 1810)	171,0	80,0
<i>Gomphotherium</i> sp. (FCT-DCT 4944)	116,52	72,8
<i>G. inopinatum</i>	149,0	62,0
<i>G. sylvaticum</i>	161,0	68,0
<i>G. sylvaticum</i>	161,0	70,0
<i>G. connexum</i> (RV35049)	120,01	62,08
<i>G. connexum</i> (V8572)	186,93	83,78
<i>G. connexum</i> (V8573)	170,72	82,74
<i>G. connexum</i> (V8576)	176,15	74,93
<i>G. libycum</i> (97-656)	149,5	77,70
<i>G. libycum</i> (M 14075)	148,2	65,0
<i>G. subtapiroideum</i> (1959 II 384)	128,0	67,0
<i>G. subtapiroideum</i> (1959 II 3722)	127,5	76,0

<i>G. subtapiroideum</i> (1959 II 4783)	137,0	75,5
<i>G. subtapiroideum</i> (1959 II 11380)	123,0	70,0
<i>Gomphotherium</i> sp. (Museu 10607)	124,73	63,76
<i>Gomphotherium</i> sp. (Museu 10610)	107,21	65,80
<i>Gomphotherium</i> sp. (Museu 10612)	153,84	79,53
<i>Gomphotherium</i> sp. (Museu 10614)	101,99	58,77
<i>Gomphotherium</i> sp. (Museu 10615)	125,86	59,74
<i>Gomphotherium</i> sp. (Museu 7971)	153,98	84,16
<i>Gomphotherium</i> sp. (Museu 7974)	148,05	71,74
<i>Gomphotherium</i> sp. (Museu 7975)	102,07	57,30

App 1.6. Measurements (mm) of lower m3. **Data.** *G. tassyi* (Wang et al., 2017); *Gomphotherium* sp. (FCT-DCT); *G. inopinatum* (Wang, 2014); *Serridentinus productus* (Frick & Rak, 1926); *G. cooperi* (Osborn, 1932; Wang et al., 2015); *Serridentinus mongoliensis* (Osborn, 1924; Wang et al., 2015); *G. connexum* (Wang et al., 2015); *G. libycum* (Sanders & Miller, 2002); *G. subtapiroideum* (Gohlich, 2010); *Gomphotherium* sp. (Museu Geológico de Lisboa).

List of the data consulted	Length	Width
<i>G. tassyi</i> (HNV 1945)	188,5	86,0
<i>G. tassyi</i> (HNV 1807)	165,0	75,5
<i>Gomphotherium</i> sp. (FCT-DCT 5363)	87,9	53,88
<i>Gomphotherium</i> sp. (FCT-DCT 4945)	154,14	77,63
<i>G. inopinatum</i> (IVPPV 18700)	149,0	68,0
<i>Serridentinus productus</i> (AM21111)	153,0	60,55
<i>G. cooperi</i> (M 12181)	147,0	63,0

<i>Serridentinus mongoliensis</i> (19152)	138,0	63,0
<i>G. connexum</i> (RV35015)	148,52	51,45
<i>G. connexum</i> (V18701)	191,09	68,10
<i>G. connexum</i> (V8571)	172,02	76,04
<i>G. connexum</i> (V8575)	169,99	64,27
<i>G. libycum</i> (97/1245)	147,10	68,40
<i>G. libycum</i> (DPC 2579)	113,0	69,10
<i>G. subtapiroideum</i> (1959 II 384)	132,0	60,0
<i>G. subtapiroideum</i> (1959 II 3723)	150,0	73,0
<i>G. subtapiroideum</i> (1959 II 11383)	152,0	74,0
<i>G. subtapiroideum</i> (1959 II 11381)	161,0	74,0
<i>G. subtapiroideum</i> (1959 II 11382)	131,0	63,0
<i>G. subtapiroideum</i> (1959 II 11384)	133,0	62,0
<i>G. subtapiroideum</i> (1959 II 11385)	155,0	79,0
<i>Gomphotherium</i> sp. (Museu 10637)	153,88	77,43
<i>Gomphotherium</i> sp. (Museu 10640)	148,17	73,42
<i>Gomphotherium</i> sp. (Museu 10643)	165,02	79,01
<i>Gomphotherium</i> sp. (Museu 10644)	169,51	77,20
<i>Gomphotherium</i> sp. (Museu 16701)	128,94	77,16
<i>Gomphotherium</i> sp. (Museu 10606)	182,83	68,71
<i>Gomphotherium</i> sp. (Museu 10611)	153,93	80,79
<i>Gomphotherium</i> sp. (Museu 10613)	158,88	65,71

<i>Gomphotherium</i> sp. (Museu 7962)	134,99	61,43
<i>Gomphotherium</i> sp. (Museu 7963)	131,27	58,7
<i>Gomphotherium</i> sp. (Museu 7964)	136,35	56,70
<i>Gomphotherium</i> sp. (Museu 7965)	139,97	64,98
<i>Gomphotherium</i> sp. (Museu 7966)	143,54	65,73
<i>Gomphotherium</i> sp. (Museu 7967)	122,31	58,92
<i>Gomphotherium</i> sp. (Museu 7968)	127,65	64,07
<i>Gomphotherium</i> sp. (Museu 7969)	182,78	87,56
<i>Gomphotherium</i> sp. (Museu 7970)	153,88	79,56
<i>Gomphotherium</i> sp. (Museu 7987)	153,93	70,82
<i>Gomphotherium</i> sp. (Museu 7988)	147,72	62,0
<i>Gomphotherium</i> sp. (Museu 7989)	180,62	73,91
<i>Gomphotherium</i> sp. (Museu 7990)	153,92	73,92
<i>Gomphotherium</i> sp. (Museu 7991)	184,65	79,04
<i>Gomphotherium</i> sp. (Museu 7992)	142,99	68,31

B

APPENDIX

Tables of the Biochemistry results, each entry in the table includes the following information:

- "Sample": Indicates the sample being analyzed.
- "Nº SAI": Refers to the Sample Number (SAI) for identification purposes.
- " $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ ": Represents the Carbon Isotope Composition ($\delta^{13}\text{C}_{\text{VPDB}}$) measured in per mil (‰).
- " $\delta^{18}\text{O}_{\text{VPDB}} (\text{‰})$ ": Indicates the Oxygen Isotope Composition ($\delta^{18}\text{O}_{\text{VPDB}}$) measured in per mil (‰).

App 2.1. Results of the isotopic analysis. Sample; "Nº SAI" - Sample Number (SAI) " $\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$ " - Carbon Isotope Composition ($\delta^{13}\text{C}_{\text{VPDB}}$) in per mil (‰) " $\delta^{18}\text{O}_{\text{VPDB}} (\text{‰})$ " - Oxygen Isotope Composition ($\delta^{18}\text{O}_{\text{VPDB}}$) in per mil (‰).

Sample	Nº SAI	$\delta^{13}\text{C}_{\text{VPDB}} (\text{‰})$	$\delta^{18}\text{O}_{\text{VPDB}} (\text{‰})$
4943.X1	2022/30752	-9,95	-4,0
		-10,09	-4,16
4944.S1.1	2022/30767	-9,74	-4,19
		-9,63	-4,05
4944.S1.2	2022/30768	-9,69	-3,30
		-9,79	-3,06
4944.S1.3	2022/30769	-9,97	-3,40
		-10,12	-3,61
4944.S2.1	2022/30770	-9,70	-3,93

		-9,72	-3,61
4944.S2.2	2022/30771	-9,95 -9,97	-3,09 -2,73
4945.S1.1	2022/30756	-9,36 -9,34	-2,45 -2,43
4945.S1.2	2022/30757	-9,30 -9,29	-3,63 -3,70
4945.S1.3	2022/30758	-9,73 -9,70	-5,61 -5,34
4945.S1.4	2022/30759	-9,32 -9,37	-2,68 -2,96
4945.S2.1	2022/30753	-9,61 -9,59	-3,62 -3,43
4945.S2.2	2022/30754	-9,85 -9,84	-3,83 -3,64
4945.S2.3	2022/30755	-9,96 -9,94	-6,72 -6,58
4945.S3.1	2022/30760	-9,70 -9,69	-2,65 -2,52
4945.S3.2	2022/30761	-9,63 -9,66	-3,34 -3,84
4945.S3.3	2022/30762	-9,80 -9,84	-3,20 -3,67
4945.X1	2022/30763	-9,19 -9,23	-3,90 -3,75
4945.X2	2022/30764	-9,28 -9,29	-2,30 -2,30
4945.X3	2022/30765	-9,19 -9,16	-1,76 -2,07
4945.X4	2022/30766	-9,56 -9,55	-3,08 -3,06



⟨2024⟩ PRISCILA MOREIRA LOHMANN

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