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Palaeoecology of Early Miocene proboscideans from the Aragonian type area (Iberian Peninsula)[☆]

Francisco Alquézar-Blesa [a], Beatriz Azanza [a,b], Daniel DeMiguel [a,b,c], Flavia Strani [a,b,*]

[a] Departamento de Ciencias de La Tierra, Universidad de Zaragoza, 50009 Zaragoza, Spain
[b] Instituto Universitario de Investigación en Ciencias Ambientales de Aragón (IUCA), Universidad de Zaragoza, 50009 Zaragoza, Spain
[c] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193 Barcelona, Spain

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ABSTRACT

The northeast Iberian Peninsula preserves fossil localities that record the Miocene Climatic Optimum (MCO) and the Middle Miocene Climatic Transition (MMCT). Specifically, the Calatayud-Daroca Basin is the reference area for European Early-Middle Miocene mammal palaeocommunities (Aragonian type area), and includes the Artesilla locality (~16.49 Ma) which contains the earliest records of diverse proboscideans (Gomphotheriidae and Deinotheriidae), following their dispersal from Africa to Europe at the onset of the MCO. In this paper, we study the palaeoecology of *Gomphotherium* and *Prodeinotherium* from the Aragonian type area to investigate habitat adaptation during the early phases of the MCO and compare results with the palaeoecology of *Gomphotherium* specimens from Tarazona (~14.50 Ma), a rich Middle Miocene locality in the nearby Ebro Basin at the onset of the MMCT. Proboscideans are among the best-studied examples of the evolutionary response of herbivorous mammals to changes in vegetation following Neogene C4 grassland expansion. A clear transition from a "mastodont-like" low-crowned bunolophodont tooth morphology with a reduced number of loph(*id*)s to an "elephant-like" high-crowned lophodont teeth adapted to grass-consumption is observed between Early and Late Neogene forms. We analyse ecometric parameters (hypsodonty, enamel thickness and number of loph(*id*)s) and dental wear patterns of individuals from Artesilla and Tarazona. We find that while both taxa, *Gomphotherium* and *Prodeinotherium*, displayed dental morphologies that are concordant with a low-abrasion diet, as observed in other early forms of these groups, dietary signals indicate more abrasive feeding behaviours. These results suggest that some lineages of proboscideans adapted to grass-rich diets more than 7 Myr before the Late Neogene expansion of open grasslands.

1. Introduction

The order Proboscidea (Afrotheria, Mammalia) includes large mammals that originated in Africa whose earliest known representative were of Paleocene age, near the beginning of the placental radiation (Gheerbrant, 2009). Proboscideans first dispersed into Europe during the Early Miocene (23.04–15.98 Ma, International Chronostratigraphic Chart v2024/12) in multiple migration waves through the temporal passage that originated by the tectonic collision between the Afro-Arabia and Eurasia plates. This so-called *Gomphotherium* land bridge allowed terrestrial mammal exchanges between both landmasses (Harzhauser et al., 2007). These dispersion events occurred between latest MN3 to early MN4 (from ~18.5 to ~16.5 Ma) (Tassy, 1990; Göhlich, 1999; Harzhauser et al., 2007; Konidaris and Tsoukala, 2022) just before or coincident with the onset of the Miocene Climatic Optimum (MCO, ~16.9–14.7 Ma; Steinthorsdottir et al., 2021), a major climatic event characterised by the rise of global mean temperatures (~7–8 °C higher than present day; Steinthorsdottir et al., 2021) (Böhme, 2003; You et al., 2009; Westerhold et al., 2020; Larrasoaña et al., 2025). After this interval, during the Middle Miocene Climatic Transition (MMCT, ~14.7–13.8 Ma; Steinthorsdottir et al., 2021), cooler global conditions facilitated the expansion of more open landscapes and promoted the spread and diversification of numerous mammal lineages across Eurasia and Africa, including the proboscideans (Flower and Kennett, 1994; Westerhold et al., 2020; Cantalapiedra et al., 2021). In the European continent, three proboscidean families became

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[*] Corresponding author at: Departamento de Ciencias de La Tierra, Universidad de Zaragoza, 50009 Zaragoza, Spain.
E-mail address: flavia.strani@unizar.es (F. Strani).

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widespread during the Early Miocene. Deinotheriidae (deinotheres) were characterised by downward-curved mandibular tusks, and include *Prodeinotherium cuvieri* as the first European representative (Gasamans et al., 2021). Gomphotheriidae (sensu Shoshani and Tassy, 2005) were represented by the trilophodont-bunolophodont gomphotheres with four tusks, especially *Gomphotherium* and *Archaeobelodon* (amebelodont). Mammutidae, with zygodont cheek teeth, were represented by the less common genus *Zygolophodon* (Göhlich, 1999). Among *Gomphotherium, G. subtapiroideum* shows combined characteristics of both bunodont and zygodont teeth (Göhlich, 2010; Wang et al., 2017). The late Early Miocene locality of Artesilla (Calatayud-Daroca Basin, Iberian Peninsula) represents the oldest known Iberian record of a diverse proboscidean fauna represented by *Gomphotherium*, *Archaeobelodon* and *Prodeinotherium* and also records other possible African origin immigrants as creodonts (*Hyainailouros*) and felids (*Afrosmilus*) (Azanza et al., 1993).

Proboscideans are a group of herbivorous mammals whose dietary adaptations have varied considerably during their evolutionary history. They have progressively adapted to habitat changes following major Neogene and Quaternary climatic shifts (Cantalapiedra et al., 2021; Saarinen and Lister, 2023). One of the most distinctive features of this group is therefore the diverse tooth morphologies recorded in fossil taxa. While the earliest Palaeogene proboscideans were small-bodied tusk-less animals, subsequent taxa displayed major cranial and dental specialisations. These included hypertrophied incisors (tusks) and increasingly complex premolar and molar morphology, and high-crowned (hypsodont) and crest-rich (lophodont) teeth (Nabavizadeh, 2024). These major modifications in proboscidean molar morphology have been explained as an adaptation to the Late Neogene expansion of open grasslands, although some key innovations like lamelliform lophs and increased loph number compared to Palaeogene early lophodont taxa, have been recorded already around 10 Ma (Edwards et al., 2010; Saarinen and Lister, 2023). In proboscideans, hypsodont teeth with a significant number of loph(*id*)s and a thin enamel layer reflect an adaptation that allows them to efficiently chew on abrasive items, such as phytolith-rich grasses. In contrast, brachydont teeth with few loph(*id*)s and a thicker enamel layer are associated with taxa that feed in wooded areas (Ferretti, 2003; Damuth and Janis, 2011; Kaiser et al., 2013; Saarinen and Lister, 2023).

During the Early and Middle Miocene, the Northern Hemisphere experienced increasingly warm and humid conditions followed by a phase of greater aridity occurring during the Late Miocene (Eronen et al., 2012). However, the dietary patterns and hypsodonty indices of late Early Miocene fossil ungulates from the Iberian Peninsula suggest that the onset of the aridification phase occurred earlier in this region than elsewhere in Europe (DeMiguel et al., 2012; Eronen et al., 2010, 2012). In this context, it is also worth noting that biozones established in the Aragonian type area provide a more precise biostratigraphic framework (Daams et al., 1999; Freudenthal, 2006; Van der Meulen et al., 2012) for interpreting these environmental changes (DeMiguel et al., 2012).

Here, we investigate the feeding behaviours of *Gomphotherium* and *Prodeinotherium* from the Aragonian type area (the site of Artesilla; ~16.49 Ma, biozone Ca correlated with the European MN4 zone; Freudenthal, 2006; Van der Meulen et al., 2012) (Fig. 1A) to understand how proboscideans lacking dental adaptations for grass-consumption responded to a shift towards drier conditions. To do so, we analyse molar ecometric variables and dental wear patterns, as these reflect, respectively, phylogenetic information about dietary adaptation of species and a more direct signal about the type of vegetation consumed by individuals (Grine, 1986; Saarinen et al., 2015; Strani et al., 2025).

2. Material and methods

Macroscopic ecometric traits of proboscidean dentition reflecting adaptive strategies to feed in different habitat conditions include dental crown height (hypsodonty), the number of loph(*id*)s, and enamel thickness (Saarinen and Lister, 2023). Dental meso- and microwear patterns represent a taxon-free signal of a species diet providing information respectively on the long- and short-term feeding behaviours of

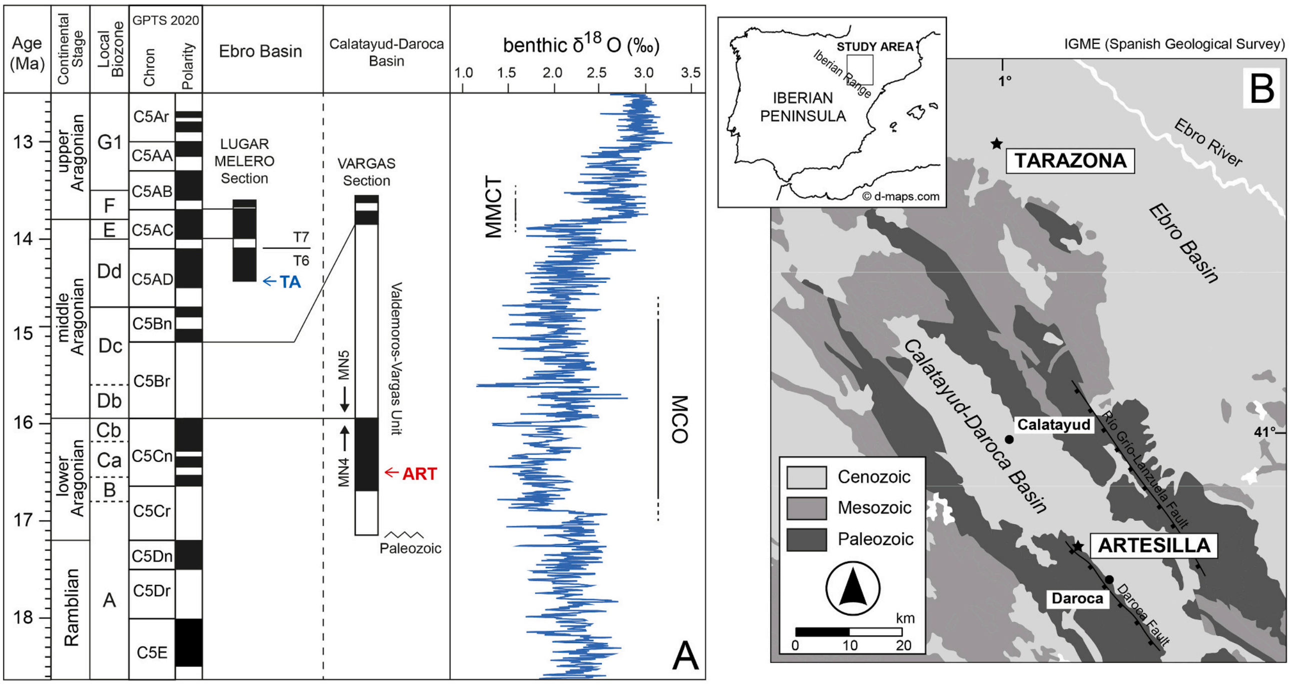

Fig. 1. Chronology for the Early and Middle Miocene faunas from the Iberian Peninsula showing the position of Artesilla (ART) and Tarazona (TA) with respect to the Miocene Climatic Optimum (MCO) and Middle Miocene Climatic Transition (MMCT) (Lugar Melero and Vargas Sections modified from Pérez-Rivarés et al., 2018 and Van der Meulen et al., 2012; benthic $\delta^{18}O$ curve modified from Westerhold et al., 2020) (A); Geological context of the Calatayud-Daroca and Ebro Basins (Iberian Peninsula) and location of Artesilla and Tarazona (AB) (maps from IGME – Spanish Geological Survey and d-maps.com).

extinct taxa (Grine, 1986; Solounias and Semprebon, 2002; Saarinen et al., 2015). We analysed ecometric variables and dental wear patterns of the gomphotheres and a deinothere from Artesilla (*Gomphotherium subtapiroideum*, *Prodeinotherium cuvieri*). At this site, *Archaeobelodon* is only represented by a juvenile upper tusk (Azanza et al., 1993), and was excluded from the present work. Raw data are included in Supplementary Dataset 1 (SI1). The studied material is stored at the Museum of Natural Sciences of the University of Zaragoza.

We compare the data obtained from late Early Miocene proboscideans of Artesilla with data from early Middle Miocene specimens of *Gomphotherium angustidens* from Tarazona (~14.50 Ma, Pérez-Rivarés et al., 2018; biozone Dd, correlated to MN5, Álvarez-Sierra et al., 2006) from the southern edge of the nearly Ebro Basin (SI2) (Fig. 1B), as well as data from other fossil and modern proboscideans (Solounias and Semprebon, 2002; Saarinen and Lister, 2016; Semprebon et al., 2016; Rivals et al., 2019; Xafis et al., 2020; Konidaris et al., 2023; Saarinen and Lister, 2023; Strani et al., 2025).

2.1. Ecometric variables

2.1.1. Hypsodonty

In herbivorous mammals, high-crowned (hypsodont) teeth are associated with abrasive diets, as they are resistant to wear over extended lifespans and indicate an adaptation to open, grass-dominated landscapes. Conversely, low-crowned (brachydont) teeth are linked to softer, less abrasive diets typical of browsing taxa usually feeding in wooded habitats (Damuth and Janis, 2011; Kaiser et al., 2013; but see DeMiguel et al., 2016). Following Saarinen and Lister (2023), we measured with a caliper the distance (in mm) from the root to the tip of the cusp of unworn or minimally worn upper (M3) and lower third molars (m3) (Fig. 2A, B). Then, we measured the maximum width (in mm) of the tooth's occlusal surface perpendicular to the anteroposterior axis. Hypsodonty was calculated as crown height/crown width × 100 to obtain an index that we compared with Saarinen and Lister (2023) dataset and calculated for eight specimens (six of *G. subtapiroideum* and one of *P. cuvieri* from Artesilla, and one of *G. angustidens* from Tarazona) (Table 1).

2.1.2. Number of loph(id)s

The number of lophs (upper molars) and lophids (lower molars) is also linked to dietary specialisation, as these structures increase the occlusal surface area and improve the processing of fibrous and abrasive plant matter (Saarinen and Lister, 2023). We measured the number of loph(*id*)s in both upper (M3) and lower (m3) third molars (Fig. 2A, B). A total of seven specimens where studied (five for *G. subtapiroideum* and one of *P. cuvieri* from Artesilla, and one for *G. angustidens* from Tarazona) (Table 1). Data were compared with the dataset of Saarinen and Lister (2023).

2.1.3. Enamel thickness

Thick enamel protects against phytolith abrasion and exogenous particles (grit, dust) that are typically ingested alongside plants growing at soil level such, as grasses and shrubs (Lakhal et al., 2025). In proboscideans, as molars developed higher number of lophs and higher crown heights, enamel was redistributed across the expanded occlusal surfaces. In some cases, this yielded relatively thinner enamel without reduced resistance (Ferretti, 2003; Saarinen and Lister, 2023). We only measured enamel thickness in areas where wear permitted a reliable assessment, selecting sections of the tooth where the enamel surface was sufficiently worn. As the tips of the cusps are typically the first areas to experience wear, our measurements were taken from these regions, which also tend to have the thickest enamel layer (Saarinen and Lister, 2023) (Fig. 2C). In very unworn teeth (Fig. 2D), enamel thickness was measured at those points where diagenetic fractures allowed reliable measurement to be taken as close as possible to the cusps. Enamel thickness was measured in both upper (M1–M3) and lower (m1–m3) molars of 25 individuals (17 of *G. subtapiroideum* from Artesilla, seven of *G. angustidens* from Tarazona and one of *P. cuvieri*) (Table 1).

2.2. Dental mesowear

Mesowear analysis is one of the most widely applied methods to reconstruct the feeding behaviour of fossil herbivorous mammals, as it is based on molar wear patterns produced by consumed plants during the mastication process over a long period of time (Fortelius and Solounias, 2000; Ackermans, 2020). Initially developed for ungulates by Fortelius and Solounias (2000), the method was later adapted for proboscideans by Saarinen et al. (2015). Rather than focusing on cusp shape scoring, as described by Fortelius and Solounias (2000), Saarinen et al. (2015) proposed measuring the angles formed between worn lamellae and the dentin valley (or the enamel bands and the dentin valley of a loph or lophid in bunolophodont taxa), as they observed that narrower angles in modern proboscideans reflect a browsing feeding behaviour, whereas wider angles are typically associated with a grass-rich diet. Mesowear angles below 106° are associated to a browsing diet, angles between 106° and 117° are associated to a mixed behaviour, and above 117° are associated to a grazing diet (Saarinen and Lister, 2023). Following the protocol described by Saarinen et al. (2015) which is also reliable for deinotheres and other bilophodont mammals (Wilson et al., 2025), measurements were taken using a modified digital goniometer equipped with two thin metal extensions on its arms. In this study, the method was applied to bunolophodont gomphothere and bilophodont deinothere teeth from Artesilla and Tarazona. For each specimen, two or three measurements were taken by setting the angle vertex at the lowest point of a worn dentin valley within a loph(id) and aligning its sides with the tops of the enamel ridges. These measurements were then averaged (Fig. 2C). We excluded unworn teeth from the analysis and selected preferably upper or lower molars, although third or fourth premolars were also included to increase the sample size (SI1). A total of 18 individuals (13 for *G. subtapiroideum* and one for *P. cuvieri* from Artesilla, and four for *G. angustidens* from Tarazona), were analysed using this method (Table 1).

2.3. Dental microwear

Dental microwear analysis is a technique used to reconstruct the short-term feeding behaviour of both extant and extinct mammals by examining the microscopic wear patterns produced on tooth enamel during food processing (Grine, 1986; Solounias and Semprebon, 2002; Mihlbachler and Beatty, 2012). Microwear features were examined under low (35×) magnification using a Leica S9i stereomicroscope on high-resolution epoxy casts of teeth, following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). The occlusal surface of the fossil cheek teeth was cleaned with acetone and (95%) alcohol (ethanol 96%) and the relevant area was moulded using high-resolution silicone (vinylpolysiloxane; Provil Novo Putty and Light regular set). Casts were created using clear epoxy resin (Araldite LY 55 with Renlam MS-1). Moulds were made exclusively on the first loph or lophid of each tooth—on the posterior part of the cusp on the lingual side and on the anterior part of the cusp on the labial side—using both premolars and molars from upper and lower dentitions, as this portion is primarily employed by proboscideans for shearing plant material during mastication (Calandra et al., 2010). We calculated the following variables: average number of pits (AP), average number of scratches (AS), percentage of individuals with >4 large pits (%Lp); percentage of individuals with gouges (%G), percentage of individuals with >4 cross scratches (%XS), percentage of pits (%P), scratches width score (SWS), percentage of specimens with between 0 and 17 scratches (%0–17), percentage of individuals with predominantly fine scratches (%FS), percentage of individuals with a mix of fine and coarse scratches (%MS) and percentage of individuals with predominantly coarse scratches (% CS). Photographs of 21 specimens (15 for *Gomphotherium*

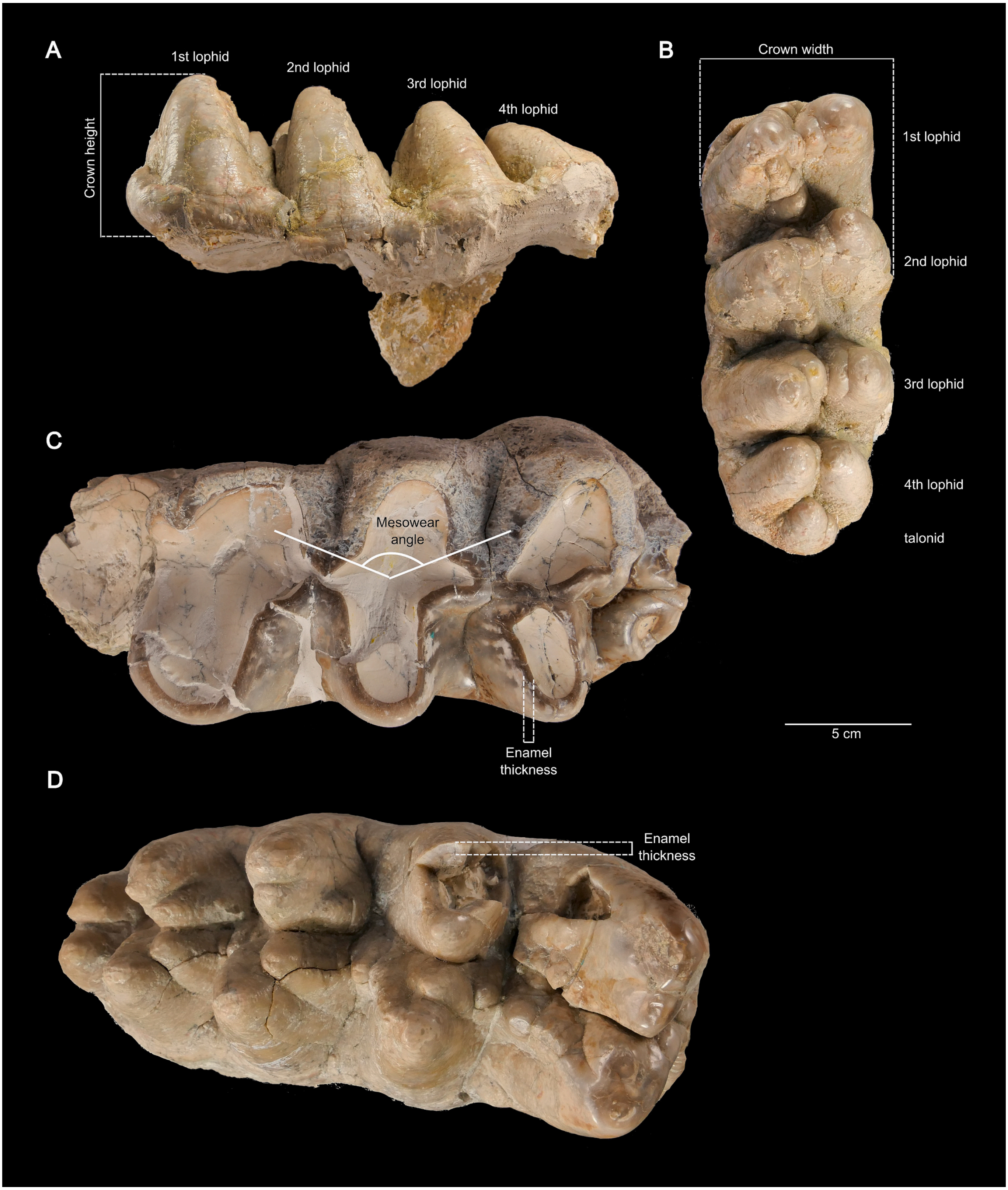

Fig. 2. Fossil molars of *Gomphotherium subtapiroideum* from Artesilla. (A, B) Labial and occlusal views of specimen MPZ 2026/218 (left m3) showing crown height, crown width and number of lophids; (C) Occlusal view of specimen MPZ 2026/220 (right m3) showing enamel thickness in a fractured molar; (D) Occlusal view of specimen MPZ 2026/221 (left m3) showing mesowear angle and enamel thickness in a worn molar.

Table 1

Summary of mean measurements of the other ecometric variables. Abbreviations: number of individuals measured (N).

Species	Locality	Age (Ma)	N	Enamel thickness (mm)	N	N° loph(*id*)s	N	Hypsodonty
Gomphotherium subtapiroideum	Artesilla	~16.49	17	2.9	5	3.4	5	71.9
Prodeinotherium cuvieri	Artesilla	~16.49	1	2.9	1	2.0	1	61.1
Gomphotherium angustidens	Tarazona	~14.50	7	3.9	1	4.0	1	71.5

subtapiroideum, one for *Prodeinotherium cuvieri*, and five for *Gomphotherium angustidens*) (Table 2; Fig. 3) were analysed using ImageJ (Schneider et al., 2012). Data were compared with those of modern taxa with known diets (Solounias and Semprebon, 2002) and with Middle Miocene *G. angustidens* and *P. bavaricum* from Gračanica (Bugojno Basin, Bosnia-Herzegovina) (Xafis et al., 2020).

We quantified microwear in a standard square area of 0.16 mm^2. Features were divided into five categories: small pits, large pits, fine scratches, coarse scratches, and gouges. The presence of cross scratches was also recorded. All microwear marks were classified following established criteria: 1) scratches (length-to-width ratio > 4), subdivided into fine (≤ 3 μm wide) and coarse (> 3 μm wide); 2) pits (ratio ≤ 4), subdivided into small (≤ 8 μm in diameter) and large (> 8 μm); and 3) gouges, which are irregularly shaped, larger, and deeper features reflecting more intense wear processes. In modern herbivorous mammals, browsing species, which feed mostly on leaves and fruits, generally display dental microwear patterns characterised by a higher proportion of pits on the tooth enamel. In contrast, grazers, which tend to consume a larger proportion of abrasive grasses rich in silica phytoliths, usually display a higher density of scratches on the dental enamel. Mixed feeders typically show intermediate or variable patterns (Solounias and Semprebon, 2002).

Scratch textures were also converted into a Scratch Width Score (SWS) following Rivals (2012): a score of 0 was given to teeth with predominantly fine scratches per tooth surface, 1 to teeth with a mixture of fine and coarse types of textures, and 2 to teeth with predominantly coarse scratches. Individual scores for a sample were then averaged to get the SWS value. Coarse scratches are mostly observed in modern C4 grazers, bark eaters and fruit browsers (Solounias and Semprebon, 2002). We also calculated the percentage of individuals with scratch numbers falling in a low scratch range (%0–17), as described by Semprebon and Rivals (2007). This index can also help to differentiate between grazing, browsing and mixed feeding signals in modern herbivorous mammals: grazers have 0–22.2% of individuals with scratches between 0 and 17; mixed feeders have 20.9–70% of individuals with scratches between 0 and 17; and leaf-dominated browsers have 72.7–100% of individuals with scratches between 0 and 17.

2.4. Statistics

A discriminant analysis was also performed using the following independent microwear variables: 1) percentage of pits, 2) percentage of individuals with predominantly fine scratches, 3) percentage of individuals with predominantly coarse scratches, 4) percentage of individuals with a mixture of fine and coarse scratches, 5) percentage of individuals with >4 large pits, and 6) percentage of individuals displaying gouges. The dietary classification of modern taxa modified from Solounias and Semprebon (2002) was used as the grouping variable. All analyses were performed using IBM SPSS Statistics 24. A total of 20 specimens (15 for *G. subtapiroideum* and the individual for *P. cuvieri* from Artesilla, and four for *G. angustidens* from Tarazona), were analysed using this method (Table 2). We also included *G. angustidens* and *P. bavaricum* from Gračanica (Xafis et al., 2020).

3. Results

3.1. Ecometric

Results indicate that the gomphotheres from Artesilla and Tarazona exhibit a higher degree of hypsodonty (71.9 and 71.5, respectively) than the deinothere (61.1) (Table 1). This is consistent with the more derived position of the family Gomphotheriidae, with taxa displaying hypsodonty comprised between 62.1 (*Progomphotherium maraisi*) and 83.5 (*Choerolophodon ngorora*) in relation to the more basal Deinotheriidae which instead display hypsodonty values around or lower than 60 (Fig. 4). In particular, *G. subtapiroideum* from Artesilla and *G. angustidens* from Tarazona show hypsodonty values comparable to other Early Miocene gomphotheres (*Afrochoerodon kisumuensis*, 69; *Protanancus macinnesi*, 71), while *P. cuvieri* from Artesilla display hypsodonty comparable to that recorded for the Early Miocene *P. hobleyi* (60). Gomphothere molars display a greater average number of loph(*id*)s (3.6 for *G. subtapiroideum* of Artesilla and 4 for *G. angustidens* of Tarazona) compared to the deinothere from Artesilla (which only has 2 as typical of this group in the M3/m3). (Table 1). These results of *G. subtapiroideum* and *G. angustidens* are in line with those recorded for other gomphotheres of similar age such as *A. kisumuensis* (4), *P. macinnesi* (4.15) and *Archaeobelodon* sp. (4) (Fig. 4). *Gomphotherium subtapiroideum* from Artesilla display thinner enamel (2.9 mm) than *G. angustidens* from Tarazona (3.9 mm) (Table 1), however both show thinner enamels compared to other gomphotheres species which on average have enamel thickness values around 5 mm both before and after the MCO and MMCT (Fig. 4). The single individual of *Prodeinotherium cuvieri* display thinner enamel (2.9 mm) than Early Miocene *P. hobleyi* (3.6 mm) (Fig. 4).

3.2. Dental mesowear

We obtained mean values of 119.2° for *G. subtapiroideum* and 81.7° for *P. cuvieri* (Fig. 5), pointing to different levels of abrasion in the diet of the two taxa. *Gomphotherium angustidens* from Tarazona displays a mean mesowear angle of 121.3° comparable to that of the Artesilla gomphothere. The mean mesowear angles of both gomphotheres from Artesilla and Tarazona mostly fall within the range of mixed and grazing interval (Fig. 5). These values are higher than those recorded in other gomphotheres which are generally lower than 120° falling within the mixed feeders or browsing range (Fig. 5), overlapping instead with those of Pleistocene *Mammuthus meridionalis* (119.3°), which display a flexible feeding behaviour that can include more or less grass in their diet depending on locality and age (Saarinen and Lister, 2016; Rivals et al., 2019). In contrast, the single individual of *P. cuvieri* displays a considerably lower mesowear angle falling in the browsing interval and consistent with the range observed in other Miocene and Pliocene deinotheres (Fig. 5).

3.3. Dental microwear

Microwear analysis (Fig. 6, Table 2) of proboscideans from Artesilla shows that both taxa exhibit a dominance of scratches over pits (*G. subtapiroideum* AP = 11.4; AS = 32.3; S/*P* = 3.1; %0–17 = 6.7; *P. cuvieri* AP = 10.5; AS = 36.5; S/*P* = 3.5; %0–17 = 0), a signal consistent with an abrasive diet. A similar pattern is observed in the gomphothere of Tarazona (*G. angustidens* AP = 11.0; AS = 30.0; S/*P* = 2.7; %0–17 = 0). All of the studied taxa display a predominance of fine

Table 2

Summary of dental microwear results obtained for Artesilla and Tarazona and Gračanica (data from Xafis et al., 2020). Abbreviations: Diet: predicted diet based on discriminant analysis (*Extant seasonal and non-seasonal mixed feeders are grouped together into a single dietary category referred to as "mixed feeders").

Species	Locality	Age (Ma)	N	AP	AS	S/P	%P	%S	SWS	% 0–17	%LP	%G	% XS	%FS (0 SWS)	%MS (1 SWS)	%CS (2 SWS)	Diet	Diet*
Gomphotherium subtapiroideum	Artesilla	~16.49	15	11.4	32.3	3.1	26.1	73.9	0	6.7	26.7	33.3	0.0	100.0	0.0	0.0	seasonal mixed	mixed
Prodeinotherium cuvieri	Artesilla	~16.49	1	10.5	36.5	3.5	22.3	77.7	0	0.0	0.0	0.0	0.0	100.0	0.0	0.0	seasonal mixed	mixed
Gomphotherium angustidens	Tarazona	~14.50	4	11.0	30.0	2.7	26.8	73.2	0	0.0	0.0	50.0	0.0	100.0	0.0	0.0	seasonal mixed	mixed
Gomphotherium angustidens	Gračanica	~14	2	54.5	16.8	0.1	76.5	23.5	0	100	100	0	0.0	100.0	0.0	0.0	leaf browser	fruit browser
Prodeinotherium bavaricum	Gračanica	~14	8	81.6	13.7	0.2	85.6	14.4	0	100	87.5	0	0.0	100.0	0.0	0.0	leaf browser	leaf browser

scratches (%FS = 100) and small pits, except for *G. subtapiroideum* from Artesilla, which shows %Lp = 26.7). Some individuals of *G. subtapiroideum* from Artesilla and *G. angustidens* from Tarazona display a relative abundance of gouges (%G = 33.3 and 50, respectively). None of the studied individuals display high number of cross scratches. Overall, both fossil gomphotheres and the deinothere from the Aragonian type area display scratch-dominated microwear patterns to a greater extent than fossil proboscideans from other localities and modern elephants which AS usually fall within a ~ 20–30 range (Fig. 6). Compared to proboscideans from Artesilla and Tarazona, the Gračanica species display an abundance of pits over scratches (*G. angustidens* AP = 54.5; AS = 16.8; S/*P* = 0.1; %0–17 = 100%: *P. bavaricum* AP = 81.6; AS = 13.7; S/*P* = 0.2; %0–17 = 100%) (Table 2) which are comparable to that observed in modern browsing taxa (Fig. 6).

All fossil proboscideans are classified as seasonal mixed feeders (Fig. 7A, Table 2) (67.4% of modern taxa correctly classified, 52.2% in cross-validation). Because meal-by-meal mixed feeders are virtually indistinguishable from grazers in terms of the average number of scratches, but differ in terms of the average number of pits (which are lower in grazers) and scratch texture (which is finer in meal-by-meal mixed feeders) (Fig. 6) (see also Solounias and Semprebon, 2002), we run a discriminant analysis grouping together extant seasonal and non-seasonal mixed feeders into a single dietary classification (mixed feeders) (Fig. 7B). In this case, all fossil proboscideans were classified as mixed feeders (Fig. 7B, Table 2) (76.1% of modern taxa correctly classified, 63.0% in cross-validation).

4. Discussion

During the early phase of the MCO at Artesilla (~16.49 Ma), *Gomphotherium* and *Prodeinotherium* display ecometric variables in line with their basal and less derived forms, with generally low tooth crown heights, and a reduced number of loph(*id*)s (particularly in the case of *P. cuvieri*, which has only 2), which are dental features typical of early browsing proboscideans (Saarinen and Lister, 2016, 2023). Traditionally, *G. subtapiroideum* is also considered less bunodont than *G. angustidens* (Wang et al., 2017) a characteristic usually linked to a less generalist diet. *Gomphoterium subtapiroideum* shows however dental mesowear angles consistent with a diet comprised of higher content of abrasive items than other coeval African early elephantoids (sensu Shoshani and Tassy, 2005) like *Protanancus macinnesi* and *Afrochoerodon kisumuensis* (Fig. 5), and dental microwear patterns also coherent with a more abrasive mixed diet. During the onset of the MMCT (~14 Ma), *G. angustidens* from Tarazona, while displaying hypsodonty index comparable to that of *G. subtapiroideum* from Artesilla, is also characterised by a higher number of lophs and thicker enamel (Fig. 4) and similarly high levels of abrasion, suggesting that through the MCO *Gomphotherium* underwent a process of adaptation to consume also abrasive and resistant plant parts.

A browsing long-term feeding behaviour is recorded only in the single individual of *P. cuvieri*, in line with what is observed in other Miocene or Oligocene *Prodeinotherium* spp. (Fig. 5). This individual displays microwear patterns which are more consistent with a more abrasive diet. However, this taxon is represented only by a single specimen that, while not juvenile, display unworn M3 and a M2 in the early stage of use that may had not yet recorded the full mesowear signal. For this reason, both mesowear and microwear results should be tentatively taken.

The exceptionally high number of scratches recorded in the Artesilla and Tarazona sample (around or above 30 in all species) compared to modern grazing taxa, may be due the fact that comparison data for extant species are comprised mostly of ungulates (artiodactyls and perissodactyls) (Solounias and Semprebon, 2002), that display different mastication patterns compared to proboscideans (Koenigswald, 2016; Schultz et al., 2020). Modern ungulates display a mostly bucco-lingually directed power stroke with continuous phase I and phase II, while at

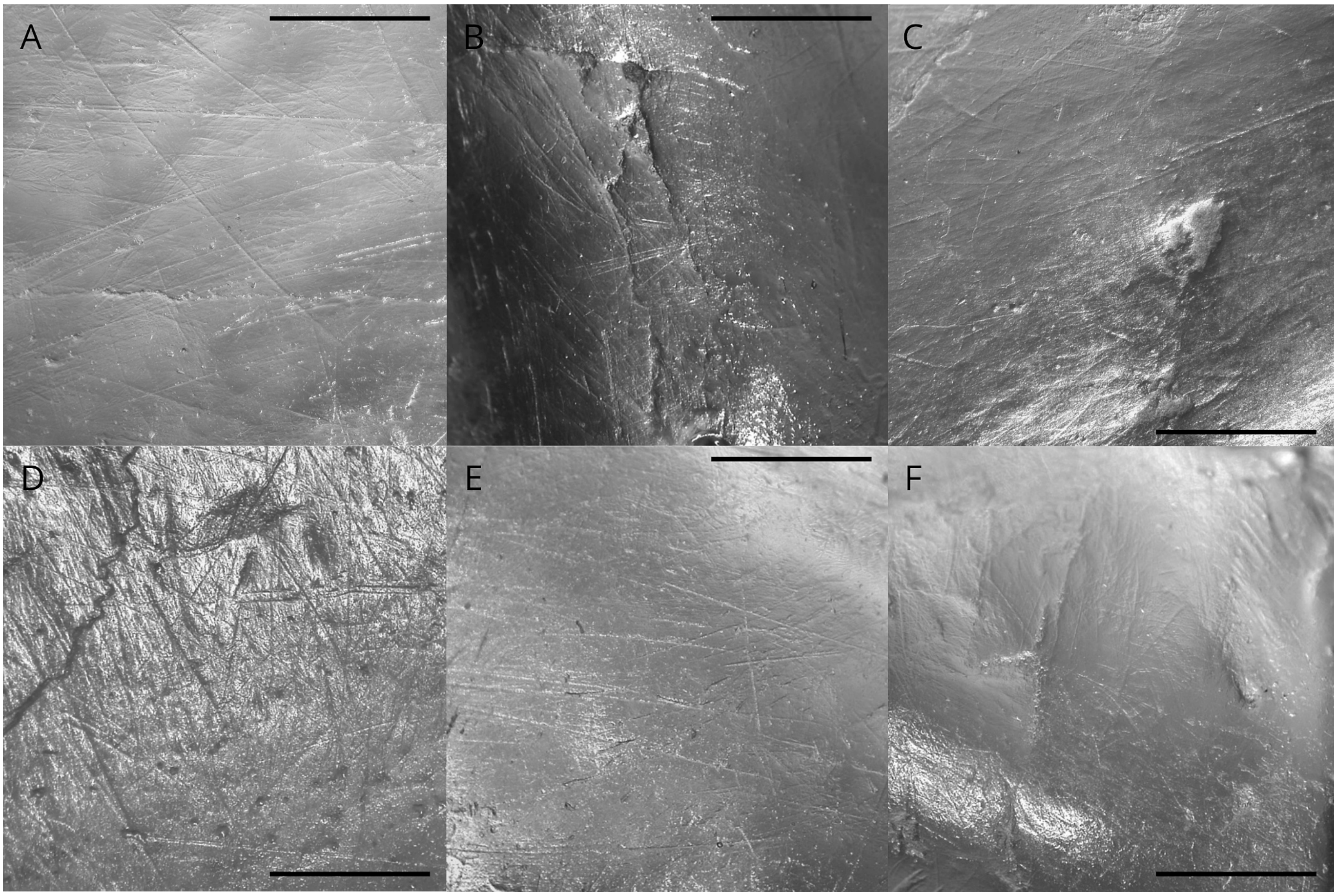

Fig. 3. Photomicrographs of enamel surfaces at 35× magnification of selected teeth. *Gomphotherium subtapiroideum* (Artesilla): (A), MPZ 16546, left m2; (B), MPZ 2026/212, left M2; (C), MPZ 2026/220, right m3. *Prodeinotherium cuvieri* (Artesilla): (D), MPZ-6408, right M3. *Gomphotherium angustidens* (Tarazona): (E), MPZ 97/566, left M2; (F), MPZ 97/574, right m1. Scale bars: 1 mm.

least three different patterns are observed in proboscideans: Deinotheriidae displays a one-phased shearing pattern, Mammutidae and Gomphotheriidae compress food during phase I followed by lower jaw lateral movement during phase II and Elephantidae shears and grinds food with a proal movement of the lower jaw (Koenigswald, 2016; Schultz et al., 2020). Solounias and Semprebon (2002) highlight that some modern mixed feeders can display a greater number of scratches compared to extant grazers, possibly due to the difficulty of resolving separate scratches in grazers where scratches are etched over an already abundantly scratched surface, rather than due to a higher absolute number of scratches present in nongrazers. This scenario would explain why *G. subtapiroideum, G. angustidens* and *P. cuvieri* all display a high average number of scratches (around or above 30 in all species) but are classified as mixed feeders when microwear variables reflecting overall coarseness are taken into account (Table 2, Fig. 7).

Trace and isotopic analysis (Coimbra et al., 2025) of *G. angustidens* from Portugal suggest a periodic intake of sediment in its diet (geophagy) that it has been observed in modern African elephants during dry seasons. A higher concentration of particles such as dust or grit on plant parts in very arid environments may lead to a heavily scratched microwear “grazing-like” pattern that can mask the species' true feeding behaviour (Solounias and Semprebon, 2002), as observed in the exceptionally high average number of scratches in the Artesilla and Tarazona proboscideans (Fig. 6). This “dirty” feeding behaviour, however, is usually reflected by an abundance of coarse features (coarse scratches, gouges and large pits) (Solounias and Semprebon, 2002), a pattern that is not observed in the gomphotheres *G. subtapiroideum*, *G. angustidens* or the deinothere *P. cuvieri*, that on the contrary display an abundance of fine scratches with (few) large pits and gouges being recorded only in *G. subtapiroideum* (Table 2). This suggests that the scratch-dominated microwear patterns are not a result of the ingestion of grit-infested plant parts or of geophagy but of a grass-rich diet.

The overall higher degree of abrasion detected in *G. supbtapiroideum* and *G. angustidens* through dental wear patterns contrasts with data of similarly aged *Gomphotherium* from the Somosaguas succession (14.075–13.78 Ma, Madrid Basin), where stable isotopic analysis suggests that *G. angustidens* consumed mostly browse although in increasingly colder and arid habitat conditions (Domingo et al., 2009, 2012). This discrepancy might be attributable to methodological differences (tooth wear vs. stable isotopes) as well as different environmental conditions in the Calatayud-Daroca, Ebro and Madrid basins. Somosaguas is in fact dated around the peak of cold (Mi3) of the MMCT and was characterised by long drought periods (10 months) and savannah/semi-desertic conditions (Menéndez et al., 2017). In modern African savannah ecosystems, it has been observed that elephants switch to a browsing diet during droughts (Birkett and Stevens-Wood, 2005). A similar scenario may explain why *Gomphotherium* was a browser in the Madrid basin where conditions were more arid than in both Artesilla and Tarazona. Mesowear angles compatible with a less browsing behaviour (within the 106° and 117° range) are also reported for isolated *Gomphotherium* molars attributed to *G. angustidens* from various Iberian localities (Xafis et al., 2020), however uncertain information about datation and provenance, does not allow for a direct comparison with our sample. Nevertheless, the mean mesowear angle of this sample (111.7°) (Xafis et al., 2020) is lower than those recorded in both *G. subtapiroideum* from Artesilla (119.2°) and *G. angustidens* from

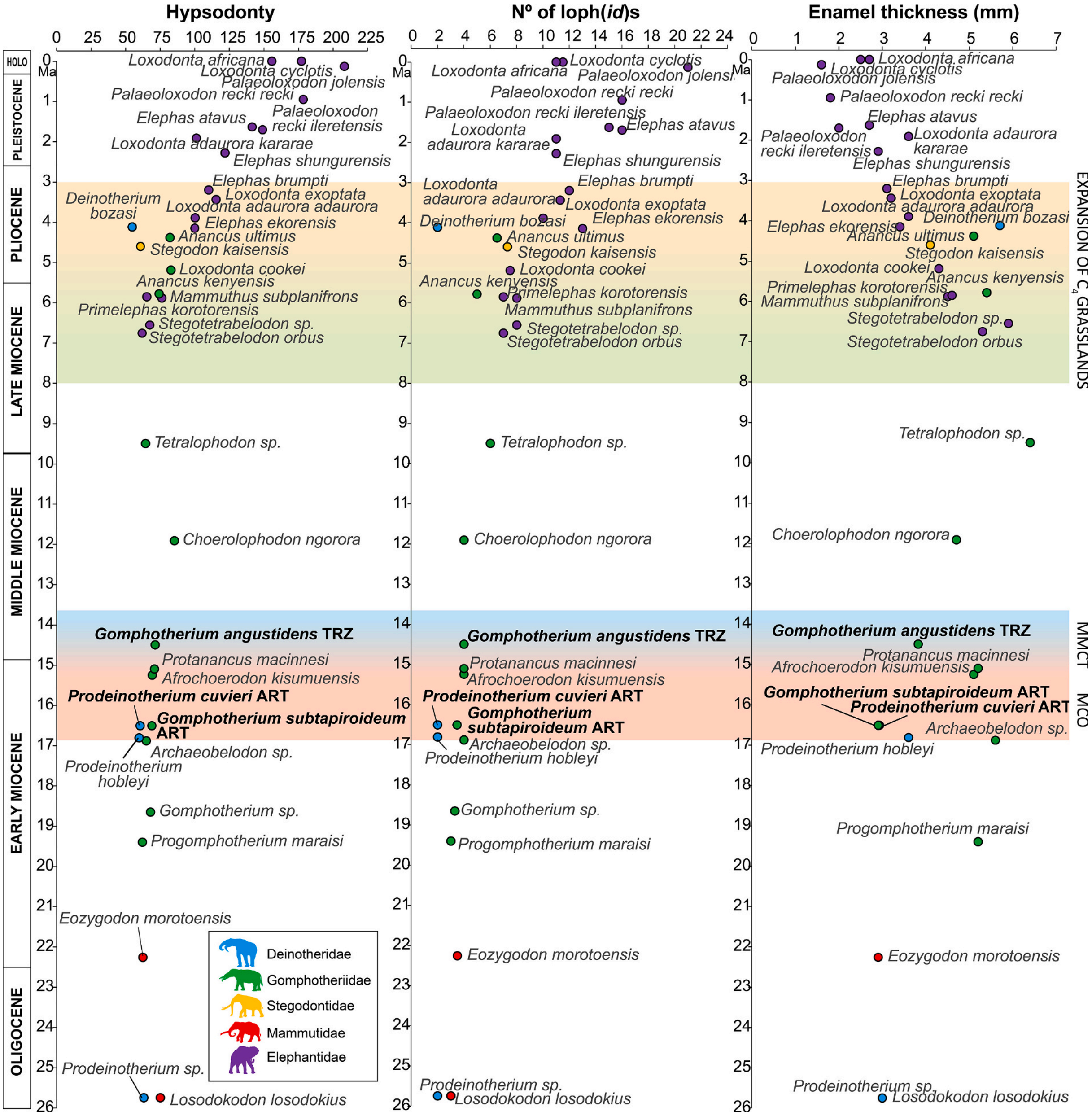

Fig. 4. Comparative figure showing hypsodonty, the number of loph(*id*)s and enamel thickness measurements from specimens recovered at the Artesilla and Tarazona sites (in bold), alongside additional data compiled from Saarinen and Lister (2016, 2023). Proboscidean silhouettes taken from PhyloPic by T. Michael Keesey (*Mammut*, *Gomphotherium*), Steven Traver (*Prodeinotherium*), Margot Michaud (*Loxodonta africana*) and Julián Bayona (*Stegodon*).

Tarazona (121.3°).

Gomphotheres and deinotheres from other European sites such as Sandelzhausen (Germany, Middle Miocene, 15.3 Ma), Sansan (France, Middle Miocene, 14.1 Ma), Gračanica (Bugojno Basin, Bosnia-Herzegovina, Middle Miocene, ~14 Ma), Hammerschmiede (Germany, Late Miocene, 11.42 Ma) and also display feeding behaviours characterised by a low degree of abrasion (Calandra et al., 2010; Xafis et al., 2020; Konidaris et al., 2023) (Figs. 5, 6). Isotopic values of North American *Gomphotherium* also indicate that this proboscidean adopted a mostly browsing or mixed diet dominated by C_3 plant through the Middle and Late Miocene (Fox and Fisher, 2004). Dental mesowear angles from *Gomphotherium* spp. from East Africa (Saarinen and Lister, 2023) are lower than those from both Artesilla and Tarazona (Fig. 5), suggesting a more browsing diet typical of tropical forests. These fossils, which date to the Burdigalian (20.45–15.98 Ma, International Chronostratigraphic Chart v2024/12), represent a time when East Africa was likely covered by dense forests (Cerling et al., 1998; Jacobs et al., 1999; Lukens et al., 2017) and herbivores were primarily browsing on leaves and fruits. A grazing diet has been however reported for Middle Miocene *Gomphotherium* from Central Asia (Wu et al., 2018).

In the European continent, a diet based mostly on grasses in proboscideans has been recorded only in the Late Miocene choerolophodonts *Choerolophodon anatolicus* and *C. pentelici* (Konidaris et al., 2016). This could suggest that in Europe proboscideans adapted to a diet richer in grass and open environments earlier than what has been recorded until now, possibly following the opening of landscapes and the increased availability of grasslands during the Late Miocene (Böhme, 2003; Kovar-Eder et al., 2021).

In Artesilla, the absence of herbivores commonly associated with open landscapes, such as hypsodont equids and bovids, alongside the presence of taxa typical of wetter environments, like (rare) tragulids (*Dorcatherium*) listriodontine suids (*Bunolistriodon*), suggest that

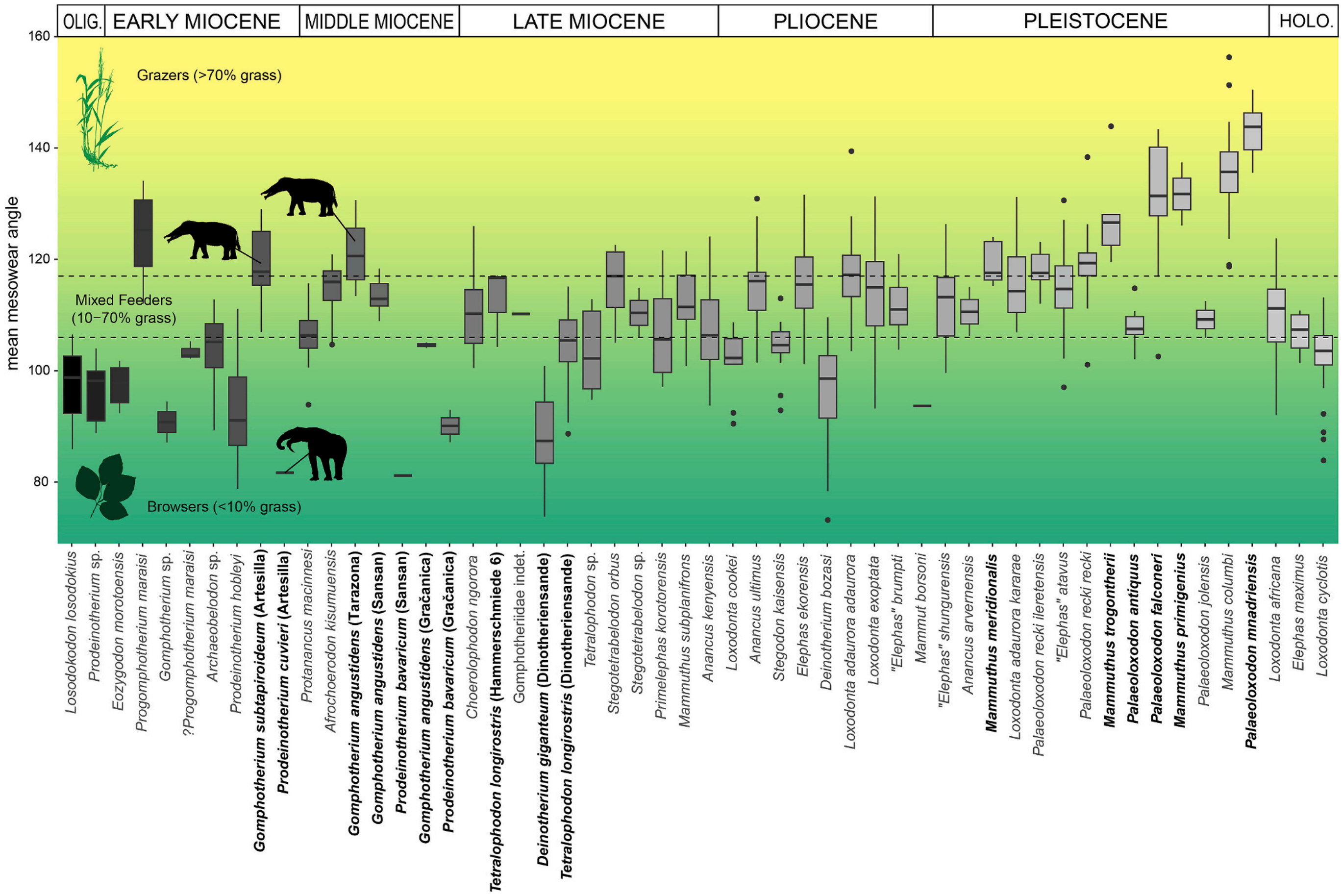

Fig. 5. Mesowear angles of *G. subtapiroideum* (Artesilla), *P. cuvieri* (Artesilla) and *G. angustidens* (Tarazona) compared with those of modern and other fossil proboscideans. Comparative data from Rivals et al. (2019), Xafis et al. (2020), Konidaris et al. (2023), Saarinen and Lister (2023), Strani et al. (2025). In bold European taxa. Thresholds in mesowear angle between browsing (below 106°), mixed feeding (between 106° and 117°) and grazing (above 117°) are indicated according to Saarinen and Lister (2023). *Mean based on specimens collected from different localities. Boxes represent the interquartile interval (with the mean indicated), and the whiskers represent the range of variation. Proboscidean silhouettes from PhyloPic by T. Michael Keesey (*Gomphotherium*) and Steven Traver (*Prodeinotherium*).

forested habitats were particularly abundant (Azanza et al., 1993). However, the mixed diet recorded for the cervid *Procervulus ginsburgi* from Artesilla points to the presence of somewhat open landscapes or seasonally more arid habitats than expected in this area during the MCO (DeMiguel et al., 2008). In Tarazona the trend towards cooler and more arid conditions linked to the onset of the MMCT is testified by the decrease in vertebrate diversity, micromammals associations and mineralogical analysis (Murelaga et al., 2008). It should also be noted that even if C4 grasslands became globally widespread (to a lesser extent in Europe) only during the Late Neogene (Cerling et al., 1997; Edwards et al., 2010), palynological data from the nearby Rubielos de Mora basin (Teruel province), suggest that C4 grasses were already present and relatively abundant in northeastern Iberian Peninsula during the Early and Middle Miocene (Urban et al., 2015).

5. Conclusions

The proboscideans *Gomphotherium* and *Prodeinotherium* from the Aragonian type area exhibit ecometric traits (e.g. low-crowned molars and a reduced number of loph(*id*)s) that are consistent with those of other Early Miocene representatives of the group. These traits are all indicative of adaptations for feeding on relatively soft vegetation (i.e. browsing). Direct dietary proxies derived from dental mesowear and microwear reveal instead a greater degree of trophic flexibility than would be expected for such early forms. *Gomphotherium* shows high mesowear angles—which are indicative of a long-term grazing diet—in the Aragonian type area, both during the onset of the MCO (in the site of Artesilla, ca ~16.49 Ma) and before the MMCT (in Tarazona, ca ~14.50 Ma), whereas *Prodeinotherium* retains in Artesilla the lower angles—that are typically associated with browsing. Dental microwear patterns consistently point to mixed-feeding behaviours in both taxa, suggesting that short-term dietary variability is likely linked to seasonal environmental changes with *P. cuvieri* being forced to incorporate more abrasive plants in its diet for sustenance, although this result should be tentatively taken due to the sample being representend by a single individual. The evidence of a more abrasion-dominated diets in Early Miocene *Gomphotherium* supports a scenario of an early adaptation of European proboscideans to increasingly open habitats that spread in the Iberian Peninsula before the MMCT.

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CRediT authorship contribution statement

Francisco Alquézar-Blesa: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Beatriz Azanza:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Daniel DeMiguel:** Writing – review & editing, Validation, Resources, Project administration, Funding acquisition. **Flavia Strani:** Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Formal analysis, Data

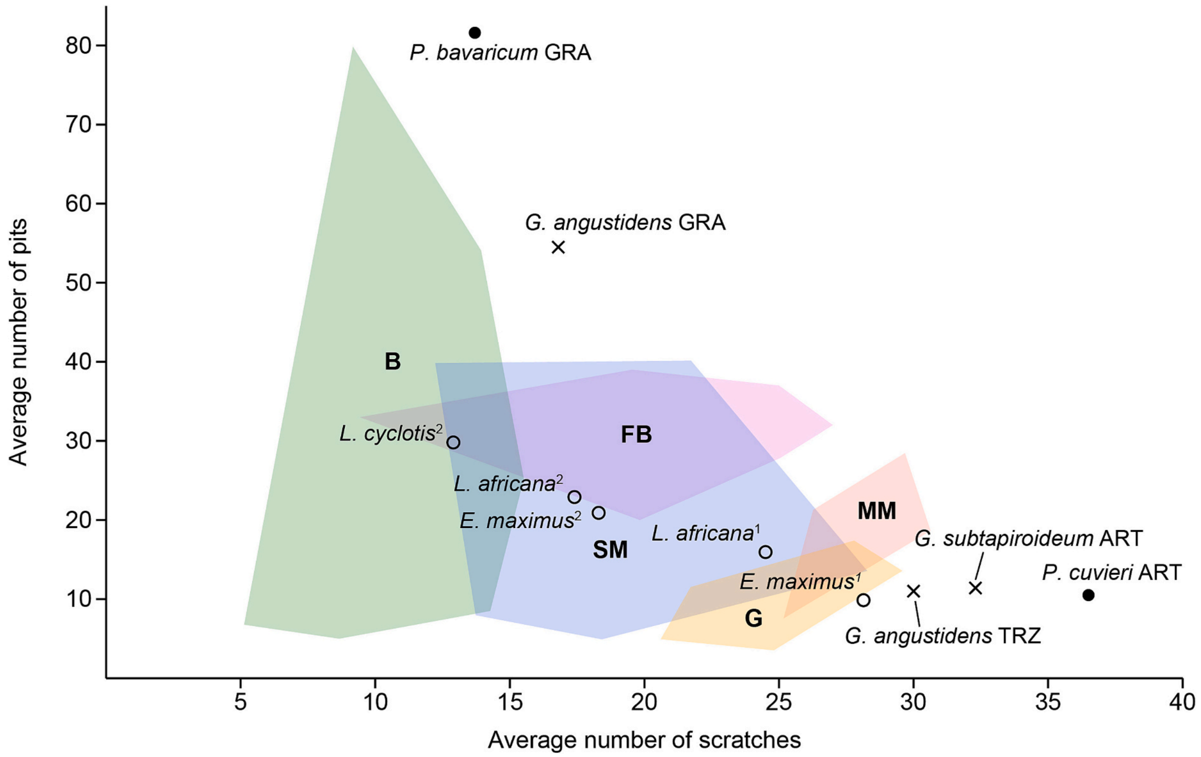

Fig. 6. Scatterplot showing the relationship between the average number of scratches and the average number of pits in modern and fossil taxa. The figure includes specimens from the sites of Artesilla (ART) and Tarazona (TRZ), as well as from Gračanica (GRA) (Xafis et al., 2020) and extant proboscideans (Solounias and Semprebon, 2002; Semprebon et al., 2016) and extant ungulates (Solounias and Semprebon, 2002). Abbreviations: leaf browsers (LB); fruit browsers (FB); seasonal mixed feeders (SM); meal-by-meal mixed feeders (MM); grazers (G); [1]Solounias and Semprebon (2002); [2]Semprebon et al. (2016).

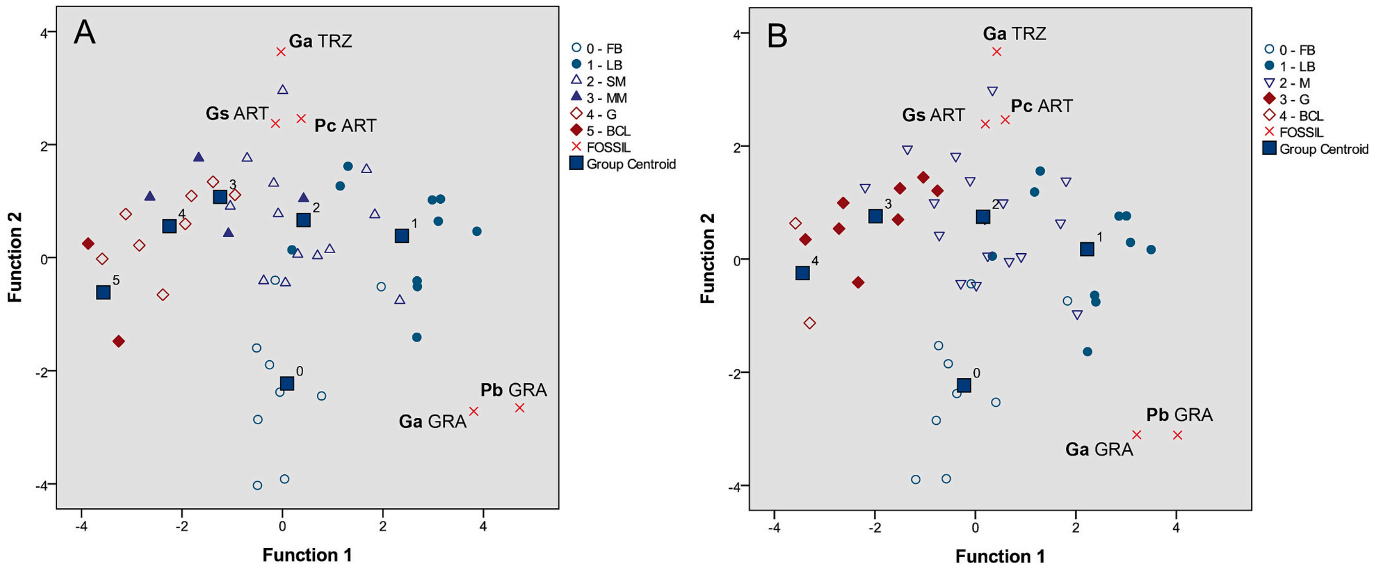

Fig. 7. Bivariate diagrams based on discriminant microwear analysis. A, Classification using extant ungulate dietary types as grouping variables: fruit browsers (0-FB); leaf browsers (1-LB); seasonal mixed feeders (2-MF); meal-by-meal mixed feeders (3-MM); grazers (4-G); and bark, coarse stem, and leaf feeders (5-BCL). B, Classification grouping extant seasonal and non-seasonal mixed feeders in a single dietary category (mixed feeders): fruit browsers (0-FB); leaf browsers (1-LB); mixed feeders (2-MF); grazers (3-G); and bark, coarse stem, and leaf feeders (4-BCL). Square symbols indicate group centroids. Extant data from Solounias and Semprebon (2002).

curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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