



New proboscidean specimens from the Late Miocene of Romania: the huge-sized deinothere *Deinotherium proavum*, the rare “*Mammut*” cf. *obliquelophus* and the first description of the shovel-tusker *Konobelodon* from the country

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Abstract

In this article, we describe so far unpublished proboscidean specimens from several Late Miocene localities of Romania. A partial mandible and the complete upper/lower cheek tooth rows of a deinothere individual from the site of Ghergheşti 1 belong to *Deinotherium proavum* and comprise one of the few examples of entire cheek tooth rows of the same individual of this species. Ghergheşti 1 is geographically close to Mânzaţi from where the celebrated skeleton of “*Deinotherium gigantissimum*” was discovered at the end of the nineteenth century, and thus further highlights the importance of Romania in the study of this emblematic deinothere. *Deinotherium proavum* represents the last deinothere species in Europe and corresponds to the terminal stage of the size increase characterizing the evolution of European deinotheres. Two zygodont molars are attributed to the rare “*Mammut*” cf. *obliquelophus* and add to the scarce record of “*Mammut*” in the Miocene of Eurasia. They document the secure presence of “*Mammut*” in the Miocene of Romania. The small size of the studied molars compared to known specimens of the Pliocene “*Mammut*” *borsoni* and the weak development of the distal cingulum in the lower third molars may have taxonomic and biostratigraphic importance. Furthermore, the presence of an amebelodontid is documented by a large-sized and dorsoventrally flattened lower tusk fragment that shows tubular dentine in its inner part and is attributed to the tetralophodont shovel-tusker *Konobelodon*. This specimen marks the first record of the genus in Romania. Finally, the biostratigraphic distribution of the taxa is discussed.

Keywords Deinotheriidae · Mammutidae · Amebelodontidae · Miocene · Turolian · Romania

Introduction

The Late Miocene proboscideans of Romania are investigated since the end of the nineteenth century and the long palaeontological research in the country has revealed a wealth of proboscidean specimens from a plethora of localities, significantly enriching the Miocene proboscidean archive. Unfortunately, a lot of specimens are isolated finds and/or lack precise stratigraphic information, as it is usual in historical collections, prohibiting a detailed biostratigraphic study. Nonetheless, most of the Late Miocene proboscidean species known from Europe have been reported from the country: the deinotheres *Deinotherium giganteum* Kaup, 1829 (e.g. Ţibuleac 2018 and references therein) and *Deinotherium proavum* (Eichwald, 1831) [including Găiceana, the type locality of its junior synonym “*Deinotherium gigantissimum*” Stefanescu, 1892, as well as Verneşti and

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Mânzați (Stefanescu 1892, 1895, 1910; Codrea et al. 2016 and references therein), the tetralophodont gomphotheres *Tetralophodon longirostris* (Kaup 1832) (e.g. Codrea and Ursachi 2007) and *Anancus* [e.g. Derşida; Jurcsák (1973) and Codrea et al. (2002); as *Anancus arvernensis* Croizet and Jobert 1828, but considering the presence of *D. proavum* and the overall Turolian character of the fauna might belong instead to *Anancus lehmanni* (Gaziry 1997); see Konidaris and Roussiakis 2019], the choerolophodonts *Choerolophodon anatolicus* (Ozansoy 1965) and *Choerolophodon pentelici* (Gaudry and Lartet 1856) (e.g. Ştiucă 2003; Ţibuleac 2014, 2019), and perhaps the mammutid “*Mammut*” [Curtea de Argeş; Athanasiu (1907); see Markov (2008) for possible attribution to “*Mammut*” *obliqueolophus* (Mucha 1980), if indeed of Late Miocene age].

In this article, we study so far unpublished specimens from several Late Miocene sites of Romania housed at the Museum Vasile Pârvan of Bârlad, and we document the secure presence of “*Mammut*” during the Late Miocene of Romania and the first record of the tetralophodont amebelodontid *Konobelodon* in the country. In addition, we study in detail the complete upper and lower cheek tooththrows of *Deinotherium proavum*, belonging to a partial skeleton preliminarily reported in Ratoi et al. (2015) from Ghergheşti 1 (a site geographically adjacent to Mânzați from where the skeleton of “*Deinotherium gigantissimum*” originates), enriching further the material of this huge-sized deinotherid species from Romania.

Materials and methods

The studied material includes mandibular and dental specimens originating from the localities Ghergheşti 1, Banca, Hălăreşti, Iana, Siliştea and Puieşti in eastern Romania (Fig. 1). The specimens are stored at the Museum Vasile Pârvan, Natural Sciences Branch of Bârlad. Terminology follows Pickford and Pourabrishami (2013) for the deinotheriid teeth and Tassy (1996a) for the elephantimorph ones. The letters p/m and P/M denote the lower and upper premolars/molars, respectively. For the cheek teeth, the dimensions measured are the mesiodistal crown length (L), the buccolingual crown width (W) at each loph(id), and the maximum crown height (H). Measurements (taken by L.U.) are given in Table 1. Comparative measurements for deinotheriid and mammutid teeth were obtained from the literature or directly from specimens (Tables 2 and 3). For the amebelodontid lower tusk, the dorsoventral diameter (height) and the mediolateral diameter (width) at its cross-section were measured. The compression index (CI) was calculated as $\text{height} \times 100 / \text{width}$. The CI box-and-whisker plot was made with PAST v. 4.13 (Hammer et al. 2001; <https://www.nhm.uio.no/english/research/resources/past/>).

Institutional abbreviations. AMPG, Athens Museum of Palaeontology and Geology, Athens, Greece; HGI, Hungarian Geological Institute, Budapest, Hungary; HLMD, Hessisches Landesmuseum Darmstadt, Germany; HHNM, Hungarian Natural History Museum, Budapest, Hungary; MVP-SN, Museum Vasile Pârvan, Natural Sciences Branch, Bârlad, Romania; NHMW, Naturhistorisches Museum Wien, Austria; SU, Palaeontological Museum of the Sofia University Sofia, Bulgaria.

Geological setting and localities

At the Serravallian/Tortonian boundary (11.6 Ma), the fragmentation of the initial Paratethys Sea resulted into two large lake systems, the Central Paratethys (Pannon Lake) to the west and the Eastern Paratethys to the east (Palcu et al. 2019; Krijgsman et al. 2020). The Eastern Paratethys extended between 11.6 and 6.8 Ma from the present-day Black Sea–Caspian Sea region and experienced major fluctuations in water levels as a response to palaeoclimatic changes (Palcu et al. 2019). Particularly during the late Tortonian (9.6–7.6 Ma; Khersonian regional stage), the dry climatic conditions resulted in stratigraphic sequences composed mainly of continental deposits alternating with lacustrine/brackish sediments (Palcu et al. 2019, 2023; Lazarev et al. 2020). The Dacian Basin of Romania, located to the east and south of the Carpathians, comprised the westernmost branch of the Eastern Paratethys (Jipa and Olariu 2009; Lazarev et al. 2020). Its terrestrial settings were inhabited by a diverse biota, of which fossils of large mammals, including the herein studied ones, are quite common (e.g. Ursachi 2016; Ţibuleac 2018, 2019).

The proboscidean specimens of the present study originate from the broader area delimited by the Tutova river in the west and the Bârlad river in the east (Fig. 1), which belongs to the Scythian Platform (Săndulescu 1984) and specifically to the westernmost area of this platform, the so-called “Bârlad Platform” (sensu Ionesi 1994). The Neogene sedimentary deposits that crop out in this area are dated to Khersonian (upper part of Sarmatian s. l.)–Dacian (Fig. 1).

The Maeotian succession includes the volcanic cinerites of the Nuşasca – Ruseni Formation (Jeanrenaud 1971). These layers are excellent marker horizons that can be easily identified in the field, in both the deltaic and brackish facies areas of the Maeotian deposits. The Maeotian sediments in the region were mainly deposited in a fluvial environment. The lower part of the Maeotian succession is composed of brown andesitic tuffs in paragenesis with cinerites, which are gradually replaced by yellow greenish cineritic/tuffic sands. So far, three cineritic layers have been described. The upper part of the Maeotian deposits comprises complex alternations of fine yellow sands, which are poorly sorted, as well as layers of clays and silts. Some sands show intercalations

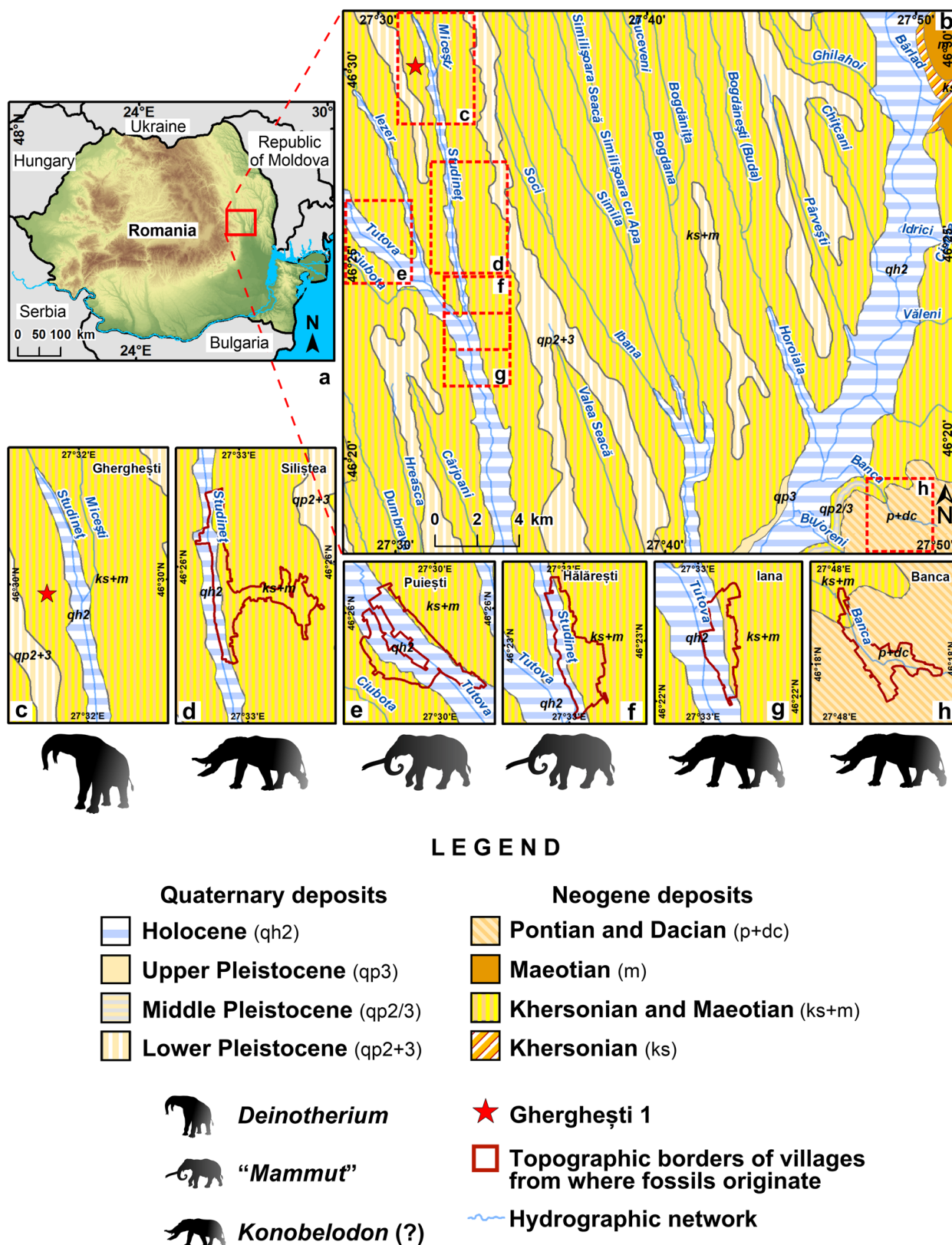


Fig. 1 a Geographic position of the fossiliferous localities in eastern Romania. b geological map of the studied region (shown in red inset in a) c–h detail of the geological map (corresponding to the dashed insets in (b)) showing the fossiliferous localities and the identified

proboscidean taxon in each of them; c Gherghești 1, d Silișteea, e Puiеști, f Hălărești, g Iana, h Banca. Proboscidean silhouette images (not to scale) modified from PhyloPic (phylopic.org)

Table 1 Dental measurements (in mm) of *Deinotherium proavum*, “*Mammut*” cf. *obliquelophus*, *Konobelodon* sp. and *Konobelodon*? From the herein studied localities of Romania

Taxon	Inventory number	Site	Tooth	Side	L	W1	W2	W3	W4	W5	W6	H			
<i>Deinotherium proavum</i>	MVP-SN-C5559	Gherghești 1	p3	Right	77		67					(49)			
				Left	76		63						(51)		
			p4	Right	84	70	74							(49)	
				Left	84	70	72							(46)	
			m1	Right	98	72	70	65						(36)	
				Left	(91)	73	66	–							
			m2	Right	100	84	85								(56)
				Left	100	95	88								(49)
			m3	Right	106	97	81								(50)
				Left	106	98	84								(45)
			P3	Right	91	95	98								(67)
				Left	92	98	93								(61)
			P4	Right	79	100	93								(55)
				Left	78	101	93								(49)
			M1	Right	101	78	92	98							(35)
				Left	(85)	66	95	–							(40)
			M2	Right	106	112	103								(65)
				Left	107	115	105								(57)
			M3	Right	103	107	94								(48)
				Left	104	113	94								(52)
“ <i>Mammut</i> ” cf. <i>obliquelophus</i>	MVP-SN-C240	Hălărești	m2	Right	110	60	67	71				55			
	MVP-SN-C5708	Puiești	m3	Left	154	88	82	86	69			(61)			
<i>Konobelodon</i> sp.	MVP-SN-C5240	Iana	m3	Left	(125)				65	50	33	(64)			
<i>Konobelodon</i> ?	MVP-SN-C5239	Banca	m3	Right	(87)			74	66	51		(37)			

Measurements in parentheses indicate the greatest measurable value of a parameter in incomplete or inadequately preserved specimens or worn cusps in case of height values

of lenticular sandstones which reach a diameter of 2.5 m, as identified on the Studineț and Tutova valleys (near the Perieni locality). The upper member also includes some sandy layers with accumulations of the bivalve mollusk *Unio wetzleri*.

Most of the past surveys resulted in the discovery of fortuitous and isolated fossil finds and usually concern a single taxon. Iana is a commune in Vaslui County and includes five villages: Siliștea, Hălărești, Iana, Recea, and Vadurile. The lower tusk fragment of *Konobelodon* from Siliștea (MVP-SN-C4657) was found by Ilie Chirilă in the 1960ies in a sandy open pit located 250 m from the village. A mammutid second molar (MVP-SN-C240) was found at Hălărești. Macarovic (1960) described the Maeotian stratigraphy of the Tutova Valley and reported (no photos or description are provided) a mandible with molars of the mammutid *Mastodon* cf. *turicensis* from a sand pit (originally assigned to the Lower Pliocene) located at 180 m altitude in the Hălărești village (supposedly stored at the collections of the Museum Vasile Pârvan in Bârlad, but it could not be located). The sedimentary deposits that crop out in the region of the

Hălărești village consist of yellow sands with some cineritic intercalations at the base, overlain by yellow and blue clays and white sands with sandstone concretions. There is no information regarding the specimens from Puiești (m3 of “*Mammut*”, MVP-SN-C5708) and Banca (m3 fragment of *Konobelodon*?, MVP-SN-C5239). In the Puiești area there are several open pits which consist of cross bedded white sands that are covered by yellow sand with sandstone intercalations. In the Băcani area, Macarovic (1960) identified in the yellow sands the mollusk *Unio wetzleri* and assigned an upper Maeotian age for the deposits.

Therefore, despite that the herein studied elephantimorph specimens (“*Mammut*”, *Konobelodon*) concern accidental and isolated finds collected in the past without precise stratigraphic control, they originate from localities whose outcrops expose Khersonian–Maeotian deposits (Fig. 1). The Khersonian (late Tortonian) and Maeotian (early Messinian) regional stages of Eastern Paratethys are dated to 9.6–7.6 and 7.6–6.1 Ma, respectively, and are correlated to the late Vallesian–Turolian, i.e., MN10–MN13 of the European Land Mammals MN zones (Palcu et al. 2019; Krijgsman et al. 2020).

Table 2 Comparative sample of deinotheriid premolars and molars used in the analyses

Species	Locality	Country	Source
<i>Deinotherium levius</i>	Atzelsdorf	Austria	Göhlich and Huttunen (2009)
	La Grive	France	Bergounioux and Crouzel (1962)
	Montréjeau	France	Crouzel (1947)
	Saint-Gaudens	France	Ginsburg and Chevrier (2001)
	Tournan	France	Ginsburg and Chevrier (2001)
	Hinterauerbach	Germany	Gräf (1957)
	Ingolstädter Straße 166	Germany	Stromer (1938)
	Massenhausen	Germany	Gräf (1957)
	Sprendlingen 2	Germany	Böhme et al. (2012)
	Sopron	Hungary	Gasparik (2004)
	Husiatyn	Ukraine	Svistun (1974)
<i>Deinotherium giganteum</i>	Montredon	France	Tobien (1988)
	Breitenfeld	Germany	Mottl (1969)
	Eppelsheim (only the type specimen)	Germany	Gräf (1957)
<i>Deinotherium proavum</i>	Ezerovo	Bulgaria	Kovachev and Nikolov (2006)
	Dorn-Dürkheim 1	Germany	Pickford and Pourabrishami (2013)
	Gela	Greece	Poulakakis et al. (2005)
	Maronia	Greece	Athanassiou (2004)
	Zakros	Greece	Fassoulas and Iliopoulos (2011)
	Baltavár	Hungary	Gasparik (2004)
	Curtea de Argeş	Romania	Athanasiu (1907)
	Gaiceana	Romania	Stefanescu (1895)
	Mânzați	Romania	Stefanescu (1895, 1899)
	Vernesti	Romania	Athanasiu (1907)
Obuhovka	Russia	Bajgusheva and Titov (2006)	

Gherghești 1 (Fig. 1; discovered in 2015 by L.U. and R.G.B.) represents a fluvial accumulation and consists of yellow sands with sandstone intercalations in the lower part (fossiliferous layer) covered by white sands in the upper part (Fig. 2). These deposits are correlated to Maeotian. In terms of taphonomy, the proximate spatial accumulation of the deinother remains (mandible, upper jaw, vertebrae, ribs, humerus), the absence of duplicate dental elements and their consistency in dental wear, combined with the fact that there are no other surrounding faunal finds belonging to other taxa, indicate that all teeth and bones belong to a single, adult, individual. Before final burial the bones were possibly transported by water stream losing their anatomical connections. A few bones show poor preservation, but this is due to a small landslide that occurred in the last decades, after construction works carried out for the road where the deinother remains were found. This landslide resulted in the circulation of rainwater on the bones, and fissured and even broke some of them. On the opposite, where such processes did not affect, the preservation is fairly good (mandible and in particular the resistant teeth).

Systematic palaeontology

Order **Proboscidea** Illiger, 1811

Family **Deinotheriidae** Bonaparte, 1845

Genus ***Deinotherium*** Kaup, 1829

Deinotherium proavum (Eichwald, 1831)

Material. Partial right hemimandible with p3–m3; left lower tooththrow with p3–m3; right and left upper tooththrows with P3–M3; all specimens belong to the same individual with the inventory number MVP-SN-C5559 (associated, but severely fragmented, postcranial remains include ribs, vertebrae, the humerus and perhaps the pelvis; described here are only the mandibular and dental remains).

Locality. Gherghești 1 (Vaslui District, Scythian Platform).

Description. The hemimandible (preserved length: 545 mm; preserved height: 314 mm; height behind the m3: 128 mm; width behind the m3: 145 mm) preserves the corpus and the

Table 3 Comparative sample of mammutid molars used in the analyses

Species	Locality	Country	Source
<i>Zygodiphodon turicensis</i>	Malarctic	France	Tassy (1977)
	Pontlevoy	France	Stehlin (1925)
	Freising	Germany	Lehmann (1950)
	Tutzing	Germany	Lehmann (1950)
	Bitola	North Macedonia	Garevski et al. (2012)
"Mammut" <i>obliqueolophus</i>	Ahmatovo	Bulgaria	Nikolov and Kovacev (1966)
	Curtea de Argeş	Romania	Athanasiu (1907)
	Balta Sands	Ukraine	Kubiak (1972)
	Romanovka	Ukraine	Mucha (1980)
"Mammut" <i>praetypicum</i> "	Păgaia	Romania	Schlesinger (1922), Jurcsák (1973), Codrea et al. (2005)
"Mammut" <i>borsoni</i>	Bossilkovtsi	Bulgaria	Chalwadjev (1986)
	Peichinovo/Pejeinovo	Bulgaria	G.K. at SU
	Pisarevo	Bulgaria	Bakalov and Nikolov (1962)
	Vialette	France	Ros-Montoya (2010)
	Kaltensundheim	Germany	von Koenigswald et al. (2022)
	Milia	Greece	Tsoukala and Mol (2016)
	Hidveg	Hungary	Schlesinger (1922)
	Százhalombatta (Batta–Érd)	Hungary	Schlesinger (1922)
	Olteni	Romania	Alekseeva and Furu (1962)
	Hajnáčka	Slovakia	Schlesinger (1922), Fejfar (1964)
	Baza 1	Spain	Ros-Montoya (2010)

rostral part of the ramus including the coronoid process; the rostral part of the mandible with the symphysis, the caudal part of the ramus, including the condyle, as well as the angle of the mandible, are missing (Figs. 3, 4). A circular mental foramen is situated at the lateral side of the corpus, at the level of the distal end of the p3. Corpus and rostral part of ramus are almost vertical.

The p3 has a triangular shape with short and mesially pointed first lophid and wider second lophid (Fig. 5a, f). Protoconid, metaconid, ectolophid and hypolophid are in advanced stage of wear, and the dentine is confluent. The mesial spur is weak. The median valley at the lingual side is open, separating clearly first and second lophids. A buccal, shallow, notch is positioned low in the crown. A cingulum, formed by a series of cusplets, is present at the distal end of the tooth.

The p4 has a subrectangular shape, longer mesio-distally than buccolingually wide; the two lophids have roughly the same width (Fig. 5b, f). The exposed dentine merges the metalophid and the preprotocristid, which is connected to the mesial cingulum, forming a shallow mesial fovea. Postprotocristid and prehypocristid are connected buccally in the transverse valley, resulting in the formation of a buccal fovea; lingually the valley is open. The dentine is confluent also in the hypolophid and the

worn posthypocristid is connected with the low but relatively strong distal cingulum.

The right m1 is much worn with dentine exposure in all of its three lophids (Fig. 5g). Yet, the degree of wear of its left antimeres is readily more advanced with confluent dentine on the whole occlusal surface; its mesial and distal ends are damaged (Fig. 5c). In the right m1 the width of the first and second lophids is almost equal, whereas the left m1 is tapering distally, with its second lophid being much shorter than the first one (Table 1). In the right m1, the mesial cingulum and the metalophid are united due to wear. Hypolophid and the median accessory cusplet are united, the latter blocking the first transverse valley toward the buccal side; lingually the valley is open. The distal transverse valley is open. The dentine in the tritolophid is also confluent.

The subrectangular right and left m2 are less worn than their preceding m1 (Fig. 5d, h). The wear is stronger in the left m2. The m2 is slightly longer than wide. Although metalophid and hypolophid are almost equally wide in the right m2, in the left one the metalophid is wider. Preprotocristid and premetacristid are rather weak in the right molar, yet stronger than prehypocristid and pre-entocristid. The transverse valley is open, and the ectoflexus is marked. The distal cingulum is low but strong.

The m3 exhibits a lower degree of wear than the preceding dentition (Fig. 5e, h). It is the longest of the tooth row.



Fig. 2 The excavation site of Gherghești 1 (field season summer 2015) showing the find-bearing sediments and *Deinotherium proavum* remains in situ. **a** Right and left hemimandibles in upside down

position; the left hemimandible collapsed and only the teeth are preserved. **b** Distal part of humerus. **c** The site at the end of the excavation. **d** Ribs and vertebrae

The metalophid is wider than the hypolophid. The metalophid is straight, and the premetacristid is slightly stronger than the preprotocristid, particularly in the left molar. The transverse valley is open. The hypolophid is almost parallel to the metalophid in the right molar, whereas it is set slightly diagonal in the left one. The prehypocristid is well-developed. The talonid is well-separated from hypolophid, it is formed by a series of cusplets and is directed slightly buccally.

The P3 has a subtrapezoidal occlusal shape, being somewhat wider than long (Fig. 6a, f). The mesial cingulum is moderately curved and slightly anteriorly pointed mesiobuccal. The parastyle at the mesiobuccal side is weak and merged with the ectoloph in the more worn left P3. The tooth is an advanced stage of wear, and the exposed dentine merges the first loph, the ectoloph and the second loph, delimiting the deep valley in the central part of the tooth.

In the lingual side, a rather deep fovea is formed due to the contact of the worn protocone and hypocone. The distal cingulum is low and rather weak.

The P4 is subrectangular and is wider than longer (Fig. 6b, g). It is much worn and dentine is exposed along the first loph, the ectoloph, and the second loph. The right P4 is less worn, and the central valley is open lingually, whereas in the left P4, the valley is closed due to the contact of the worn protocone and hypocone. The mesial cingulum is rather strong, especially at the buccal side with the parastyle. The entostyle is stronger in the left P4, whereas it is very weak in the right one. The distal cingulum is formed by a series of low, but relatively strong, cusplets.

The left M1 is completely preserved, whereas in the right M1, the lingual part of the metaloph and the distal part of the tooth are missing (Fig. 6c, h). The description is based on the left M1. The tooth is trilophodont and mesio-distally



Fig. 3 Partial right hemimandible (MVP-SN-C5559) of *Deinotherium proavum* from Gherghești 1, in **a** lateral, **b** medial, and **c** dorsal view

elongate, with wider first loph and distally tapering. It is much worn, and the dentine is exposed along the protoloph, the metaloph and the tritoloph, the latter two merged at the center of the distal transverse valley. The mesial cingulum is rather low but strong, and the parastyle is prominent. The first ecto- and entoflexus are marked. The worn postparacrista and postmetacrista are strong, particularly the former. The distal cingulum is not well preserved.

The M2 has a subrectangular shape in occlusal view, being wider than longer; the first loph is wider than the second one (Fig. 6d, i). They are moderately worn; slightly more is the left one. The mesial cingulum is formed by a series of cusplets; mesiolingually the worn parastyle is strong. The postmetacrista is slightly stronger than the postprotocrista. The transverse valley is open buccally and lingually, and a weak entostyle is present. The second loph is

mesially curved. The distal cingulum is elongate and formed by a series of relatively weak cusplets.

The M3 has a subtrapezoidal shape in occlusal view, and like the M2 wider than long, and with wider first than second loph (Fig. 6e, j). In the left molar, both mesial cingulum and first loph are rather aligned, whereas in the right one, they are more curved. The transverse valley is open buccally and lingually. At the lingual side, there is bulge, stronger in the right M3. The second loph is mesially curved, and the posthypocrista extends until the convolute, which is stronger in the right M3. The distal cingulum is weak, even more in the right M3.

Remarks. Several cranial, dental, and postcranial traits render deinotheriids a unique clade within proboscideans, close to the base of the lineage, and markedly different from the more derived elephantimorphs. Dental traits, such as

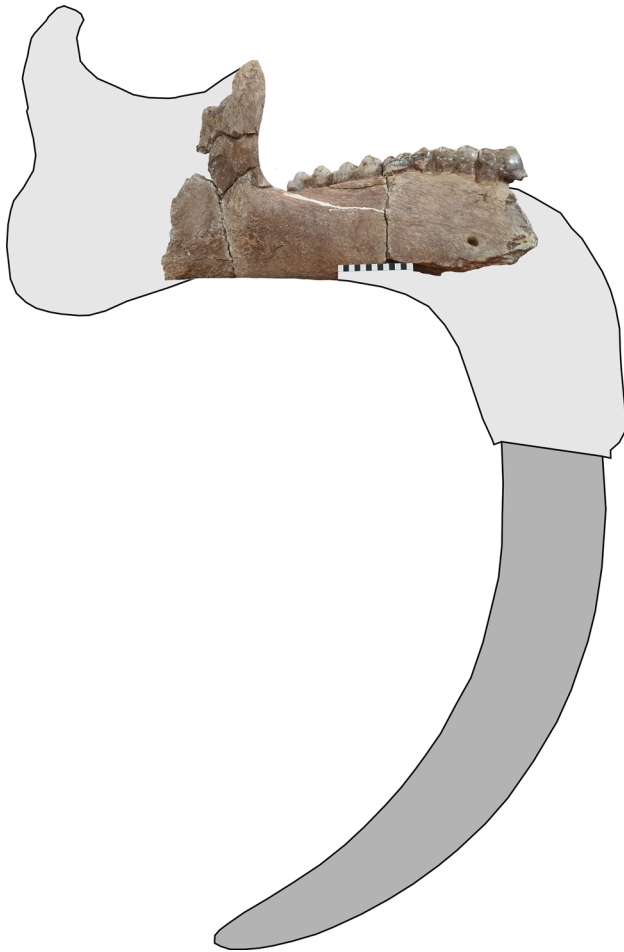


Fig. 4 Anatomical position and hypothetical reconstruction of the Gherghești 1 partial hemimandible (MVP-SN-C5559) based on the right hemimandible of *Deinotherium proavum* from Gela, Aghia Photia (Greece; Fassoulas and Iliopoulos 2011; Iliopoulos et al. 2014); not to scale

the low-crowned, lophodont and bilophodont cheek teeth (apart from the trilophodont dp4/DP4 and m1/M1), the simple occlusal morphology, the replacement of the deciduous dentition by the permanent one in a vertical manner, and the simultaneous function of all permanent cheek teeth are primitive characters that remained unchanged throughout the long (~25.0 myr), but conservative, evolutionary history of the family (Harris 1973; Shoshani et al. 1996; Sanders et al. 2010). On the other hand, the most distinctive feature of deinotheres is the downcurved mandibular symphysis that possesses the almost vertically emerging strong lower tusks (Fig. 4), combined with the absence of upper ones.

As part of the first major radiation of proboscideans, deinotheres originated in Africa during the Late Oligocene but were one of the first proboscidean groups that migrated

toward Eurasia at the beginning of the Miocene. Deinotheres arrived in Europe during the Early Miocene (MN 3; Koufos et al. 2003), and they were continuously present in the continent until the Late Miocene (MN 13) with two genera, the smaller-sized *Prodeinotherium* from the Early–Middle Miocene and the larger-sized *Deinotherium* from the Middle–Late Miocene (Huttunen 2002a). Three species of European *Deinotherium* are recognized (e.g. Böhme et al. 2012; Aiglstorfer et al. 2014; Konidaris et al. 2019): *Deinotherium levius* Jourdan 1861 (late Astaracian), *Deinotherium giganteum* Kaup 1829 (Vallesian) and *Deinotherium proavum* (Eichwald 1831) (latest Vallesian–Turolian). *Deinotherium gigantissimum* Stefanescu 1892 and *Deinotherium thraeciensis* Kovachev and Nikolov 2006 are considered junior synonyms of *D. proavum* (e.g. Codrea 1994; Markov 2008). Distinguishing features among these species include (a) dental dimensions, (b) traits of the mandibular symphysis and angle, and (c) morphology of the p3 and the dp2/DP2. Further details on the taxonomy of European deinotheres are given in Aiglstorfer et al. (2014), Konidaris et al. (2017, 2019, 2023a), Alba et al. (2020) and Konidaris and Tsoukala (2022).

The shape of the mandibular symphysis and the angle, and the precise morphology of the p3 cannot be evaluated in the Gherghești deinotheres. Therefore, we focus our comparison on the dental dimensions, which have proven to have both taxonomic and biochronologic significance, because throughout the evolutionary history of the European deinotheres during the Miocene dental dimensions increased progressively from the older to the younger species. Excluding the smaller-sized deinotheres *Prodeinotherium* from the Early–Middle Miocene of Europe (e.g. Huttunen 2002b), the metric comparison of the cheek teeth shows that although some overlap in the size ranges for certain tooth positions exists between the chronologically successive species of *Deinotherium* (mostly between *D. levius* and *D. giganteum*), *D. proavum* shows distinctly larger dimensions from the other two species (Fig. 7). Such a size distinction allows the metric comparison of the available teeth from Gherghești 1, which reveals that for all tooth positions the Gherghești crown dimensions are clearly distinguished from both *D. levius* and *D. giganteum*, and plot with or very close to the convex hulls of *D. proavum* from several European localities (Fig. 7), including those from Romania (Mânzați, Găiceana, Curtea de Argeș). Therefore, the Gherghești deinotheres can be safely attributed to *D. proavum*.

Family **Mammutidae** Hay, 1922

Genus **Mammut** Blumenbach, 1799

“*Mammut*” cf. *obliqueolophus* (Mucha, 1980)

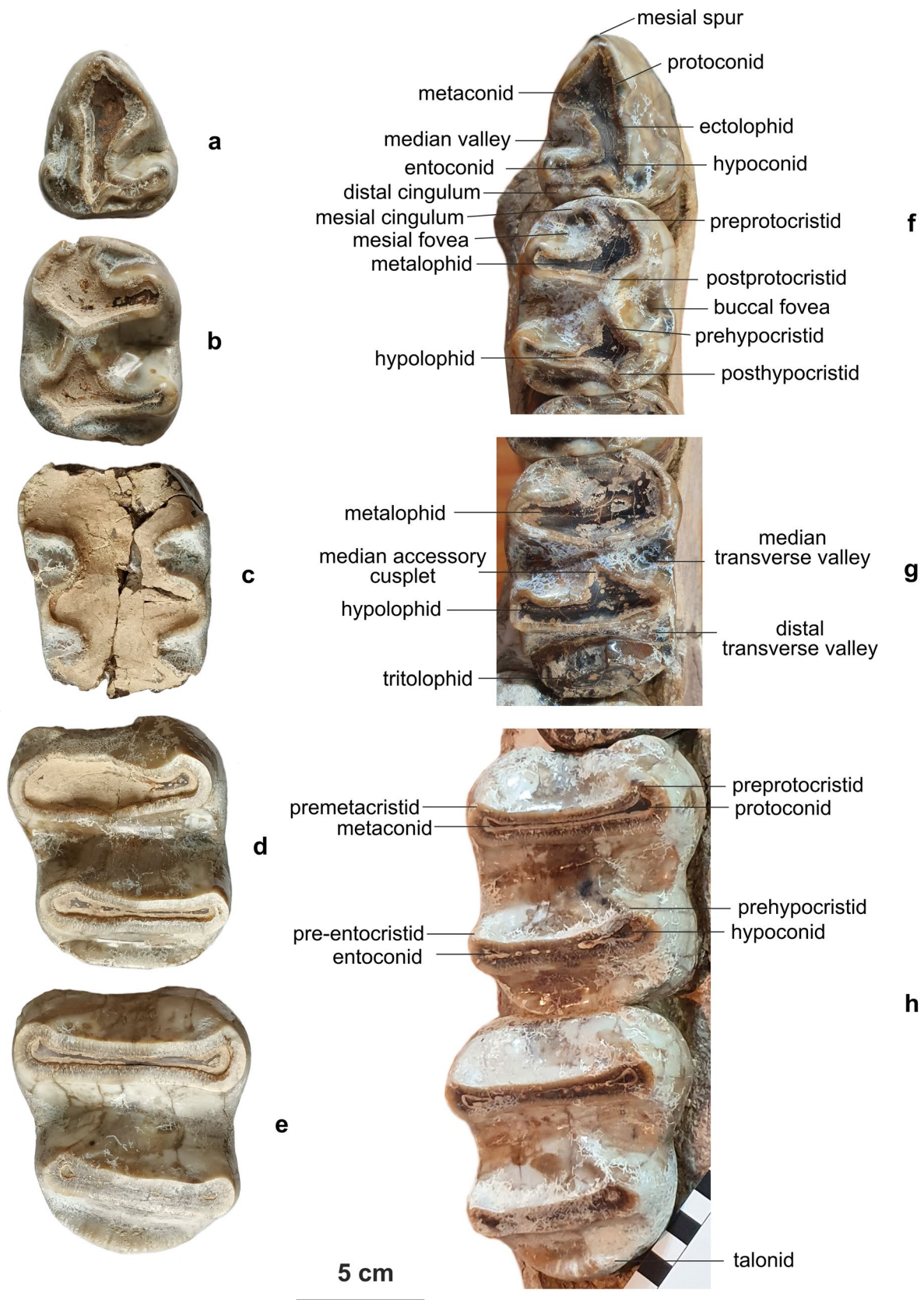


Fig. 5 Left **a–e** and right **f–h** lower premolars and molars of *Deinotherium proavum* from Gherghești 1 (MVP-SN-C5559). **a** p3; **b** p4; **c** m1; **d** m2; **e** m3; **f** p3–p4; **g** m1; **h** m2–m3

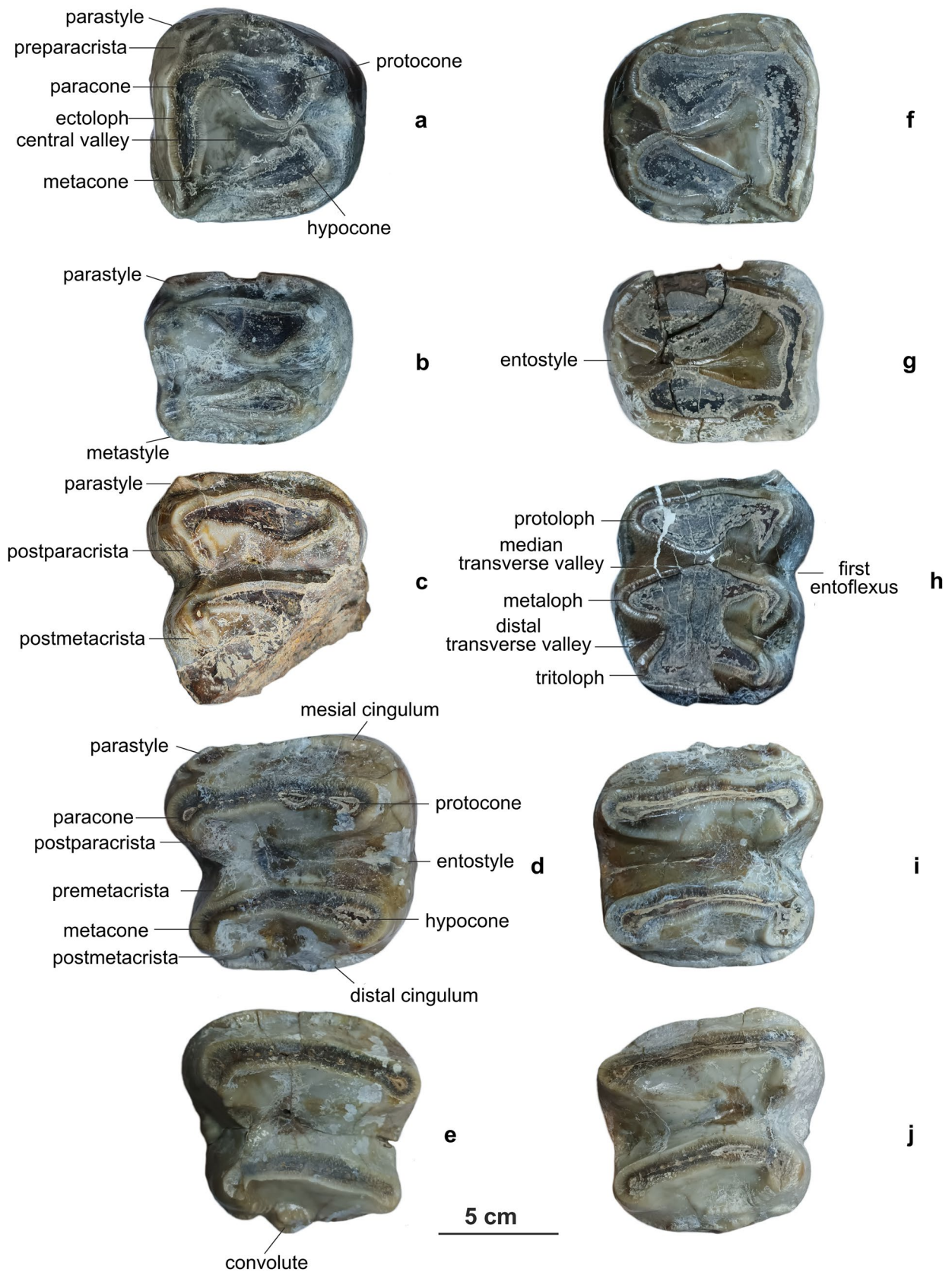


Fig. 6 Right **a–e** and left **f–j** upper premolars and molars of *Deinotherium proavum* from Gherghești 1 (MVP-SN-C5559). **a** P3; **b** P4; **c** M1; **d** M2; **e** M3; **f** P3; **g** P4; **h** M1; **i** M2; **j** M3

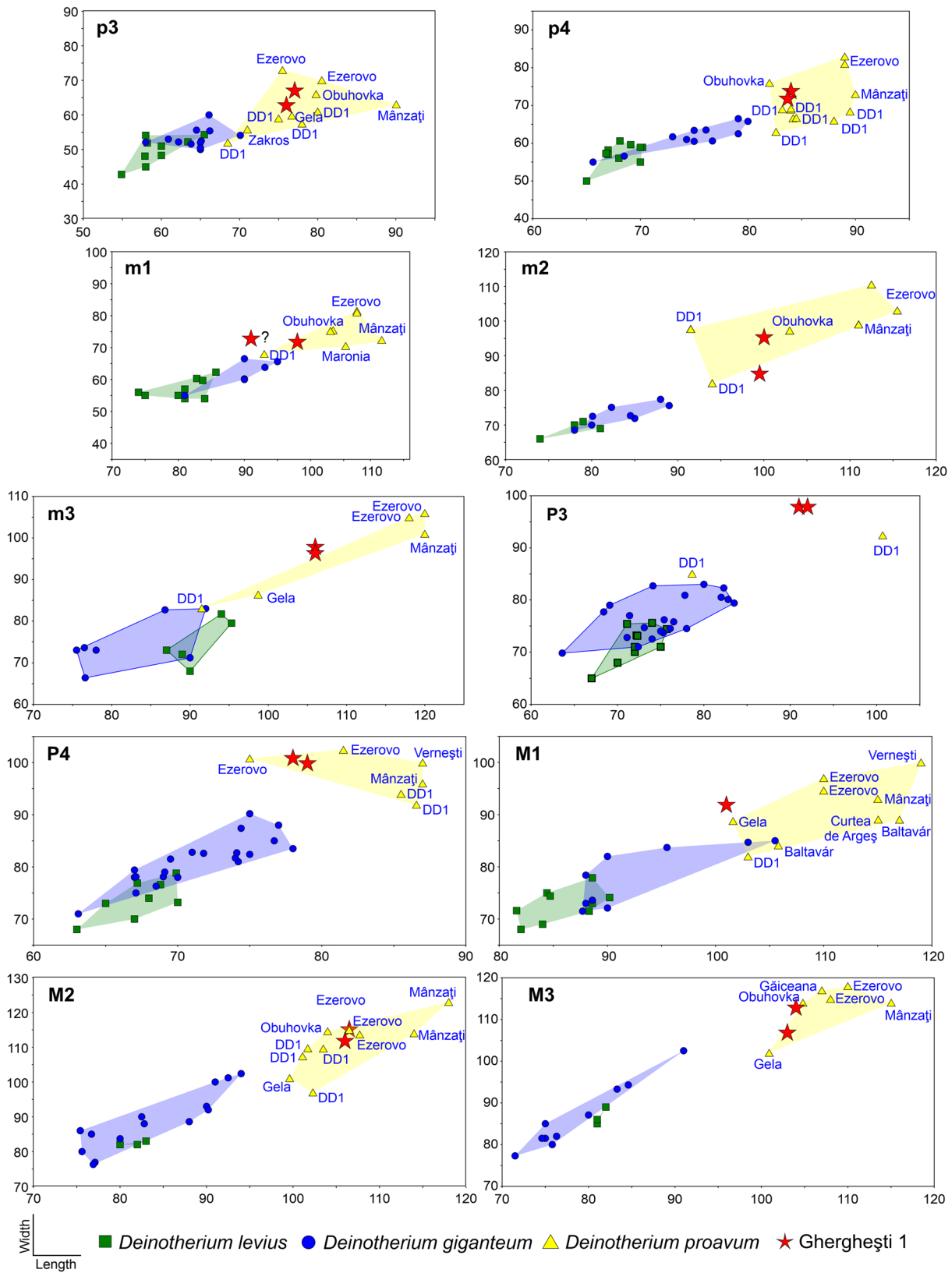
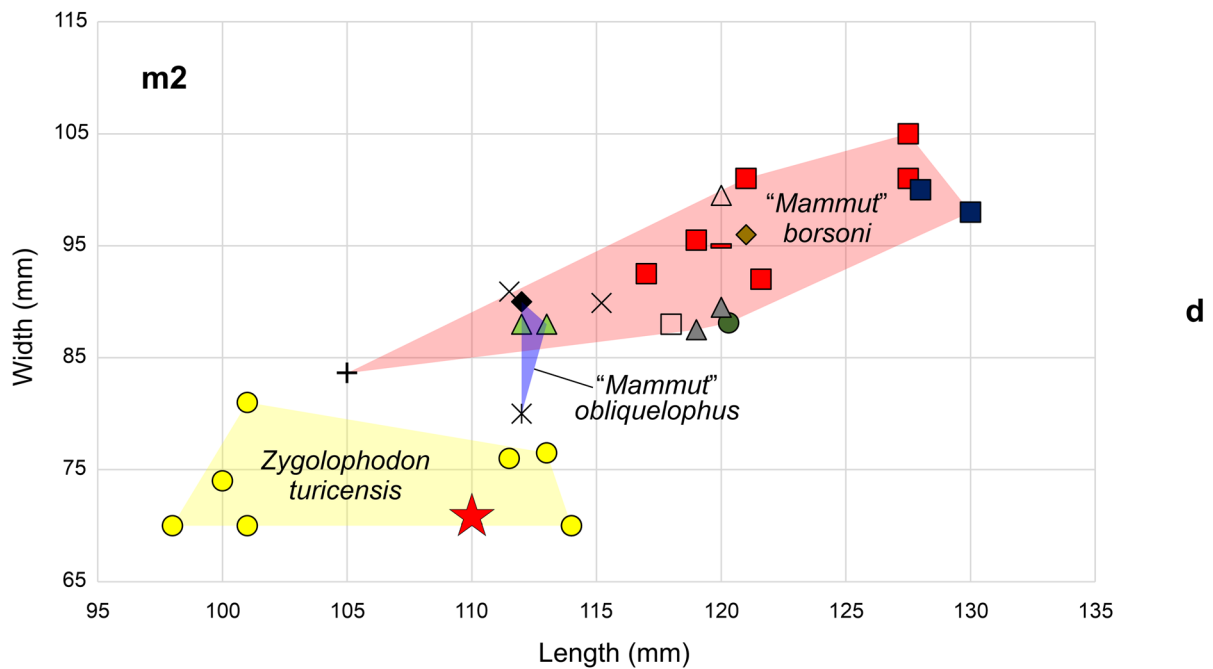
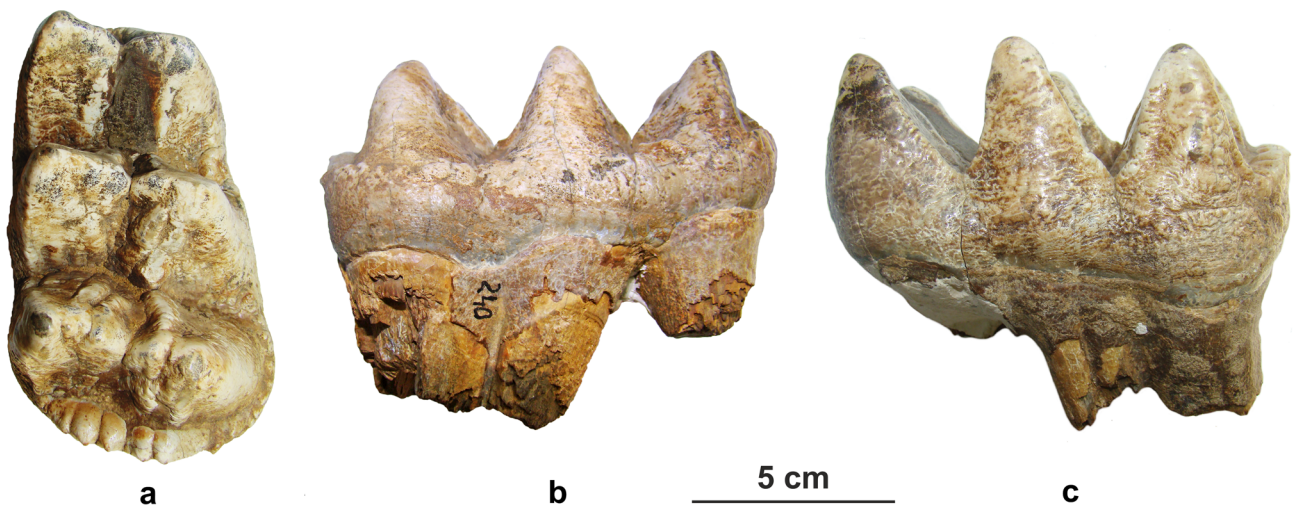


Fig. 7 Bivariate plots of length vs. maximum width (in mm) comparing lower and upper premolars and molars of *Deinotherium levius*, *Deinotherium giganteum* and *Deinotherium proavum* from various

localities; the symbol “?” indicates inadequately preserved left m1 from Gherghești 1; the convex hulls for the species are also shown. For the comparative sample see Table 2



- | | | | | |
|---|-------------------|------------|-----------|------------------|
| ● <i>Zygolophodon turicensis</i> | ◆ Romanovka | ■ Milia | ● Baza 1 | ▲ Pisarevo |
| □ " <i>Mammut praetypicum</i> ", Păgaia | ▲ Balta Sands | × Vialette | ■ Hidveg | △ Peychinovo |
| ★ Hălărești | ⊗ Curtea de Argeș | ◆ Hajnáčka | — Oltenia | + Kaltensundheim |

Fig. 8 Morphology and metric comparison of the right m2 (MVP-SN-C240) of "*Mammut*" cf. *obliquephus* from Hălărești. **a–c** The m2 in **a** occlusal, **b** labial, and **c** lingual view; **d** bivariate plot of

length vs. maximum width (in mm) for m2 of *Zygolophodon turicensis*, "*Mammut*" *obliquephus* and "*Mammut*" *borsoni* from various localities. For the comparative sample, see Table 3

Material and localities. Right m2, MVP-SN-C240 (Hălărești); left m3, MVP-SN-C5708 (Puiești).

Description. The m2 is incipiently worn (Fig. 8a–c). It consists of three lophids, of which the third one is the widest.

There exist mesial, labial, and distal (the stronger) cingula, which are comprised of several cusplets in a row; the lingual side is void of any trace of cingulum. The lophids are arranged oblique relative to the long axis of the tooth, and in its lophid the main cusps and the mesoconelets are situated

in line. Anterior and posterior pretrite zygodont crests are present (the pretrite ones more developed) and contact each other in the interlophids. In lingual view, the interlophids are V-shaped and the crown at their base is high (Fig. 8c). The roots are partially preserved; there is a single mesial one located below the first lophid, whereas there are two united ones below the second and third lophids.

The m3 is slightly worn; dentine is exposed on the first three lophids, more on the pretrite one and less on the posttrite ones (Fig. 9a–c). The tooth consists of four mesio-distally compressed lophids (the first one is the widest) with a weak mesial cingulum attached to the first lophid, and a stronger but narrow distal cingulum. Pretrite zygodont crests are very weak; slightly more expressed but worn is the pretrite zygodont crest of the third lophid. This feature, combined with the absence of posttrite zygodont crests, and lingual and labial cingula results in the completely open transverse valleys without any element blocking them. In lingual view, the interlophids are V-shaped and the crown at their base is high. The roots are mostly preserved; the two mesial ones below the first and second lophids, respectively, are isolated whereas the two distal ones below the third and fourth lophid are united.

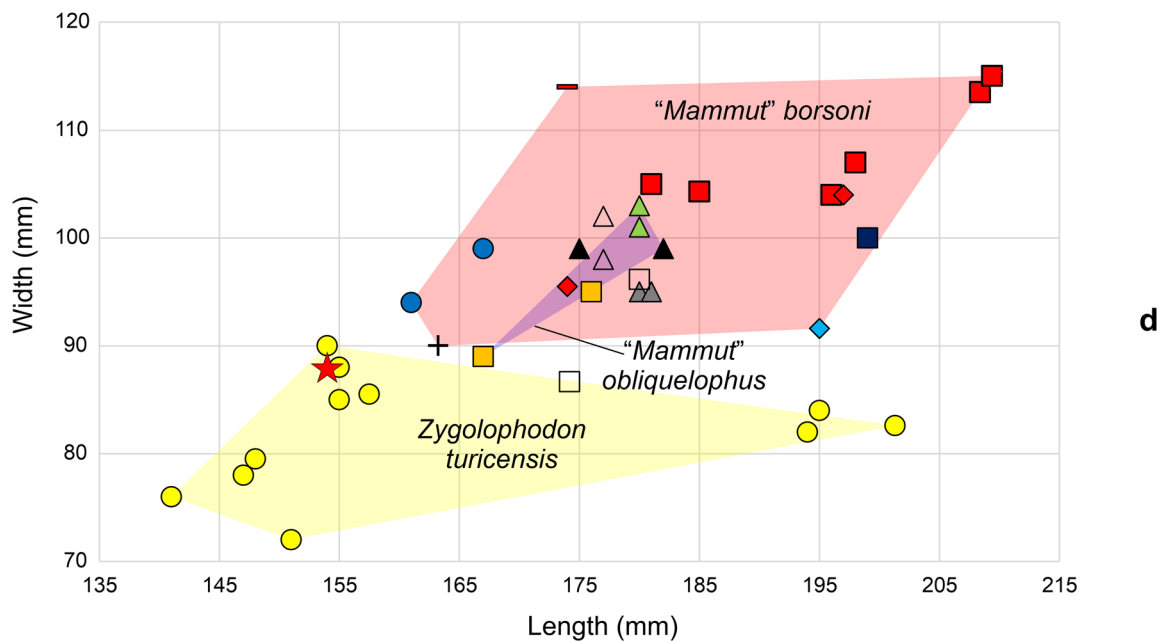
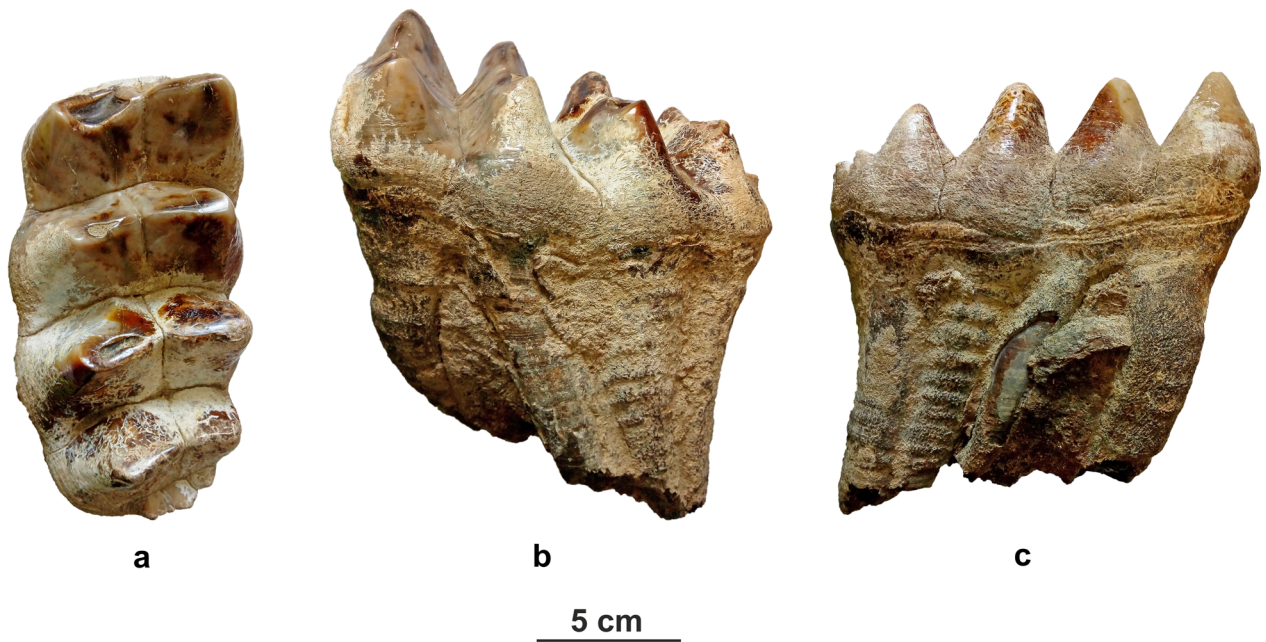
Remarks. The family Mammutidae includes elephantimorph proboscideans identified by their zygolophodont cheek teeth (presence of yoke-like transverse crests, mesio-distally compressed and sharp transverse ridges, absence of accessory conules, and presence of zygodont crests), and trilophodont intermediate molars throughout its evolutionary history (Tassy 1996b; Tobien 1996). Like the deinotheriids, mammutids are also regarded as part of the first major radiation of proboscideans, and both their origin during the Late Oligocene and their initial diversification during the Early Miocene took place in Africa (Shoshani and Tassy 1996; Sanders et al. 2010). During the Early Miocene mammutids, alongside deinotheriids, gomphotheriids and amebelodontids migrated to Europe where they existed until the Pliocene/Pleistocene boundary (Konidaris and Tsoukala 2022).

Presence of zygolophodonty (yoke-like transverse crests), mesio-distally compressed and sharp transverse ridges, absence of accessory conules, and presence of zygodont crests indicate an attribution of the m2 C240 and the m3 C5708 to the family Mammutidae (Tassy 1996b; Tobien 1996). In western Eurasia, two genera are present, *Zygodon* and “*Mammut*”, whose distinction is based on cranial, mandibular, and dental (tusk and cheek teeth) features (Tobien 1996). The herein studied material includes exclusively molars, and therefore its comparison and identification rely on their morphology and dimensions. Of the two European mammutids, the more basal *Zygodon* retains a more bunodont character on its cheek teeth, whereas in the more derived “*Mammut*” the absence of conules results in

the reinforcement of the zygodont character (Tobien 1996). Furthermore, in the lower molars of “*Mammut*” *borsoni* (Hays 1834), the crown at the base of the interlophids of the lingual side is high, a feature that distinguishes them from those of *Zygodon turicensis* (Schinz 1824) (Tassy 1985: p. 516, Fig. 202). The less-expressed zygodont crests, and the absence of crescentoids and of additional conules that block the valleys indicate a well-expressed zygodonty (and accordingly a less bunodont character), and combined with the high crown at the base of the interlophids of the lingual side, in the Hălărești and Puiești specimens, are traits clearly different from *Zygodon* (e.g. Tobien 1975, 1996; Tassy 1977, 1985) and permit the attribution of the Hălărești and Puiești molars to the genus “*Mammut*”.

In western Eurasia, two species of “*Mammut*” are generally recognized, the Late Miocene “*Mammut*” *obliquelophus*, and the Pliocene “*Mammut*” *borsoni* [the generic name *Mammut* for the Eurasian representatives is in question, pending revision of the whole sample and comparison with the North American specimens; see discussion in Markov (2008) and von Koenigswald et al. (2022)]. According to Markov (2008) “*M.*” *obliquelophus*, shows the same cheek tooth morphology like “*M.*” *borsoni*. Indeed, the molars from Hălărești and Puiești cannot be morphologically placed to one or the other species, as the zygodont character is practically identical between the species. The distal cingulum in the m3 from Puiești is much weaker than in the m3s of “*M.*” *borsoni* from Milia (Tsoukala and Mol 2016) and Százhalombatta (Batta-Érd; Schlesinger 1922: pl. 15, Fig. 4), but this trait appears to be variable, as a developed distal cingulum is present in the m3 of “*M.*” *obliquelophus* from Podolia (Kubiak 1972) and Ferladani (Pavlov 1894); however, such a weak distal cingulum as this from Puiești is not reported as yet from “*M.*” *borsoni*. On the other hand, the m3 of “*M.*” *obliquelophus* from Morskaya-2 (Russia; Titov and Tesakov 2013) bears five lophids plus a distal cingulum. Intraspecific variability is observed also in the “*M.*” *borsoni* from Milia, as in the m3 MIL-562, 663 the distal cingulum is weaker than MIL-202, where it takes the form of a fifth lophid (Tsoukala and Mol 2016).

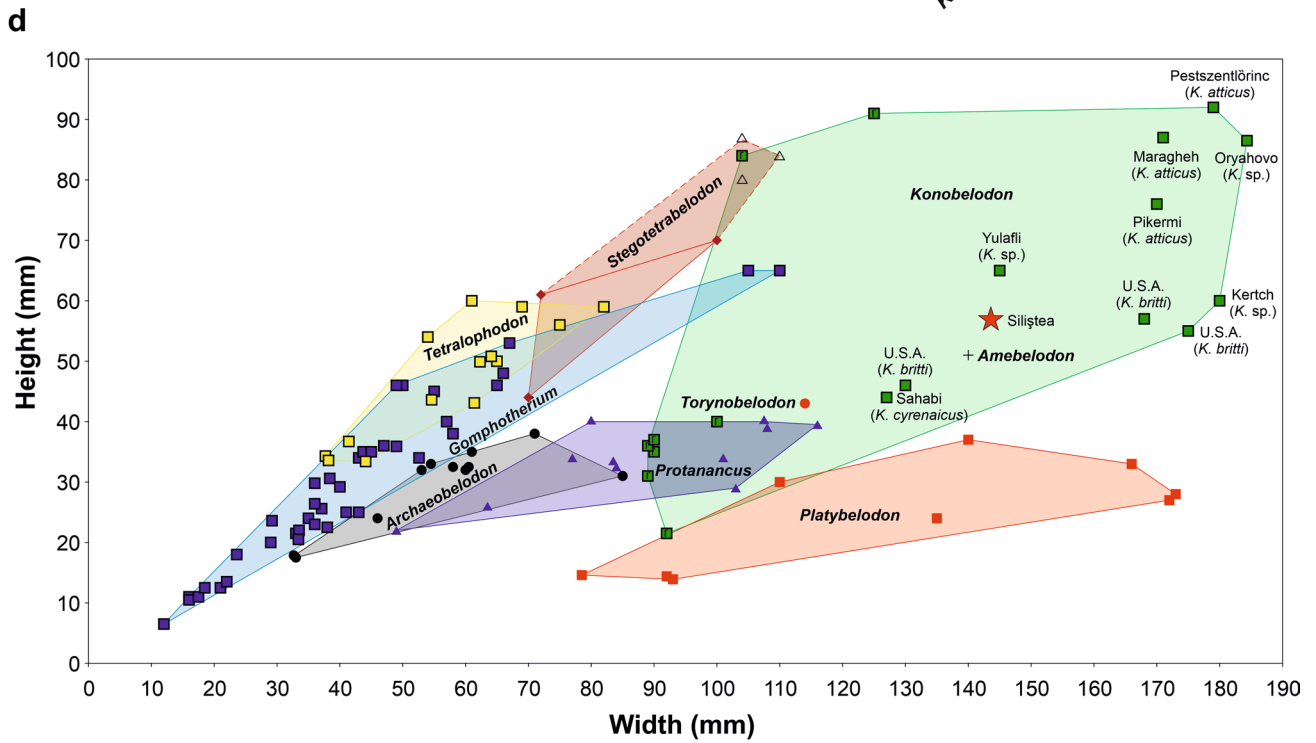
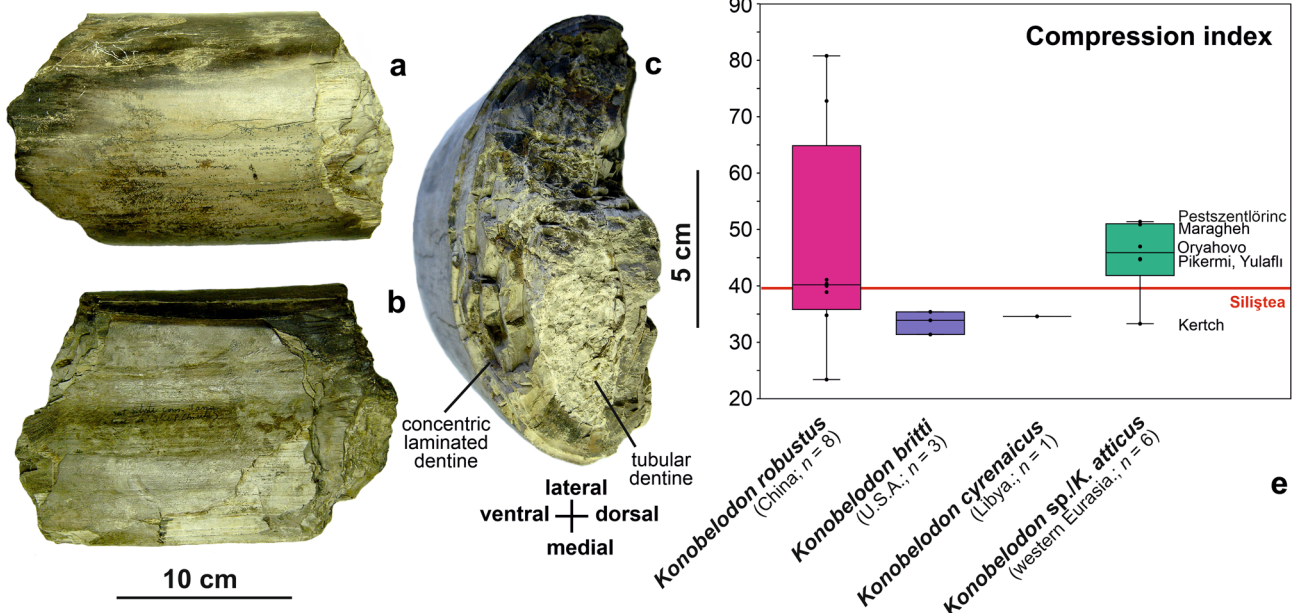
Metrically, m2 and m3 of “*M.*” *obliquelophus* overlap with those of “*M.*” *borsoni*, but in the lower values of the latter species (Figs. 8d, 9d). For the studied material in particular, the length of the m2 from Hălărești is close to that from “*M.*” *obliquelophus* from Romanovka and the Balta Sands, and “*M.*” *borsoni* from Vialette, however, it is much narrower. The closest metric match from the “*Mammut*” sample is with the m2 from Curtea de Argeș (Romania; Athanasiu 1907). The latter locality is referred to as “Pontian” by Athanasiu (1907), who attributes a mammutid mandible from there to *Mastodon borsoni* “Junge Form”. Schlesinger (1922: p. 135–136) allocates this material to the transitional morph “*Mastodon* (*Zygodon*)



- | | | | | |
|--|---------------|----------------|-------------|------------------|
| ● <i>Zygolophodon turicensis</i> | ◆ Romanovka | ■ Milia | ◆ Batta-Érd | ▲ Pisarevo |
| □ " <i>Mammuth praetypicum</i> ", Păgaia | ▲ Balta Sands | ● Bossilkovtsi | ■ Hidveg | △ Psychinovo |
| ★ Puiеști | ■ Ahmatovo | ◆ Hajnáčka | — Oltenia | + Kaltensundheim |

Fig. 9 Morphology and metric comparison of the left m3 (MVP-SN-C5708) of "*Mammuth*" cf. *obliquelophus* from Puiеști. **a–c** The m3 in **a** occlusal, **b** labial, and **c** lingual view; **d** bivariate plot of length vs.

maximum width (in mm) for m3 of *Zygolophodon turicensis*, "*Mammuth*" *obliquelophus* and "*Mammuth*" *borsoni* from various localities. For the comparative sample see Table 3



- *Gomphotherium* (En Péjuan, Simorre and Tournan, France; Steinheim, Babing, Gweng bei Mühldorf and Sandelzhausen, Germany)
- *Tetralophodon* (Esselborn and Bermersheim, Germany; Breitenfeld, Laaerberg and Großweiffendorf, Austria; Rudabánya, Hungary; Hammersmiede 6, Germany)
- ◆ *Stegotetralodon* (Cessaniti, Italy; Sahabi, Libya; Lothagam 1, Kenya)
- △ ?*Stegotetralodon* (Gebel Sémène, Tunisia; Crevillente 2, Spain)
- *Archaeobelodon* (Sansan, France; Mwit, Kenya)
- ▲ *Protanancus* (Yürükali, Turkey; Maboko, Kenya; Alengerr, Kenya; Chinji, Pakistan; China)
- *Platybelodon* (Belomechetskaya, Russia; Arapli, Turkey; Loperot, Kenya; Danghe area and Tungur, China)
- *Torynobelodon* (Sand Canyon-Nebraska, U.S.A.)
- + *Amebelodon* (Freedom-Nebraska, U.S.A.)
- *Konobelodon* (Pikermi, Greece; Maragheh, Iran; Pestszentlörinc, Hungary; Oryahovo, Bulgaria; Yulafli, Turkey; Kertch, Ukraine; Sahabi, Libya; Florida, Texas and Kansas, U.S.A.)
- *K. robustus*, Linxia basin, China)
- ★ *Konobelodon*, Siliştea

Fig. 10 Morphology and metric comparison of the lower tusk fragment (MVP-SN-C4657) of *Konobelodon* sp. from Silișteța. The lower tusk in **a** ventral, **b** dorsal, and **c** cross-sectional view; **d** bivariate plot (width vs. height) comparing the lower tusk of *Konobelodon* from Silișteța with lower tusks of various Miocene proboscideans. Note that the lower tusks belong to individuals of different ontogenetic ages and the location of the measurements differs among them (e.g. maximal preserved diameters if isolated or in front of the mandibular symphysis if embedded). Bivariate plot based on Konidaris and Tsoukala (2020: Fig. 5d) and Konidaris et al. (2023a), and references cited in the corresponding captions; **e** box-and-whisker plot comparing the compression index of the lower tusks of *Konobelodon* spp. from various localities with MVP-SN-C4657 from Silișteța (red horizontal line). Black horizontal lines represent the median, boxes the 25 and 75 percentiles (interquartile range); whiskers the maximum–minimum values; black circles the specimens. Data from references cited in Konidaris and Tsoukala (2020: Fig. 5d) and Konidaris et al. (2023a), and G.K. measurements at AMPG, HNHM, NHMW and SU

tapiroides/Mastodon (Mammuth) americanus” (like the one from Ferladany of “*M.*” *obliquelophus*), Markov (2008) based on the assumed age hints an attribution to “*M.*” *obliquelophus*, and Codrea and Diaconu (2007) assume a Dacian [latest Miocene–earliest Pliocene sensu Steininger (1999)] age for the find deposits. In the case that the deinotherid molar from Curtea de Argeș (Athanasiu 1907: p. 194, pl. 4, figs. 8, 9) comes from the same stratigraphic layer as the mammutid mandible, this would imply a Late Miocene age for the latter.

Concerning the m3, the Puișteți molar is the smallest one of the herein examined “*Mammuth*” specimens (Fig. 9d). Its width is similar to the m3 of “*M.*” *obliquelophus* from Ahmatovo (Turolian, Bulgaria; Nikolov and Kovacev 1966), and to the m3 of “*M.*” *borsoni* from Kaltensundheim (Late Pliocene, Germany; von Koenigswald et al. 2022), yet it is shorter. The width of the Puișteți molar is also similar with a m3 from the locality of Păgaia in Romania attributed by Codrea et al. (2005) to “*Mammuth praetypicum*” (precise age unknown but deposits of the area date to the uppermost Miocene–Pliocene; for the status of this species see Markov 2008). Other mammutid specimens from this locality (as “Usztataó bei Tasnád”) were referred to the transitional morph “*Mastodon (Zygodolophodon) tapiroides/Mastodon (Mammuth) americanus*” by Schlessinger (see also Jurcsák 1973).

Overall, although morphologically the studied molars can be safely attributed to “*Mammuth*”, in the absence of a mandible preserving the symphysis, any clear-cut taxonomic attribution to the one or the other European “*Mammuth*” species would not be solidly supported. On the other hand, the smaller dimensions of the studied specimens fit better with an attribution to “*M.*” *obliquelophus*, which is in accordance with the assumed geological age

of the specimens. Therefore, we attribute the molars from Hălărești and Puișteți to “*Mammuth*” cf. *obliquelophus*. The discovery of additional material of “*M.*” *obliquelophus* will reveal whether the smaller size and the weaker development of the distal cingulum in the m3 has taxonomic/biostratigraphic significance.

Family **Amebelodontidae** Barbour, 1927

Genus ***Konobelodon*** Lambert, 1990

Konobelodon sp.

Material and localities. Lower tusk fragment, MVP-SN-C4657 (Silișteța); distal part of left m3, MVP-SN-C5240 (Iana).

Description. The lower tusk fragment C4657 (preserved L: 220 mm; W: 144 mm; H: 57 mm; CI = 39.6) represents a permanent tusk of an adult individual (Fig. 10a–c). It is large-sized and dorsoventrally flattened. Dorsally, it bears a longitudinal deep but open dorsal concavity and an additional shallower one toward the medial side; its ventral side is convex. Its medial and lateral borders are rounded. The tusk consists of a core of tubular and closed-spaced dentine, which is surrounded by a layer of concentric laminated dentine.

The m3 C5240 preserves the 3 1/2 distal lophids and the distal cingulum (Fig. 12a–c). The cusps are much worn, and dentine is exposed, apart from the distal-most lophid; however, the median sulcus is still visible separating into pretrite and posttrite halflophids. A worn posterior pretrite central is present in the damaged, proximal-most, lophid; the two more distal ones bear anterior and posterior pretrite central conules. A posterior posttrite central conule is present in the second preserved lophid, yet weaker. The mesoconulelets, especially the posttrite ones, are in a slightly more proximal position in regard to the main cusps, and chevron structure is clearly formed in the distal-most lophid. A rudimentary cingulum is present at the middle of the distal end of the tooth. A relatively strong cingulum, formed by a series of cusplets, extends along the buccal wall of the tooth. Cement covers the transverse valleys, and the lingual and buccal walls of the tooth (Fig. 12a–c).

Remarks. An attribution of the Silișteța lower tusk to the gomphotheriids *Gomphotherium* and *Tetralophodon*, the amebelodontids *Archaeobelodon* and *Protanancus*, or the elephantid *Stegotetralodon*—including the Gebel Sémène (Tunisia) and Crevilente 2 (Spain) taxon/taxa with possible

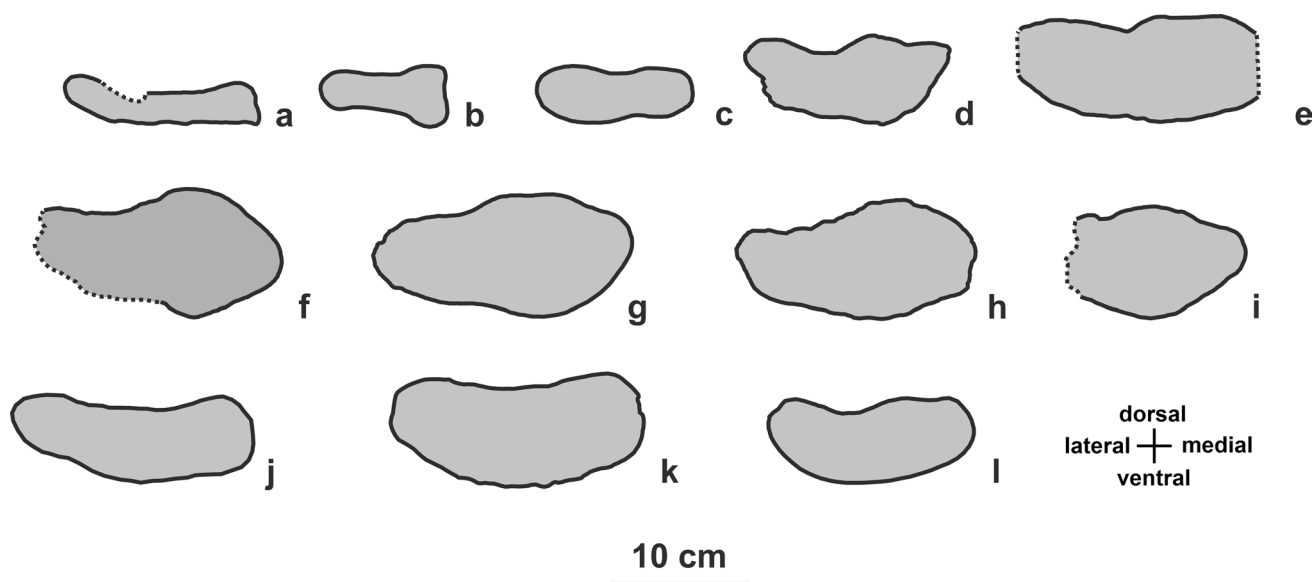


Fig. 11 Cross sections of amebelodontid lower tusks. **a** *Platybelodon* cf. *danovi*, Araplı, Turkey; **b** *Torynabelodon loomisi*, Nebraska, U.S.A.; **c** *Konobelodon cyrenaicus*, Sahabi, Libya; **d** *Konobelodon* sp., Yulaflı, Turkey; **e** *Konobelodon* sp., Kertch, Ukraine; **f** *Konobelodon atticus*, Maragheh, Iran; **g** *K. atticus*, Pestszentlőrinc, Hungary; **h**

K. atticus, Pikermi, Greece, 320 mm from base; **i** *K. atticus*, Pikermi, Greece, 950 mm from base; **j** *Konobelodon britti*, Texas, U.S.A.; **k** *K. britti*, Florida, U.S.A.; **l** *Konobelodon* sp., Siliştea, Romania. From references cited in Konidaris et al. (2014) plus Barbour (1929), and G.K observations at HNHM and NHMW

Stegotrabelodon affinities—is excluded, because the lower tusks of all these genera are formed exclusively from concentric lamellar dentine and their cross-sectional shape is more oval–pyriform (with the exception of the more flattened lower tusks of *Protanancus*), (Fig. 10d; see also Konidaris et al. 2014; Konidaris and Tsoukala 2020, and references cited in both). On the other hand, presence of tubular dentine in the dorsoventrally flattened lower tusk from Siliştea (Fig. 10c) indicates an attribution to one of the amebelodontid genera bearing internally dentinal rods, that is *Platybelodon*, *Torynabelodon* (*Torynabelodon loomisi* Barbour 1929) and *Konobelodon* (Tassy 1986, 1996b; Wang et al. 2013; Konidaris et al. 2014). Nonetheless, the lower tusks of *Platybelodon* are even more dorsoventrally flattened (plate-like) than the Siliştea one (Figs. 10d, 11a), and that of the North American *T. loomisi* has a different cross-sectional shape, with wide and roughly straight medial border, approximately the same width in the middle and lateral parts, and with shallow concavities on both dorsal and ventral sides (Fig. 11b; Barbour 1929: Fig. 98; Konidaris and Tsoukala 2022).

Both cross-sectional diameters, proportions, and morphology of the Siliştea tusk are compatible with an attribution to *Konobelodon* (Figs. 10, 11). Within *Konobelodon*, the CI of the Siliştea tusk is very close to the median value of the sample of *Konobelodon robustus* (Wang et al. 2016) from China (which shows high range in the minimum–maximum values, but the sample includes lower tusks of various ontogenetic ages; the adult mandible plots in the upper range

of CI), but the width/height dimensions of the Siliştea tusk separate it from this species (Fig. 10d, e). Although the general cross-sectional shape and the height of the Siliştea tusk are similar to *Konobelodon britti* Lambert 1990, the lower tusks of this species are wider (reflected also in their lower CI compared to the Siliştea one) and the dorsal concavity is more open (Figs. 10, 11j, k). The Siliştea tusk also exceeds the CI of the single specimen of *Konobelodon cyrenaicus* (Gaziry 1987) from Sahabi, which besides the dorsal concavity has also a ventral one (Figs. 10d, 11c). On the other hand, the CI of the Siliştea tusk is plotted within the range of the sample of western Eurasia *Konobelodon*, at its lower range, between the values of the tusk from Kertch (Pavlov 1903), and Pikermi (Konidaris et al. 2014) and Yulaflı (Turkey; Geraads et al. 2005). Compared to the lower tusk from Yulaflı, the Siliştea specimen has similar width, but the latter is higher, has a more angular medial border and bears two deeper longitudinal dorsal concavities (Figs. 10d, 11d). Two deep longitudinal dorsal concavities and additional shallower in between them extend also along the length of the tusk from Oryahovo (Bulgaria; G.K. at SU; Bakalov and Nikolov 1962). The rounded medial border and the presence of one deep dorsal concavity fit better with *Konobelodon atticus* (Wagner 1857) from the Turolian localities Maragheh (Iran; NHMW-1893/0012/0006), Pikermi (Greece; AMPG-PA1972/61) and Pestszentlőrinc (Hungary; HNHM-V.79.34) yet the Siliştea tusk has smaller dimensions (Figs. 10d, 11f–i). However, in the complete adult tusk from Pikermi, the dentine is mainly uniform in the more basal part of the

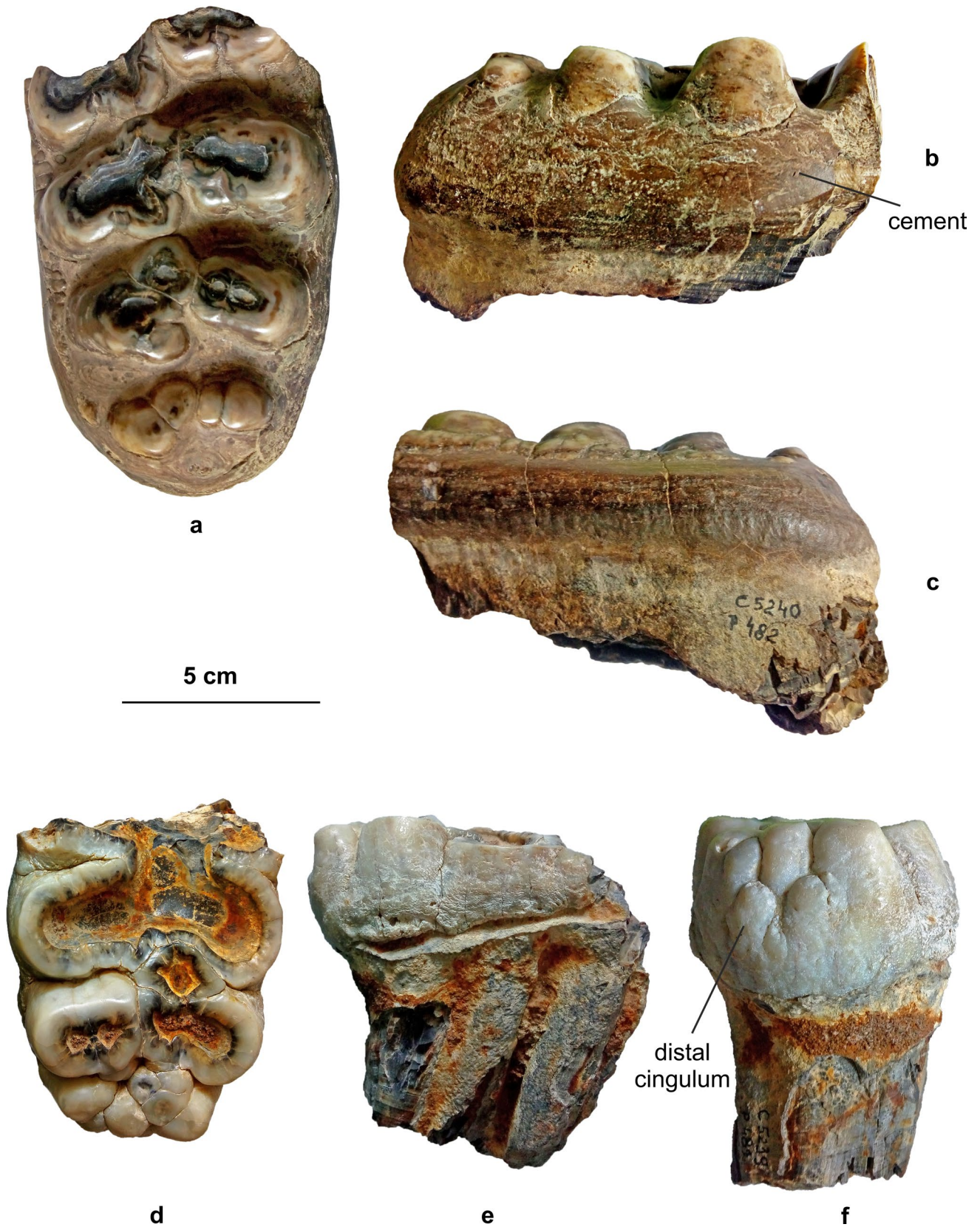


Fig. 12 a–c Distal part of left m3 (MVP-SN-C5240) of *Konobelodon* sp. from Iana, in a occlusal, b lingual, and c labial view; d–f distal part of right m3 (MVP-SN-C5239) of *Konobelodon?* from Banca, in d occlusal, e labial, and f distal view

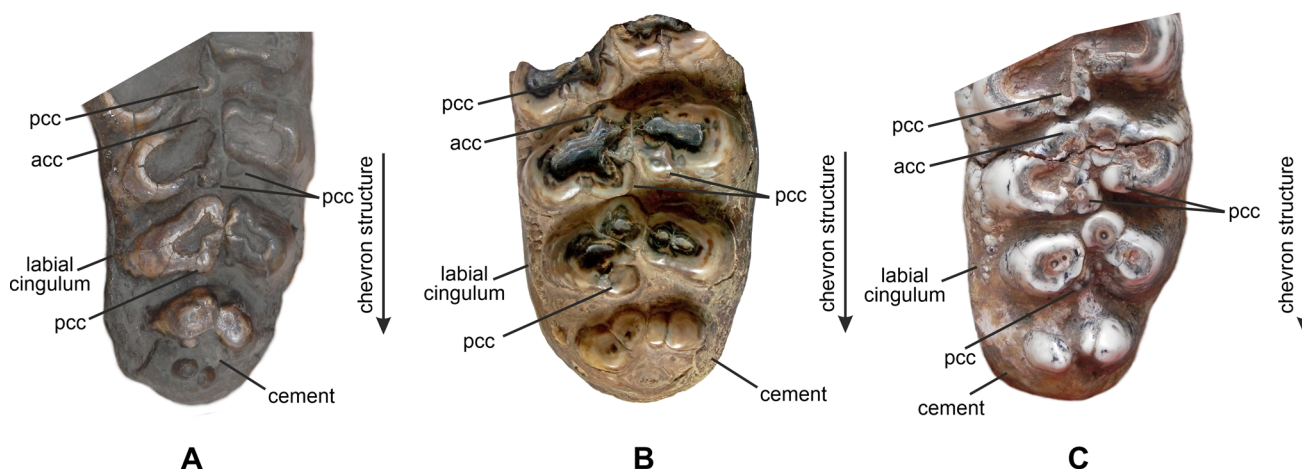


Fig. 13 Morphological comparison (in occlusal view) of the distal part of m3 of *Konobelodon*; not in scale. **A** Left m3 (SU-241) from Oryahovo, Bulgaria; **B** left m3 (MVP-SN-C5240) from Iana; **C** right

m3 (HNHM-V.79.34; reversed) from Pestszentlőrinc (Hungary). *acc* anterior central conule; *pcc* posterior central conule

tusk, whereas it becomes gradually more tubular toward the apical part. Therefore, the Siliştea specimen represents a medial fragment of the tusk, and the dimensions of its cross section at its proximal part would be potentially larger. As was also noted in Konidaris and Tsoukala (2020), the comparative lower tusk sample that is used for comparison belongs to individuals of different ontogenetic ages and the location of the measurements differ among them, while additionally differences in cross-sectional shape/dimensions and thickness of dentinal tubules occur also along the tusk's length (e.g. in the complete Pikermi and Pestszentlőrinc ones).

The comparison of the third lower molar from Iana is limited to its preserved distal part. The pretrite and posttrite ornamentation of the lophids, the substantial amount of cement covering the transverse valleys and the walls of the lophids, the developed cingulum formed by a series of cusplets along the labial side, and the chevron structure in the distal lophids are common traits in the western Eurasian *Konobelodon* (formerly "*Mastodon grandincisivus*") (Fig. 13; Schlesinger 1922; Tobien 1978; Konidaris et al. 2014). The structure of the lophids resembles the corresponding part of the m3s of *Konobelodon* from Oryahovo [SU-241; Fig. 13a; Bakalov and Nikolov (1962); these molars consist of six lophids, and such a formula can be assumed also for the Iana molar; in this case the latter preserves the posterior half of the third lophid and the remaining distal part of the tooth]. A similar structure is also observed in the m3 of *K. atticus* from Pestszentlőrinc (HNHM-V.79.34; Fig. 13c; Schlesinger 1922), but it shows a pseudo-anancoid pattern, absent in the Iana molar. The m3 of *K. atticus* from Pikermi (Vacek 1877; considered as M3 by Tassy 2016) has a rudimentary posterior pretrite central conule of the fourth lophid and lacks the one of the fifth

lophid, resulting in a somewhat simpler structure than the Iana one. However, the number of accessory conelets and of alternating contact in the distal lophids are variable traits for the taxon (Konidaris et al. 2014).

Considering the fragmentary and single status of the available material from each locality and pending the discovery of additional material, we attribute both the lower tusk and the molar to *Konobelodon* sp.

Konobelodon?

Material and locality. Distal part of right m3, MVP-SN-C5239 (Banca).

Description. Only the distal wall of the mesially preserved lophid is retained. The succeeding lophid is much worn and the dentine is confluent obscuring the original morphology. In the interloph, one worn but strong central conule blocks the transverse valley lingually. The distal lophid is slightly less worn and the visible median sulcus divides the lophid into pretrite and posttrite half-lophids. One mesoconelet is present at the posttrite side, whereas the dentine is confluent in the pretrite main cusp and the mesoconelet. The mesoconelets, especially the pretrite one, are situated in a slightly more proximal position than the main cusps. The distal cingulum is much developed and formed by several strong cusplets in its mesial part; three lower cusplets are located at the distal-most end of the tooth.

Remarks. Based on the preserved large distal root below the preserved two distal lophids, the molar fragment C5239 is identified as belonging to a tetralophodont grade elephantimorph (Fig. 12d–f). The thickness of the enamel excludes

an identification as a dp4. On the other side, considering the absence of a contact facet at its distal end that would be present due to pressure of a succeeding molar, MVP-SN-C5239 is identified as an m3.

The absence of anancoidy excludes an attribution to *Anancus*. The most characteristic part of the molar is the well-developed, double, distal cingulum (Fig. 12d–f). Such a strong and complex development of the cingulum is unknown in the large cheek tooth sample of *Tetralophodon longirostris* from the Dinotheriensande (Germany; HLMD; Kaup 1835) and Rudabánya (Hungary; HGI). This structure is also different from the m3 MVP-SN-C5240 of *Konobelodon* from Iana and from other specimens of this genus (e.g. those in Fig. 13), yet it is reminiscent of the M2 of *Konobelodon* from Yulaflı (Geraads et al. 2005: Fig. 4E). Despite of being substantially worn, the rather complex occlusal morphology of C5239 fits generally better with an attribution to *Konobelodon*. However, the fragmentary nature and advanced wear stage of the Banca specimen precludes a detailed comparison and a safe attribution, and therefore we allocate it to *Konobelodon*?

Biostratigraphic remarks—Conclusions

Deinotherium proavum was the last deinothere of Europe and perhaps of the whole Eurasia (see Pickford and Pourabrishami 2013) and by reaching enormous dimensions (average body mass 10.5 tons, while some individuals may weigh more than 13–14 tons; Larramendi 2016) corresponds to the terminal stage of size increase that characterizes the evolution of European deinotheres. The species occurred first at the latest Vallesian (Alba et al. 2020) but is well-recorded during the whole Turolian (Markov 2008; Konidaris et al. 2017). In combination with the geological data, a correlation to the Turolian is proposed for the deinothere from Gherghești.

“*Mammut*” is well-known in western Eurasia from the Pliocene with the species “*M.*” *borsoni*. Nonetheless, its first representatives are documented during the Late Miocene (Turolian) and are attributed to the distinct species, “*M.*” *obliquelophus*. The biostratigraphic distribution of this species covers the whole Turolian (see Konidaris et al. 2023b and references cited), from biozone MN 11 (e.g. Ravin des Zouaves-5, Greece; ~ 8.2 Ma; Koufos 2013) to biozone MN 13 (e.g. El Arquillo 1, Spain; ~ 6.2 Ma; van Dam et al. 2001). “*Mammut*” *obliquelophus* had a wide geographic range, from west to east of today’s Europe, and is particularly well-recorded in eastern–southeastern Europe (Konidaris et al. 2023b). Therefore, the presence of “*M.*” cf. *obliquelophus* at Hălărești and Puiesti indicates a post-Vallesian age, and if indeed the material belongs to this species, then it would be correlated to the Turolian.

The earliest occurrences of *Konobelodon* are traced in China with an estimated age at 11.1–9.8 Ma (corresponding to the European early Vallesian; Wang et al. 2016). The earliest appearance in western Eurasia is recorded at Yulaflı (Turkey), correlated to the late Vallesian (MN 10), at 9.4–9.3 Ma (Geraads et al. 2005). In the Greco-Iranian-Afghan (sensu Bonis et al. 1992; Balkano-Iranian or Sub-Paratethyan) palaeobiogeographic province, the genus is best known from the Turolian with the species *Konobelodon atticus*, whose biostratigraphic range is from biozone MN 11 to biozone MN 13 (Konidaris et al. 2014; Konidaris and Tsoukala 2022). Therefore, the presence of *Konobelodon* at Silișteea and Iana is suggestive for a late Vallesian–Turolian age.

Proboscideans are generally a rare faunal component in most Miocene fossiliferous localities, and thus any new specimen may add important morphological and biostratigraphic information and contribute to improving our knowledge of this mammal group. Even if the herein studied finds are mostly isolated, and some fragmentary, they indeed add new data on the dental morphology and size of the corresponding taxa that they are allocated: the material of *Deinotherium proavum* from Gherghești 1 is one of the few examples of complete upper and lower tooth rows of the same individual; the mammutid material adds to scarce record of “*Mammut*” in the Miocene of Eurasia; and the identification of *Konobelodon* marks the first record of the genus in Romania.

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Data availability All data analyzed in this study are included in this published article. All fossil material described in this paper is deposited in a Public Institution (Museum Vasile Pârvan, Bârlad, Romania).

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article nor have financial or proprietary interests in any material discussed in this article.

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