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First true mastodon from the Late Miocene of Iran

Sadaf Yaghoubi¹, Ali Reza Ashouri^{2*} , Majid Mirzaie Ataabadi³ and Abbas Ghaderi²

Abstract

A *mammutid* is described here for the first time from the Late Miocene (MN12 equivalent) deposits of Abkhareh village, Varzeghan region, in the North-Western part of Iran. It is identified as “*Mammut*” cf. *obliqueophus* and is represented by an isolated and moderately worn upper third molar with a zygodont crown pattern typical of mammutids. In addition, two upper incisors found associated with the molar and probably belonging to the same individual are assigned as *Mammut*. The studied material expands the geographic distribution of “*Mammut*” *obliqueophus* into Western Asia.

Highlights

There are some known localities bearing vertebrate fossil beds from Northwest of Iran like Maragheh (MN12, Mirzaie Ataabadi et al., 2013c), Ivand (MN12, Mirzaie Ataabadi et al., 2011a) and Kivi-1 (MN12, Jafarzadeh and Konidaris, 2020). However, some materials belonging to proboscideans were revealed from a village, Abkhareh (MN12), in Varzeghan area 150 km away from Maragheh. In this study, an upper third molar and a pair of upper tusks of an ancient elephant-like mammal were attributed to the mammutid “*Mammut*” cf. *obliqueophus*. This finding proves that this taxon inhabited Iran between 8–7.5 Ma, which falls in the Turolian stage of the Late Miocene. It marks the first record of this species in Iran and expands the known geographic distribution of “*Mammut*” *obliqueophus* into Western Asia.

Keywords Mammutids, *Mammut praetypicum*, MN12, Proboscideans, Late Miocene, Varzeghan

Introduction

The village Abkhareh, located 12 km to the West of Varzeghan town, about 150 km North of the well-known Late Miocene fossiliferous areas of Maragheh, yielded a relatively large number of fossil proboscideans (*Deinotherium* Kaup, 1829; *Mammut* Blumenbach, 1799) and

hipparions. These fossils were excavated more than a decade ago during a renovation of the historical building “Amir-Arshad Khaneh Bagh” in Abkhareh village (Fig. 1).

According to Mirzaie Ataabadi et al. (2011a), deinotheriid is represented in the Varzeghan area by cranial and postcranial elements, including some upper molars (right M¹, MMTT-V16; M², MMTT-V11 and M³, MMTT-V14 and left M¹, MMTT-V12; M², MMTT-V15 and M³, MMTT-V13), all belonging to a single and huge individual originally attributed to *Deinotherium giganteum* Kaup, 1829 (Mirzaie Ataabadi et al. (2011b), which has subsequently been described as *Deinotherium proavum* Eichwald, 1835, later (Pickford & Pourabrishami, 2013). Although before, the materials from Abkhareh, Varzeghan were partly studied and identified as *Deinotherium gigantissimum* Stefanescu 1892 by Pourabrishami, 2004, which following more

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recent studies (Böhme et al., 2012; Codrea, 1994; Pickford & Pourabrishami, 2013) is not a valid species, but synonymized with *Deinotherium proavum* Eichwald, 1835.

The fossils occurred on the surface, and there was no sediment exposure and its sedimentology and depositional environment are poorly understood. Deinotheres-bearing locality is a local concentration of bones within a mudstone bed and is restricted to a single horizon (Mirzaie Ataabadi et al., 2011b).

The present article only describes the mammutid remains, not the entire proboscidean materials of the fauna from this locality.

Using the name *Mammuth* for Eurasian mammutids can cause some taxonomical complications. According to Schlesinger (1922) and Tobien (1975, 1977), the Eurasian *Mammuth* ("*Mammuth*" *borsoni*, "*Mammuth*" *obliquelophus* and "*Mammuth*" *praetypicum* [if valid]) invaded North America in a second immigration phase during the Late Miocene/Pliocene and gave rise to the North American *Mammuth*. So, some European ancestors were assumed for *Mammuth americanum*. However, there is no supporting evidence so far for this hypothesis.

On the other hand, some authors believe there was a separate evolution of Eurasian and American mammutids

(Saunders, 1996; Markov, 2004; Von Koenigswald et al., 2022). The hypothesis says that during the lower Miocene *Zygolophodon* immigration to North America gave rise to *Mammuth americanum*. The most parsimonious hypothesis is to assume a second Late Cenozoic mammutid migration to North America, following the initial appearance of mammutids in the Late Early Miocene of North America (von Koenigswald et al., 2022).

In the present work, we recognize the genus *Mammuth* to encompass the offshoot of Neogene Eurasian and North American mammutid radiation, which eventually led to the Pleistocene *Mammuth americanum* of North America. Though some Late Neogene Eurasian taxa may be considered to fit morphologically with such a concept, their phylogenetic affinities remain at best, equivocal (Markov, 2004; von Koenigswald et al., 2022). Following the reasoning of Markov (2004), which we will revisit subsequently in the manuscript, we now demarcate the generic affinity of these taxa as "*Mammuth*".

To imply such a taxonomic problem with the genus name *Mammuth* and to indicate that the mammutid specimen found from Abkhareh does not represent the New World genus, we follow Markov, 2004, 2008 and Von

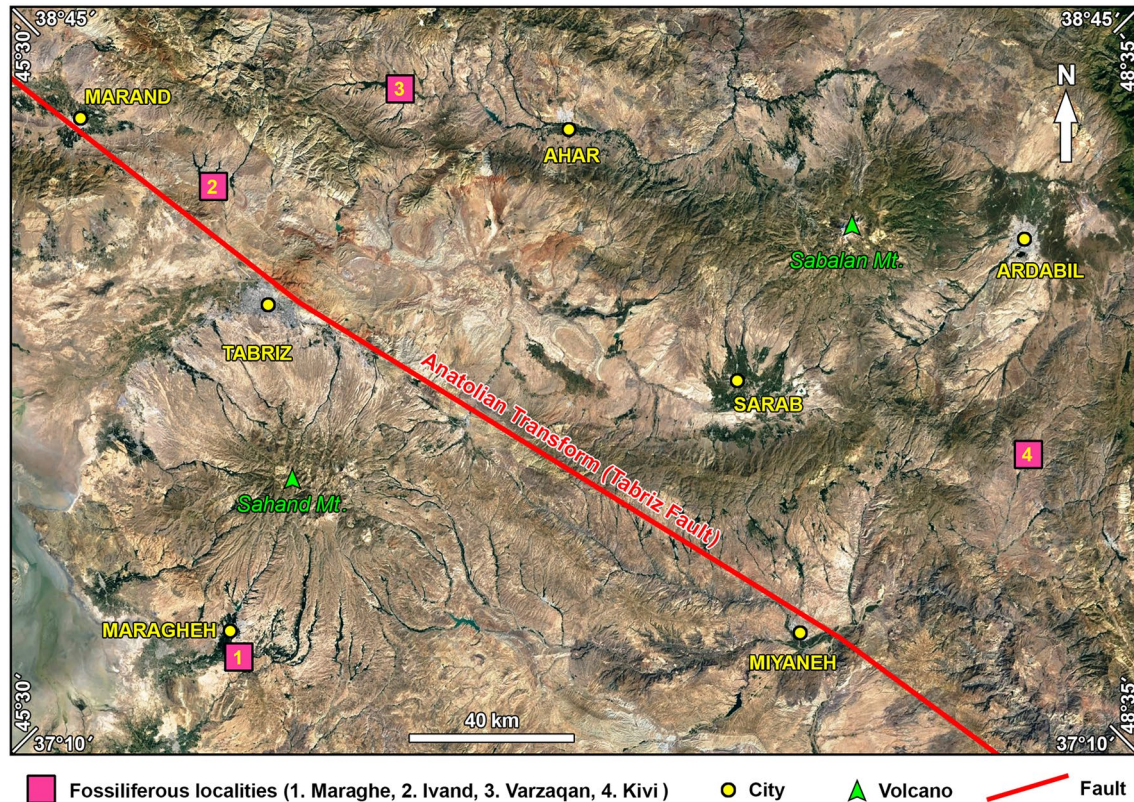


Fig. 1 Geographic location of the new late Miocene mammal fossil localities (Varzeghan, Ivand, and kivi-1) in North-Western Iran (the map modified after Jafarzadeh and Konidaris, 2019)

Koenigswald et al., 2022, as well as Konidaris et al., 2023, using genus name “*Mammut*” with quotation marks.

Geological setting

At the end of the Early Miocene, the lifting of the Iranian landmass resulted in the retreat of the Tethys. Consequently, it terminated the carbonate deposition and led to vanishing the last Tethyan seaway (Aghanabati, 2004). In the Neogene, this domain was above the sea level, covered by ancient mountain ranges and basin troughs, and had topography similar to the present conditions (Davoudzadeh et al., 1997). The area located North of Tabriz City underwent major orogenic phases during the Late Miocene–Pliocene. These activities established new erosional cycles, filling the locally close intermontane basins with fluvial and lacustrine deposits (Aghanabati, 2004). The fossil deposits of the Varzeghan area were formed in such local basins. They are environmentally different from the Maragheh Formation by not being directly influenced by volcanic activities.

The fossiliferous layer in this area was part of fluvial cycles, because channel deposits were present nearby to the fossil locality. Similar to other Late Miocene mammal fossiliferous localities in Iran, the fossils are, however, preserved in the fine-grained soil horizons, possibly belonging to an overbank deposit (Mirzaie Ataabadi et al., 2011a, 2011b; Sakai et al., 2016). Recent alluvials cover the Late Miocene sequence in the study area, and there were no exposures to be studied in detail. Unfortunately, the tiny sediment exposure near the fossil site, which was checked before, has been covered by new buildings and is no longer available for further studies.

Materials and methods

In this study, an isolated upper third molar, PRCI, V001, previously coded as Varzeghan [MMTT11], and two upper tusks (Varzeghan [MMTT1 a, b]) stored in the Paleontology Research Center of Iran in Maragheh are investigated. The dentition nomenclature of the occlusal structures of mammutid cheek teeth follows Tobien (1975, 1996). Göhlich (1998) was followed for measurement purposes. All the measurements are in millimeters.

Abbreviations

I², Upper second incisors (upper tusk in proboscideans).

MMTT, Muze Melli Tarikh Tabeie (i.e., National Museum of Natural History, in Persian).

MN, European Neogene Land Mammal Units.

M¹, M², and M³; First, second, and third upper molars, respectively.

p⁴, m¹, m² and m³; 4th lower premolar; first, second and third lower molars, respectively.

PRCI, Paleontological Research Center of Iran.

Systematic paleontology

Order Proboscidea Illiger, 1811

Unranked group Elephantimorpha Shoshani & Tassy, 1997

Family Mammutidae Hay, 1922

Genus *Mammut* Blumenbach, 1799

Type species *Mammut americanum* Kerr, 1792.

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

Synonyms: *Mammut praetypicum* Kubiak, 1972

Mastodon americanus Kerr, 1792; Hopwood, 1935, pp. 43–46, Pl. 6.5

Mammut borsoni (Hays, 1834): Tobien et al., 1988, p. 165–168, Figs. 57, 58 (see Wang et al. 2017).

Stratigraphic occurrence: Turolian; MN 11(Koufos, 2013) to MN 13 (Van Dam et al., 2001).

Geographic distribution: China (Baode Region), Southern Russia, Ukraine, Slovenia, North Macedonia, Moldova, Greece, Bulgaria, Hungary, Spain, Turkey.

Referred materials: Right M³ (MMTT11 [PRCI/V001]) and a pair of adult upper tusks (MMTT1 a, b) from Abkhareh (Varzeghan), Iran.

Description

The right M³

The specimen preserves three roots, and molar crown is adequately preserved in exhibiting zygodont characters. The tooth has three major lophs plus a reduced 4th loph at the posterior end. A median sulcus separates the pretrite and posttrite lophs.

The anterior cingulum is moderately developed. The protocone (abaxial pretrite conelet of the first loph) is strongly worn down and is connected to the anterior cingulum. The paracone (main posttrite conelet of the first loph) is slightly worn, and the number of mesoconelets seems to be two or three. Hypocone and metacone are worn to some extent, with one and two mesoconelets, respectively. Crescentoids are weak on the first and second pretrite lophs, but the third pretrite loph bears crescentoids on its anterior wall. The posttrite lophs possess zygodont crests on the posterior wall of the first posttrite cusp and on the anterior wall of the second posttrite cusp, which are hardly developed. The pretrite lateral enamel is well-developed. The pretrite third half loph consists of a cone and one mesoconelet, which are almost worn and carry crescentoids on their anterior slope. The posttrite third loph is worn so that the number of mesoconelets is unclear. The fourth loph is strong but shorter than the first three and consists of two pretrite and posttrite conelets. The posterior cingulum is moderately weak. The transverse valleys are completely open and broad (Figs. 2, 3, 4). The measurements of the third upper molar teeth is available in Table 1.

Table 1 Measurements of M^3 , “*Mammut*” cf. *obliquelophus* (MMTT11), Abkhareh, Varzeghan, Iran

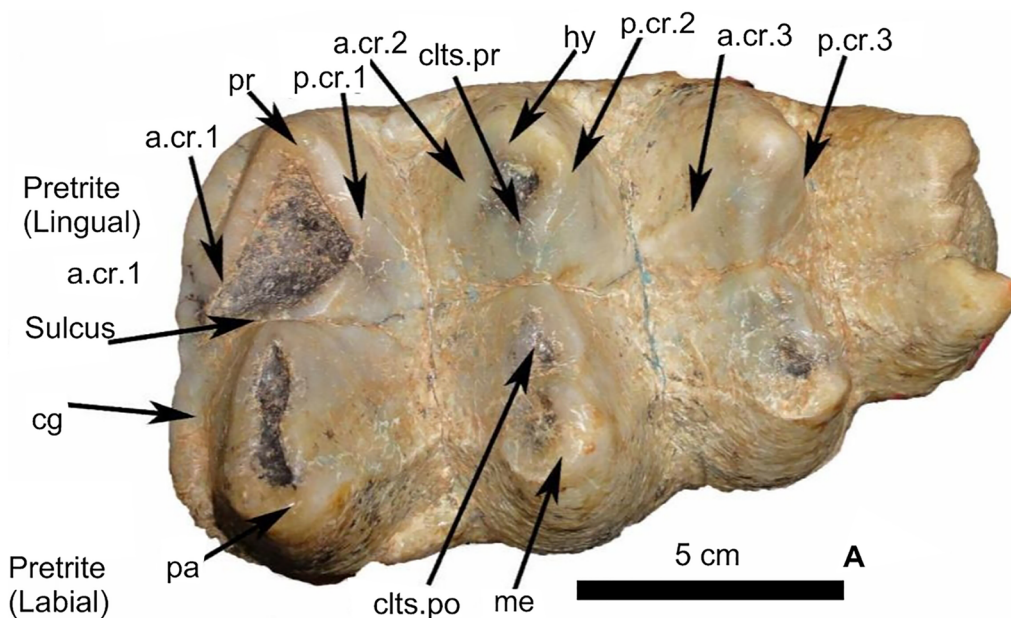
| Measurement of M^3 (MMTT11), Abkhareh | Total | First loph | Second loph | Third loph |
|---|---------|------------|-------------|------------|
| Length | 194 mm | – | – | – |
| Width | 91.5 mm | 85.5 mm | 91.5 mm | 85 mm |
| Height of second posttrite main cusp | 58 mm | – | – | – |

The cranium Kubiak (1972) described has two upper molar teeth: M^2 and M^3 . The M^2 is trilophodont, complete, but deeply worn down. The third molar is broken, and only 1st and 2nd lophs are preserved. The anterior lophs are relatively worn. There are no conules between ridges in Kubiak’s M^3 material, and half lophs are almost symmetrical in width but not in morphology. It seems that the first pretrite loph and the first posttrite loph consist of two or three mesoconelets, which are relatively worn. However, the morphology of the first and the second lophs of M^3 from Balta Sands (Podolia, Ukraine, Kubiak, 1972, pl. XII, Fig. 7) are almost similar to the Abkhareh M^3 . So, the assignments of Abkhareh tooth to “*Mammut*” cf. “*M.*” *obliquelophus* can be based on its zygodont morphology and its similarity to the Kubiak material.

Upper tusks

A pair of I^2 (MMTT 1 a, b) was found in Abkhareh village near the Varzeghan area proximate to the zygodont molar tooth (previously described in the current study). They were prepared especially in their proximal part and were covered by protective material. The left tusk is broken into two parts, but the right one is almost complete and preserved well. In situ, and in lateral view, the upper tusk is curved dorsally and seems to be directed straight or slightly downwards and then bends strongly outwards after the secondary medial of its length. So, the tip is turned upwards. Tusks are not helicoidal, without torsion, and diverged in anterodorsal view. The tusks are characterized by a polished surface on their distal ends on the medial sides of both of them. Distal tips are almost abraded, forming a partly distinct elliptical shape on each tusk. Dorsal and ventral wear facets are absent (Fig. 5a). No enamel band was recognized. There is a clear longitudinal furrow on their lateral (labial) side. Unfortunately, the pulpa of both the right and left tusks was covered with some glue during the reconstruction. So, it is not possible to see the pulpa.

The maximum lengths of MMTT1a and b (taken dorsally tangentially from the proximal end to the distal end (tip) of the tusk) are 1310 mm and 1360 mm, and their lengths are 1080 mm and 1000 mm, respectively. The maximum diameter of MMTT1a (taken at the middle

**Fig. 2** Third upper right molar tooth of “*Mammut*” cf. *obliquelophus* from Abkhareh village, Varzeghan, Iran. A, Occlusal view; Key (Tobien, 1996):

a.cr.1, anterior crescentoid of the first loph; a.cr.2, anterior crescentoid of the second loph; cg, cingulum; clts.po, conelets on the posttrite (secondary or adaxial conelets); clts.pr, conelets on the pretrite (secondary or adaxial conelets); pa, paracone; p.cr.1, posterior crescentoid of the first loph; p.cr.2, posterior crescentoid of the second loph; pr, protocone; zc, zygodont crest; p.cr.3, posterior crescentoid of the third loph; me, metacone; hy, hypocone

of the tusk) is 480 mm, and that of MMTT1b is 440 mm (Figs. 5, 6).

No sign of crossing Schreger lines was seen on the ivory's cross-section and broken surfaces. Still, their absence cannot be interpreted as definite since we could not observe the fresh sectional surface of the tusk ivory. Although the best trait to distinguish Elephantimorpha from more basal proboscideans, such as deinotheres, is the presence of Schreger lines, we relied on the tusk morphology. So, Abkhareh materials' assignment to the genus *Mammut* sp. is based on their slight curvature and untwisted morphology and absence of enamel band.

According to Jafarzadeh and Konidaris (2020), Neogene elephantimorphs from Eurasia generally have straight or less curved and untwisted upper tusks (except *Choerolophodon*), this is particularly true about

mammutids from the Miocene, including *Zygodolophodon* and *Mammut*.

The few scattered fossil bones were found on the surface sediments in Abkhareh. The close spatial accumulation of the tusks with the isolated tooth from Abkhareh may indicate that those do indeed belong to a single mammutid individual. This may also be the case with the deinotheres postcranial materials and maxilla with some teeth, which were attributed to an adult individual of *Deinotherium gigantissimum* due to their immediate proximity and consistent size (Pickford & Pourabrishami, 2013; Pourabrishami, 2004).

Therefore, it is supposed that this fossiliferous layer on the surface was a burial ground for several contemporary taxa that were washed away by seasonal rivers and buried individually.

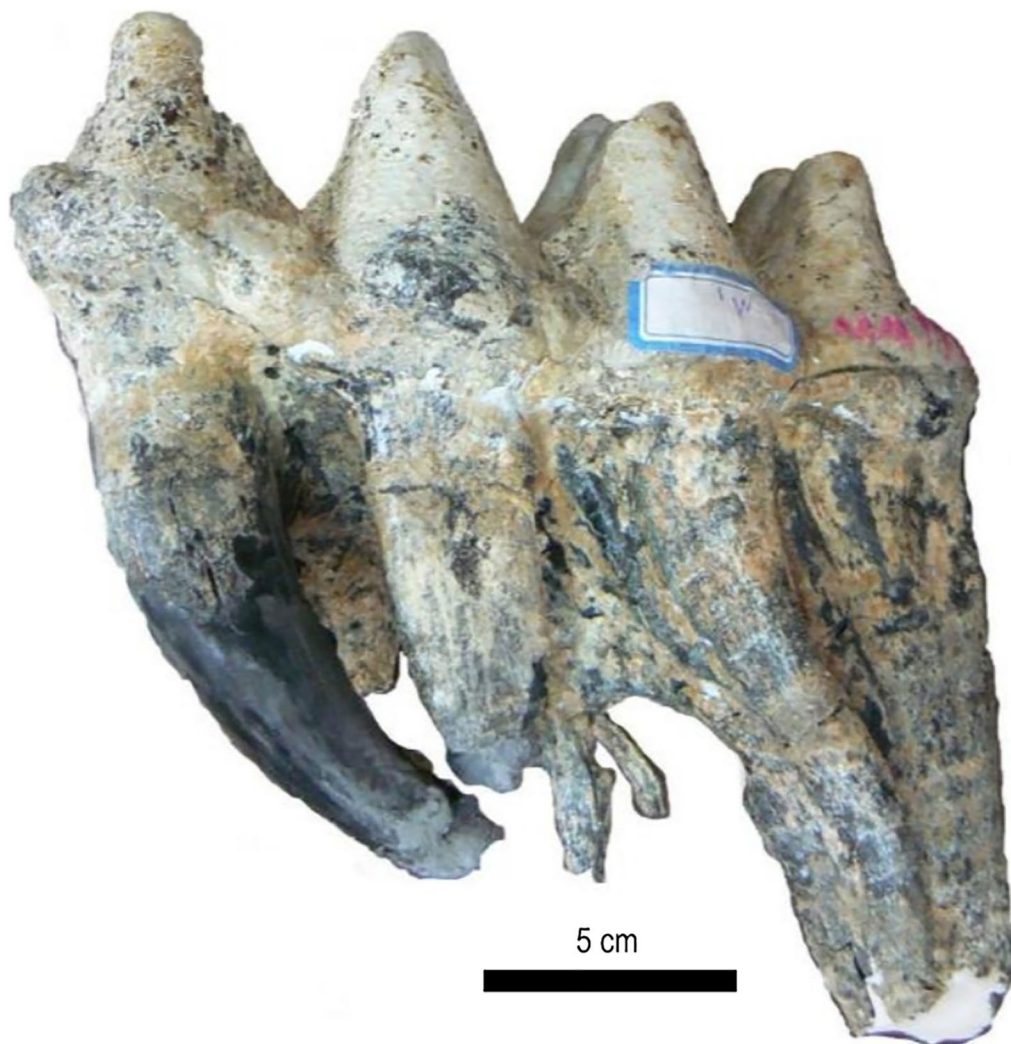


Fig. 3 Right M³ of "*Mammut*" cf. *obliquelophus*, Abkhareh, Varzeghan, Iran; lateral view



Fig. 4 M³ of “*Mammut*” cf. *obliquelophus*, Abkhareh, Varzeghan, Iran; medial view

Comparison

There are not many reports of “*Mammut*” *obliquelophus*. However, Markov (2008) argued that “*Mammut praetypicum*” (if it is taxonomically valid name) might be a senior synonym of “*M.*” *obliquelophus* presented by Kubiak (1972).

Among the Balta Sands materials in Podolia, Ukraine (Kubiak, 1972, p. 311), there is a partial skull with associated dextral I². The tusk is relatively large (1000 mm long) and almost straight. According to his notes, the tusk projects a cranium along an almost horizontally forward trajectory. However, “it is directed slightly downwards and markedly outwards and slightly turned upwards at the end”. Abkhareh tusks MMTT1a, b seem to be directed almost downward, and do not leave the skull horizontally. They are outwards and exhibit upward turns at their tips and much stronger dorsal up-curve. The cross-section in Kubiak’s I² is circular, and MMTT1 of Abkhareh shows a circular cross-section at its proximal pulp. It is almost circular in the middle of the tusk. Some “regular longitudinal streaks in the outer and inner layers of the dentine” were observed by Kubiak (1972, p. 311, PL. XIII:

F.9). However, the same feature on Abkhareh tusks is not noticeable.

Another notable upper tusk specimen from a Late Miocene Eurasian mammutid is a Turolian right tusk numbered NKP-1 from Neokaisareia in Pieria, Northern Greece, referred to as “*Mammut*” *obliquelophus* (Konidaris & Tsoukala, 2020). Its maximum length is 930 mm, and its maximum diameter is 87.3 mm, slightly shorter and slender than Abkhareh tusks (1080 mm in length).

NKP-1 tusk is almost straight with slight upward (dorsal) curvature in lateral view. It is twisted and slender (according to the author, the NKP-1 tusks belong to an ontogenetically young and/or female, which can explain why its diameter is less than the diameter of the Abkhareh one). Several longitudinal furrows run along the tusk of NKP-1, and the enamel band is absent (Konidaris & Tsoukala, 2020). Both the Balta Sands (Kubiak, 1972; Markov, 2008) and the Neokaisaria (NKP-1) right upper tusks (Konidaris & Tsoukala, 2020) have similarities in some degrees with Abkhareh tusks. All are almost straight with slight dorsal curvature in lateral view.



Fig. 5 Dextral upper tusk of “*Mammuth*” cf. *obliquelophus*, Abkhareh, Varzeghan, Iran; **A** Medial view (polished wear facet on distal end, shown by an arrow); **B** lateral view; **C** cross-section of sinistral I², “*Mammuth*” cf. *obliquelophus*, Abkhareh, Varzeghan, Iran

As mentioned, only a few I² materials are called *Mammuth obliquelophus*. The material from the Hualinsanhe locality in Gasu Province, Northwest China (almost complete cranium), belongs to a juvenile individual Wang et al. (2017). It has a pair of in situ upper tusks. The tusks are short and slender. The cross-section is round. As expected in juveniles, the apical part is covered by enamel. The skull from Hualinsanhe was attributed to *Mammuth* cf. *M. obliquelophus* by Wang et al. (2017). Although some characteristics of the tusks from Hualinsanhe, like bending ventrally in lateral view, lacking enamel band on the lateral side and slight torsion, being divergent in anterior view, and becoming slender apically are almost similar to Abkhareh ones, it does not seem feasible to compare such a specimen belonging to a very young individual with the tusk of Abkhareh belonging to a completely grown adult individual.

“*Mammuth borsoni*” (Hays, 1834) is the classic Pliocene–earliest Pleistocene mammutid recorded wide across Northern Eurasia (Tobien, 1996), yet it has never been reported from Iran. Besides, it is likely that “*M. borsoni*” has longer upper tusks than “*M. obliquelophus*”. However, the symphysis is longer than the tooth row, and lower tusks are well-developed in “*M. obliquelophus*”. As in a specimen of “*M. borsoni*” reported from Milia in Grevena, Greece (Tsoukala, 2000; Tsoukala & Mol, 2016), the length of its upper tusks reaches 4.39 m. The upper

tusks of “*M. borsoni*” are approximately straight and slightly up-curved (dorsally), slender, torsioned, without any enamel band. Longitudinal furrows are present on the proximal part, which is expected for the genus *Mammuth*. These characteristics are morphologically comparable with the NKP-1 upper tusk and the Abkhareh one, but the dimensions of the Milia upper tusks are larger than the NKP-1 and Abkhareh ones.

Upper tusks of “*Mammuth borsoni*” and “*Mammuth obliquelophus*” differ from those of *Zygodolophodon turicensis* by lacking of enamel band. Upper tusks of the genus “*Mammuth*” are straight or upturned, and lower tusks are relatively small or even vestigial.

The tusks of *Zygodolophodon turicensis* are not twisted. They are characterized by ellipsoid cross sections and straight or anteroventral located enamel bands (Tassy 1977, 2013, 2014).

Proboscideans known from the Late Miocene of the Northwest of Iran include the deinotheriid *Deinotherium*, the choerolophodontid *Choerolophodon*, the amebelodontid *Konobelodon*, and the mammutid “*Mammuth*”. The morphology of the tusks of Abkhareh, Varzeghan is obviously dissimilar from the strongly curved and robust lower tusks of *Deinotherium* (e.g., Tassy, 2016). According to Harris (1978), the mandibular tusks of *Deinotherium* are relatively short (e.g., the mandibular tusk belonging to a very large individual of *D. gigantissimum*

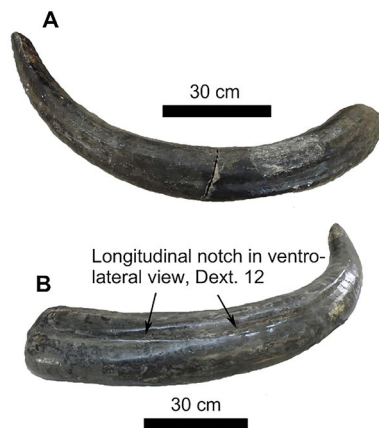


Fig. 6 **A** Lateral view of sinistral I², “*Mammut*” cf. *obliquelophus*, Abkhareh; **B** ventro-lateral view of dextral I², “*Mammut*” cf. *obliquelophus*, Abkhareh, Varzeghan, Iran (arrows show the longitudinal notch on the ventro-lateral surface of the tusk)

from Pripiceni, Moldova, with 978 mm, which is still short in comparison with Abkhareh tusks; see Harris, 1978) and recurved below symphysis and are almost vertically aligned. Normally, adult deinotheres tusks terminate in rounded conical points. Also, lower tusks of *Deinotherium* often show no signs of wear (Delmer, 2005), which contrasts with the Abkhareh tusks. However, wear facets have been observed in a few deinotheriid individuals. They are found on the anteromedial tip, suggesting wear by abrasion against one object in front of and between the tusks (Harris, 1978). So, it is supposed that the tusks of Abkhareh can be allocated to an upper tusk of an elephantoid sensu (Tassy, 1988), clade *Mammutida* (Elephantida, proboscideans) (Shoshani, 1996a, 2002).

Moreover, *Choerolophodon*, which is recognizable based on its strong curvature and double twisted (outwards and upwards) upper tusks, is markedly different from Abkhareh tusks. *Konobelodon* has less curved upper tusks than the Abkhareh one and no torsion (Pestszentlörinc, Hungry, HNHM-V.79.34; Konidaris & Tsoukala, 2020 Schlesinger, 1922).

Dental comparison

The cranium Kubiak (1972) described has two upper molar teeth: M2, M3. The M2 is trilophodont, complete, but deeply worn down. The third molar is broken, and only the 1st and 2nd lophs are preserved. The anterior lophs are relatively worn. There are no conules between ridges in Kubiak’s M3 material, and half lophs are almost symmetrical in width but not in morphology. It seems that the first pretrite loph and the first posttrite loph consist of two or three mesoconelets, which are relatively

worn. However, the morphology of the first and second lophs of M3 from Balta Sands (Podolia, Ukraine, Kubiak, 1972, pl. XII, Fig. 7) is almost similar to the Abkhareh M3. So, the assignments of the Abkhareh tooth to “*Mammut*” cf. “*M.*” *obliquelophus* can be based on its zygodont morphology and its similarity to the Kubiak material.

According to Titov and Tesakov’s study (2013), “*M.*” *obliquelophus* was reported in several Turolian (Late Miocene) vertebrate faunas in Southwestern Russia. These materials were discovered in Morskaya 2 (middle Turolian, MN12–MN13?), and include an incomplete mandible with m¹–m³ tooth rows and small, relatively straight lower tusks. The materials were attributed to “*Mammut*” cf. *obliquelophus* Mucha, 1980, due to their morphology resembling that of mastodon molars, relatively straight lower tusks, and medium-sized symphysis (Titov and Tesakov, 2013, Fig. 24.3, b–d).

Also, a left third upper molar of Yanovka-Obokhovka Sand pits deposits dated to Lower Pontian (MN12) in Russia (specimen NMIDK KP-10589/P-89, collection Novochoerkassk housed in History Museum of Don Cossacks) has close similarity with European Turolian zygodont mastodons attributed by Markov (2008) to “*M.*” *obliquelophus*. The tooth shows close morphological correspondence with upper third molar from Abkhareh, Iran submitted in this study (see Titov and Tesakov, 2013, Fig. 24.3, e). The first loph of M³ from Yanovka-Obokhovka is missing, and the antero-labial part of the second one is damaged. The third and fourth lophs are preserved enough, revealing clear zygodont characters. The length of the remaining fragments is more than 120 mm, and the width of the second loph is about 88 mm, which is almost comparable with that of the Abkhareh one, with 194 mm in length and 91.5 mm in width. The lophs are sharp-crested especially it is obvious in the third and fourth lophs, which are slightly worn. All the synclines separating the lophs are open and not blocked by conules. Pretrite conules (crescentoids) are almost completely reduced, and posterior cingulum is crenelated but low. All of these characteristics are almost similar to M³ from Abkhareh. Both molars of Abkhareh and Yanovka-Obokhovka reveal crested lophs, reduced crescentoids, and zygolophodon crests especially on posterior slopes of posttrite main cusps.

The two M³ distal fragments (TCM 19355/C and 19255/D) from Păgaia, Bihor District in NW Romania are assigned to *Mammut praetypicum* (Schlesinger, 1919) by Codrea et al., 2005 (Pl. I, Fig. 4). They show morphological similarity with Abkhareh cheek teeth. Although both are broken, and some parts of the anterior lophs are missing, they are preserved enough to reveal zygodont characteristics.

“*Mammut*” *borsoni* and “*Mammut*” *obliquelophus* have molars with larger width in comparison with *Zygodolophodon turicensis*. Cheek teeth of the genus “*Mammut*” express open valleys without additional conules, a distinguishing trait seen in more derived *Mammut*, whereas the molars of *Zygodolophodon* show a more bunodont character (Tobien, 1996). According to Garevski et al. (2012), “Height of the lophids about their anteroposterior length and the lingual cingulum height is a character distinguishing *Zygodolophodon turicensis* from the derived mammutid “*Mammut*” *borsoni* and related forms”

According to Duangkrayom et al. (2016), the upper third left molar PRY200 from the Late Miocene Tha Chang sand pits, Nakhon Ratchasima, North-Eastern Thailand is attributed to *Zygodolophodon* sp. The molar teeth has four lophids plus an anterior cingulum and a posterior cingulum. It is clearly smaller than M3 of Abkhareh. The Tha Chang molar is 152.5 mm in length and 80.8 mm in width and is seemingly smaller than “*Mammut*” *borsoni* molars measured by Tobien et al. (1988). Although crescentoids are present in both *Zygodolophodon* and “*Mammut*”, The Abkhareh M³ has stronger zygodont crests and pretrite adaxial conelets. The fourth loph in both specimens from Abkhareh and Tha Chang is well-developed, but the anterior and posterior cingulum in Tha Chang M³ is more reduced than that of Abkhareh M³.

Discussion

According to Markov (2004, 2008), “*Mammut*” *obliquelophus* (Mucha, 1980) persisted as a Turolian (Late Miocene) taxon characterized by some differences in comparison to other members of the mammutids like “*Mammut*” *borsoni* (Hays, 1834) and *Zygodolophodon turicensis* (Schinz, 1824).

“*Mammut*” *obliquelophus* was a matter of dispute and taxonomical complications. According to Tassy (1990), for a long time, Turolian mammutid materials were misidentified as Pliocene taxa, “*Mammut*” *borsoni*, and the more primitive one, *Zygodolophodon turicensis* from Orleanian to Vallesian (MN3–MN10); Huttunen & Göhlich, (2000). The possibility of this misinterpretation was already mentioned by Alexeeva (1965). Markov (2004, 2008) followed his opinion and separated the Pliocene brevirostrine “*M.*” *borsoni* from the Late Miocene moderately longirostrine Late Miocene form “*M.*” *obliquelophus*.

Although the morphology of the cheek teeth of “*M.*” *obliquelophus* bears little noticeable differences from that of “*M.*” *borsoni*, the mandibular symphysis is longer than the tooth row, bearing well-developed lower tusks in “*M.*” *obliquelophus*, while both lower incisors and symphysis are reduced in length in “*M.*” *borsoni* (Konidaris et al., 2023; Markov, 2008). Compared with the more primitive

taxon *Zygodolophodon turicensis*, which is real longirostrine, the symphysis in “*M.*” *obliquelophus* is relatively short. In both *Zygodolophodon* and *Mammut*, the posterior border of mandibular symphysis is close to the anterior end of the cheek tooth row. An elongated mandibular symphysis is universally plesiomorphic across Elephantimorpha, but underwent convergent significant reduction in all of the derived groups (Tassy, 1996, Shoshani, 1996a, 1996b).

As asserted by Tobien (1996), *Mammut* generally differs from other mammutids in having straight or upturned tusks. In lateral view, upper tusks in “*M.*” *obliquelophus* are dorsally bent with mild curvature. However, the plesiomorphic state of mammutid upper tusks is demarcated by (ventral) down-curving, as observed in *Eozygodon* (Pickford, 2004) and *Zygodolophodon* (Huttunen & Göhlich, 2000). Upper tusks in *Zygodolophodon* are diverged in anterodorsal view without torsion. They are not helicoidal, and their cross-section is ellipsoid (Březina et al., 2020). Also, the upper tusks in taxa like *Eozygodon morotoensis* and *Zygodolophodon turicensis* are covered with straight and lateroventrally located enamel bands (Von Koenigswald, 2022; Tassy 2013, 2014). Adults individuals of “*M.*” *obliquelophus*, “*M.*” *borsoni*, and *M. americanum* have no enamel band on their upper tusks. As mentioned by Tassy (1996), enamel bands are lost in most derived taxa of Elephantimorpha.

Moreover, according to Tobien (1975), *Zygodolophodon* molars differ from those of *Mammut* in the increasing number of transverse ridges in the M³ (four lophids) and m³ (four lophids plus talonid) of the latter, more derived genus. Molar crowns in *Mammut* are broader, and crescentoids (sperrleisten) are reduced. Also, the yoke character of the upper and lower molars in the genus *Mammut* is strengthened. Furthermore, “*M.*” *borsoni* and “*M.*” *obliquelophus* can be distinguished from *Z. turicensis* by the lower height of the lophids of cheek teeth about their anteroposterior length and the lower lingual cingulum (Garevski et al., 2012).

To further make the situation difficult regarding “*M.*” *obliquelophus* taxonomy, many materials have been incorrectly referred to as “*M. praetypicum*”. Markov (2008) accentuated that this name should not be used for the Turolian mammutids. The name was used by Kubiak (1972) for specimens probably from Balta Sands in Podolia in Ukraine. He elevated Schlesinger’s (1917) “*Mastodon (Mammut) americanus forma praetypica*” to a specific rank, which was a taxonomically erroneous opinion (For more explanation, see Markov, 2008). After Kubiak (1972), the name was used by other authors, for example, Göhlich (1999), Lungu and Obada (2001), and Codrea et al. (2005). However, in the case of the findings from Păgaia in Romania (Codrea et al., 2005), they lack a

mandible and are assumed to be Pliocene in age. Therefore, the Păgaia material might represent “*M.*” *borsoni*.

Moreover, it is quite possible that “*M.*” *praetypicum* is a junior synonym for “*Mammut*” cf. *borsoni* sensu Tassy (1985) from Pikermi (Greece) and a mandible from Ahmatovo (South Bulgaria) published by Nikolov and Kovacev (1966) and renamed by Markov (2004).

The fauna of Abkhareh, Varzeghan, is assigned to the second half of the Late Miocene (Middle Turolian). It is assumed that during that time, “*Mammut*” *obliquelophus* was the only representative of *Mammut* in Eurasia. “*Mammut*” *borsoni* (Hays, 1834) is best known from Pliocene European localities. *Zygodolophodon* is recognized from the Lower and Eastern Late Miocene in Eurasia.

According to Konidaris et al., 2023 “*Mammut*” *obliquelophus* was introduced by Mucha, 1980 from Romanovka, Ukraine, on the basis on a mammutid mandible and resurrected by Markov, 2008 by attributing a cranium and a mandible of an individual from the Balta Sands in Podolia (Ukraine), a mandible from Fărladani (Moldova) to this species. More recently, Konidaris et al., 2023 recorded the presence of “*Mammut*” *obliquelophus* from Sazak in South-Western Turkey (Late Miocene) on the basis of an upper deciduous premolar, as a first record of this species from Western Asia. However, “*Mammut*” was reported before from Samos Island at Mytilinii-1A locality (MN12) by Konidaris 2013; Konidaris & Koufos, 2013. During the Late Miocene, Samos was a part of Asia Minor, and its fauna shows similarity with Greco-Iranian-Afghan (subparathethyan) members. Konidaris et al., 2023 suggest that considering all other typical Turolian proboscideans (*Deinotherium proavum*, *Choerolophodon pentelici*, and *Konobelodon atticus*), the paleogeographic expansion of “*Mammut*” *obliquelophus*, increases to more Western Asia like Iran. So, the record of “*Mammut*” from Abkhareh can complete the puzzle of typical Turolian members of the Balkano-Iranian paleobiogeographic province in terms of proboscideans and expand the paleogeographic distribution of Turolian “*Mammut*” to Iran as it is expected by Konidaris et al., 2023.

Nevertheless, we hereby suggest “*M.*” *obliquelophus* to be the appropriate available name for modestly longirostrine Turolian mammutids from Eurasia with pronounced lower incisors, more primitive than the Pliocene “*M.*” *borsoni* with shorter symphysis. Still, the two species are exceedingly difficult to discriminate from cheek tooth morphology alone (see Markov, 2004).

Paleobiogeography and paleoenvironment

Several exceptional taxa are shared by the localities in Northern China and the Northwest of Iran. These include *Iranotherium*, *Alcicephalus/Samotherium*, *Honanotherium*, *Urmitherium*, and “*Mammut*”.

Iranotherium morgani, a large elasmothere rhino, occurred in Northwest China’s Linxia Basin during the Eastern Late Miocene (Deng, 2005). It was first recorded in Maragheh, the Northwest of Iran in “MN12”. This species first appeared in China during the Vallesian and immigrated to Maragheh later in the Turolian (Mirzaie Ataabadi et al., 2013a).

Honanotherium is a giraffid recently recorded from Maragheh fauna as a new species, *H. bernori* (Solounias & Danowitz, 2016). Moreover, the same authors also resurrected *Alcicephalus (Samotherium) neumayri* in Maragheh. It is the most abundant giraffid from this locality and Northwest Iran. Both genera are known primarily from North China (The NOW Community, 2023). Therefore, among giraffids, the presence of taxa from the Eastern end of the Pikermian paleobiome (i.e., China) in Northwest Iran is significant (Mirzaie Attabadi et al., 2013c).

Urmitherium, an ovibovine-like bovid, was originally discovered in Iran (Kostopoulos & Bernor, 2011). It extends in the Eastern (North-Western China) and Western (Eastern Mediterranean) reaches of the Pikermian Palaeobiome (Mirzaie Attabadi et al., 2013c; Kaya et al., 2018). It is now believed that this genus appeared first in Vallesian of Northern Greece and dispersed into Central and Eastern Asia in the form of *U. polaki* and *U. intermedium* (Lazaridis et al., 2017). The abundance of this genus in Northern China is mostly in the Late Miocene, and it is an apparent migrant from the West (Mirzaie Ataabadi et al., 2013a).

The presence of “*M.*” cf. *M. obliquelophus* in Northwest Iran’s Late Miocene (MN 12 equivalent) adds another common taxon between these areas. This taxon probably originated from *Zygodolophodon turicensis*, which was widely distributed from the Early to Early Late Miocene.

The Chinese material of “*M.*” cf. *M. obliquelophus* may serve as another example of the Eastern extension of the Pikermian Chronofauna in Eurasia. As previously shown, middle and Late Miocene chronofaunas moved into East Asia from Western Eurasia (Mirzaie Ataabadi, 2010). The Late Miocene faunas had an even higher proportion of immigrants than their precursors. Several ruminants (including *Urmitherium*) and equid lineages extended from the Eastern Mediterranean to China (Fortelius & Zhang, 2006; Watabe, 1992).

They moved across Asia in response to changing climate and humidity patterns because summer rainfall brought richer resources to Northern China in the latest Miocene (Mirzaie Ataabadi et al., 2013b).

This connection of Eastern and Western Asia was not restricted to Miocene faunas. Although it seems that the Miocene’s end coincided with the waning Pikermian chronofauna, there is evidence that the broad East–West connection of mammalian faunas also continued

into the Pliocene. For example, the presence of derived hipparionine horses like *Proboscoidipparion* in the Early Pliocene of Anatolia shows their extension of range from Anatolia to China (Bernor & Sen, 2017).

As mentioned above, the current study materials were unearthed almost next to the materials of *Deinotherium proavum*, coincidentally. According to Pickford and Pourabrishami (2013), deinotheres were present in the environments with sub-tropical to tropical (dry season–wet season cycles) climates, and they are absent from basins records during the boreal to sub-boreal (winter–summer cycles) phases. Also, their dental morphology indicates adaptation to an obligate folivorous diet (see Pickford & Pourabrishami, 2013, p. 145). It was understood that the climate of the Varzeghan region in the Northwest of Iran was open woodland during MN12 and generalized that it was the preferable paleoenvironment for “*M. obliquelophus*”, too.

Conclusion

Although “*M. obliquelophus*” was previously considered invalid by some authors (Lungu & Obada, 2001), according to Markov (2008), its validity, originally established for a mandible from Romanovka in Ukraine, is supported by a mandible with long symphysis and “*borsoni*” teeth from the Turolian locality of Ahmatove in Bulgaria.

“*M. obliquelophus*” is reported from different localities in Central and Eastern Europe and China. Accordingly, the taxon is present in Spain, Hungary, Bulgaria, North Macedonia, Greece, Romania, Moldova, Ukraine, Southern Russia (Markov, 2008), Turkey (Konidaris, 2023) and some localities of Linxia Basin and Baode region in China (Wang et al., 2017).

Despite the absence of mandibular material with symphysis in Abkhareh, Iran, which is a distinctive characteristic between “*M. obliquelophus*” and “*M. borsoni*”, the molar teeth and upper tusks can be attributed to “*M.* cf. *obliquelophus*” based on their morphology and well-expressed zygodonty without additional conules of the molar teeth. According to Konidaris (2023), chronological data and the assumed age of a fauna do not lead to valid taxonomic results but The Turolian (MN12 equal) age of Abkhareh (Mirzaie Ataabadi et al., 2011a, 2011b; Pickford & Pourabrishami, 2013) tentatively suggests an attribution to the Late Miocene representative of the genus “*M. obliquelophus*”. This probably shows the geographic extension of this species to the Northwest of Iran and its possible place between populations in the east and west.

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Author contributions

SY, and MMA described the specimens. All the authors contributed to the design and implementation of the research, to the analysis of the results, and the writing of the manuscript.

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Availability of data and materials

All data used during this study are included in this published article. The data used during the current study include the vertebrate macrofossils available at the Paleontological Research Center of Iran, Maragheh, Iran. These data are available via Sadaf Yaghoubi [yaghoubi.sa@mail.um.ac.ir] at the Ferdowsi University of Mashhad.

Declarations

Competing interests

The authors declare that they have no competing interests.

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