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Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: www.tandfonline.com/journals/ujvp20

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Juha Saarinen, Ali Taş, Elçin Şener & Ahmet Cem Erkman

To cite this article: Juha Saarinen, Ali Taş, Elçin Şener & Ahmet Cem Erkman (2025) Mammutid proboscideans (Mammalia, Proboscidea, Mammutidae) from the Upper Miocene of Hayranli-Haliminhani, Sivas Basin, Türkiye, Journal of Vertebrate Paleontology, 45:1, e2526551, DOI: 10.1080/02724634.2025.2526551

To link to this article: https://doi.org/10.1080/02724634.2025.2526551

Journal of Vertebrate Paleontology e2526551 (13 pages)
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DOI: 10.1080/02724634.2025.2526551

ARTICLE

MAMMUTID PROBOSCIDEANS (MAMMALIA, PROBOSCIDEA, MAMMUTIDAE) FROM THE UPPER MIOCENE OF HAYRANLI-HALIMINHANI, SIVAS BASIN, TÜRKIYE

JUHA SAARINEN, [1*] ALI TAŞ, [2] ELÇIN ŞENER, [2] and AHMET CEM ERKMAN [2]
[1]Department of Geosciences and Geography, P.O. Box 64, 00014, University of Helsinki, Finland, juha.saarinen@helsinki.fi;
[2] Department of Anthropology, Faculty of Science and Literature, Ahi Evran University, Kırşehir, Türkiye, alitas.paleo@gmail.com

ABSTRACT—Anatolia was a biogeographically important area between Europe, Western Asia, and Africa during the Late Miocene. Hayranlı-Haliminhanı in Sivas Basin in Central Anatolia has provided a diverse fossil mammal fauna dated between 8 and 6.5 Ma. While the presence of proboscidean fossils (Mammalia, Proboscidea) there has been noted before, those materials have not yet been described in detail. Here we describe the proboscidean fossils from Hayranlı-Haliminhanı, which we identify mostly as remains of a derived mammutid proboscidean ("*Mammut*" cf. "*M.*" *obliquelophus*), a comparatively rare taxon which has previously been reported from only one Upper Miocene locality in Anatolia. The presence of this taxon in Hayranlı-Haliminhanı supports earlier paleoenvironmental interpretations based on bovids, rodents, and mean ordinated hypsodonty of large herbivorous mammals, which suggested predominantly woodland or shrubland type vegetation. Morphometric comparisons of a proboscidean lunar (intermediate carpal bone) indicates similarity with the genus *Mammut*, supporting the affinity of Late Miocene Eurasian mammutids with this genus.

Citation for this article: Saarinen, J., Taş, A., Şener, E., & Erkman, A. C. (2025) Mammutid proboscideans (Mammalia, Proboscidea, Mammutidae) from the Upper Miocene of Hayranlı-Haliminhanı, Sivas Basin, Türkiye. *Journal of Vertebrate Paleontology.* https://doi.org/10.1080/02724634.2025.2526551

Submitted: February 10, 2025
Revisions received: June 10, 2025
Accepted: June 11, 2025
First published online: August 11, 2025

INTRODUCTION

The fossil record of Late Miocene large mammals is rich in the Anatolian Peninsula, and it offers crucial clues about paleoenvironmental conditions and biogeographic and evolutionary patterns during the Late Miocene. Proboscideans are well represented in these Late Miocene faunas (e.g., Gaziry, 1976; Geraads et al., 2005; Geraads, 2013, 2017; Konidaris et al., 2022; Sanders, 2003; Tassy, 2005, 2016). In this article we describe proboscidean fossils discovered from Hayranlı-Haliminhanı in the Sivas Basin in Central Anatolia. For the first time, we report the presence of a mammutid proboscidean ("*Mammut*" cf. "*M.*" *obliquelophus*) in Hayranlı-Haliminhanı and discuss the find in the context of paleoenvironmental interpretation of this locality. The location of Hayranlı-Haliminhanı in the Sivas Basin, and locations of other finds of Late Miocene *Mammut* sp. from surrounding areas in Europe and Western Asia, are shown on maps in Fig. 1.

The localities of Hayranlı-Haliminhanı are located in the Sivas Basin, 20 km northwest of the town of Sivas, discovered in 1993 by the Türkiye Vertebrate Fossil Research Project (Saraç, 2003). The Late Miocene mammal fossils from the Sivas Basin come from the Derindere Member of the İncesu Formation. The Sivas Basin is located in Central Anatolia between two continental tectonic blocks, the Pontides (of Eurasian affinity) in the north and the Tauride-Anatolian platform (of African affinity) towards south. The basin developed as a result of the collision of the Pontide and Tauride blocks following the closure of the Tethys Ocean during the Paleogene (Gürsoy et al., 1997). Paleocene and Eocene sequences in the basin represent marine settings, while Oligocene to Middle Miocene are mainly represented by terrestrial sequences except for marine transgressions during the Early and Middle Miocene (Kaymakci, 2000; Kaymakçi et al., 2001). The Upper Miocene fluvial and lacustrine sequences lay on top of these unconformably, forming the İncesu Formation. The fossiliferous sediments at Hayranlı-Haliminhanı consist mostly of sandy red mudstones of fluvial origins within the İncesu Formation, while the sequence transitions into preliminarily lacustrine setting towards the top of the İncesu Formation (Kaymakci, 2000).

Diverse large and small mammal fossils have been reported and described from the İncesu Formation, especially from the localities of Düzyayla (Akgün et al., 2000; De Bruijn & Mein, 1996; De Bruijn et al., 1996a, b, 1999; Fahlbusch & Bollinger, 1996; Furió et al., 2014; Made et al., 2013; Ünay, 1996), and Hayranlı-Haliminhanı (Bibi & Güleç, 2008; Demirci et al., 2007; Dumlupinar, 2023; Furió et al., 2014; Kaya & Kaymakçı, 2013; Made et al., 2013; Özkurt et al., 2015; Şahin, 2023). Both of these localities have been associated with the Neogene Eurasian mammal zones MN11–MN12, with the base of the deposits in Hayranlı-Haliminhanı suggested to represent MN11

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*Corresponding author.

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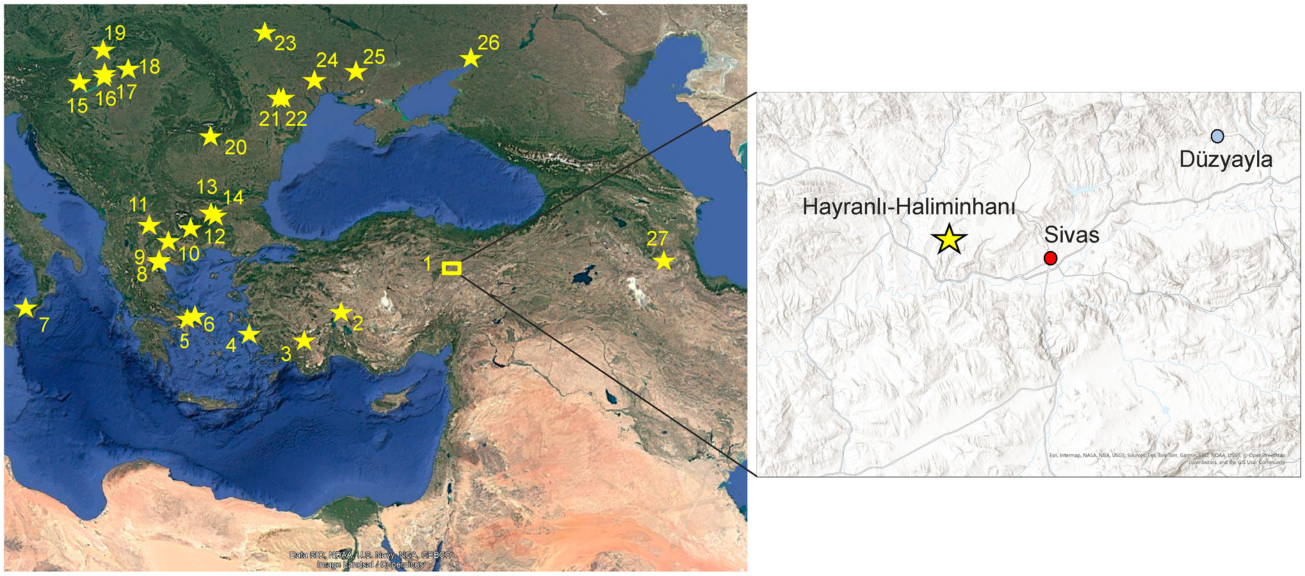

FIGURE 1. Location of Sivas Basin in Anatolia (1 in the map on the left) with other occurrences of Upper Miocene *Mammut* sp. from surrounding regions, and a close-up showing the locations of Hayranlı-Haliminhanı and Düzyayla near the town of Sivas (on the right). Occurrences of Upper Miocene *Mammut* sp. are indicated with yellow stars: **1**, Hayranlı-Haliminhanı (Sivas Basin); **2**, Tokmacık; **3**, Sazak; **4**, Mytilinii-1A-Samos; **5**, Pikermi; **6**, Halmyropotamos; **7**, Gravitelli; **8**, Neokaisareia; **9**, Palaio Keramidi; **10**, Ravin des Zouaves-5; **11**, Kiro Kuchuk; **12**, Hadjidimovo; **13**, Ahmatovo; **14**, Ezerovo; **15**, Baltavár; **16**, Polgárdi; **17**, Csákvár; **18**, Rózsaszentmárton; **19**, Vel'ké Bielice; **20**, Curtea de Argeş; **21**, Cimişlia; **22**, Taraklia; **23**, Balta Sands, Podolia; **24**, Belka; **25**, Romanovka; **26**, Morskaya 2; **27**, Abkhareh village, Varzeghan. The occurrences 2–26 are based on data presented in Konidaris et al. (2022) and references therein. The occurrence 27 is based on Yaghoubi et al. (2024). The map bases are from Google Earth Pro (left) and ArcGIS Pro (right).

based on the evolutionary stage of the suid *Microstonyx* (Made et al., 2013), while Düzyayla 1 has been interpreted to represent MN12 based on small mammals (de Bruijn et al., 1999, 2003). Meijers et al. (2022) were able to further narrow down the age range of the Hayranlı-Haliminhanı localities between 8 and 6.5 Ma based on magnetostratigraphy, associating the mammal fauna more firmly with the MN12 stage as well.

Paleoenvironmental settings of the İncesu Formation have been discussed based on fossil mammal assemblages and palynology (e.g., Akgün et al., 2000; Bibi & Güleç, 2008; Şahin, 2023). Akgün et al. (2000) indicated the Düzyayla locality to represent a mixture of riparian forests, woodland, shrubland, and some grassland environments based on pollen samples, while the mammal fauna was also interpreted by the authors to represent a mixture of forest forms (e.g., *Deinotherium*) and open-habitat forms (e.g., *Miodiceros* ("*Ceratotherium*") *neumayri*), although whether these taxa explicitly represent closed vs. open-adapted forms can be debated (see also Meijers et al., 2022). Similarly, paleoenvironmental interpretations have been made for Hayranlı-Haliminhanı based on fossil mammals (see Table 1 for revised list of fossil mammal taxa, based on Meijers et al. [2022], Şahin [2023], and the current study). The bovids at Hayranlı-Haliminhanı were interpreted by Bibi and Güleç (2008) to consist mostly of woodland and shrubland taxa, rather than those indicating extensive grassland or forest environments. More recently, the hipparionine equids at Hayranlı-Haliminhanı have been interpreted to represent a mixture of taxa adapted to wooded and open grassland habitats (Şahin, 2023). Similar interpretation of a savanna-like environment with diverse wooded and open habitats was discussed by Özkurt et al. (2015), who also considered the lack of fossil primates in the Sivas localities to indicate predominantly open environments. In contrast, Kaya and Kaymakçı (2013) noted a relatively low mean ordinated hypsodonty value for the large herbivorous mammal assemblage of Hayranlı-Haliminhanı, supporting the interpretation of a woodland-shrubland environment, as suggested by Bibi and Güleç (2008) based on the ecomorphological types of bovids. Meijers et al. (2022) suggested that the presence of a stable lakeshore environment at Hayranlı-Haliminhanı maintained wooded environments, which could explain local selection of woodland elements in the mammal fauna. Combining these interpretations seems to suggest a diverse paleoenvironment in the Sivas Basin between 8 and 6.5 Ma, which however would have been locally dominated by shrubland and woodland vegetation rather than extensive grasslands in Hayranlı-Haliminhanı.

Several groups of fossil mammals have been described from Hayranlı-Haliminhanı, including bovids (Bibi & Güleç, 2008), rodents (Kaya & Kaymakçı, 2013), suids (Made et al., 2013), insectivores (Furió et al., 2014), carnivorans (Özkurt et al., 2015) and hipparionin equids (Şahin, 2023). While proboscideans have been mentioned in previous publications, with suggested presence of *Choerolophodon* sp. (Demirci et al., 2007; Meijers et al., 2022), a systematic description of the proboscideans from Hayranlı-Haliminhanı has not yet been done. In this article we describe the proboscidean fossils from Hayranlı-Haliminhanı, noting the presence of a previously unreported derived mammutid ("*Mammut*" cf. "*M.*" *obliquelophus*), similar to the Late Miocene mammutids from Pikermi and Samos (Greece) and elsewhere in the Mediterranean realm and Western Asia. We could not confirm the presence of any other proboscidean taxa. A complete updated list of mammal taxa from Hayranlı-Haliminhanı is presented in Table 1, following Meijers et al. (2022), Şahin (2023), and our present study. We discuss the paleoenvironmental implications of this finding, considering the paleoecology of mammutid proboscideans.

TABLE 1. Updated fossil mammal list from Hayranlı-Haliminhanı with references. "*Mammut*" cf. "*M*" *obliquelophus* is added based on the current study. *The presence of *Choerolophodon* sp. could not be confirmed based on the current study, and we thus consider it dubious.

	Family	Species	Reference
Carnivora	Hyaenidae	*Hyaenictitherium wongii*	Özkurt et al., 2015; Meijers et al., 2022
		Ictitherium intuberculatum	Özkurt et al., 2015; Meijers et al., 2022
		Lycyaena dubia	Özkurt et al., 2015; Meijers et al., 2022
	Felidae	*Amphimachairodus giganteus*	Özkurt et al., 2015; Meijers et al., 2022
Perissodactyla	Rhinocerotidae	*Miodiceros neumayri*	Meijers et al., 2022
	Equidae	*Cremohipparion* aff. *moldavicum*	Şahin, 2023
		Cremohipparion aff. *proboscideum*	Şahin, 2023
		Hippotherium sp.	Şahin, 2023
Proboscidea	Gomphotheriidae	*Choerolophodon* sp.*	Demirci et al., 2007
	Mammutidae	"*Mammut*" cf. "*M.*" *obliquelophus*	this study
Artiodactyla	Bovidae	*Gazella* cf. *G. capricornis*	Bibi & Güleç, 2008; Meijers et al., 2022
		Prostrepsiceros houtumschindleri syridisi	Bibi & Güleç, 2008; Meijers et al., 2022
		cf. *Protoryx* sp.	Bibi & Güleç, 2008; Meijers et al., 2022
		Tethytragus cf. *T. koehlerae*	Bibi & Güleç, 2008; Meijers et al., 2022
		Tragoportax cf. *T. amalthea*	Bibi & Güleç, 2008; Meijers et al., 2022
	Suidae	*Microstonyx major*	van der Made et al., 2013; Meijers et al., 2022
	Giraffidae	indet.	Meijers et al., 2022
Rodentia		*Apodemus*	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Progonomys	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Myomimus maritsensis	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Microdyromys koenigswaldi	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Tamias cf. *eviensis*	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Spermophilinus bredai	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Sciurus sp. indet	Kaya & Kaymakçı, 2013; Meijers et al., 2022
		Pliopetaurista bressana	Kaya & Kaymakçı, 2013; Meijers et al., 2022
Lipotyphla		*Schizogalerix sinapensis*	Furió et al., 2014; Meijers et al., 2022
		Paenelimnoecus sp.	Furió et al., 2014; Meijers et al., 2022
		Amblycoptus oligodon	Furió et al., 2014; Meijers et al., 2022
		Petenyia dubia	Furió et al., 2014; Meijers et al., 2022
		Soricinae indet.	Furió et al., 2014; Meijers et al., 2022
		Crocidosoricinae indet.	Furió et al., 2014; Meijers et al., 2022
		Desmanella aff. *cingulata*	Furió et al., 2014; Meijers et al., 2022
		Desmanodon larsi	Furió et al., 2014; Meijers et al., 2022

MATERIALS AND METHODS

The fossil material examined in this study are housed in the paleontological collections of the Ahi Evran University in Kirsehir, Türkiye. In the specimen numbers, the number "58" is the numeric code for the Sivas area and "HAY" refers to Hayranlı, followed by a locality number (localities 2 and 14 for the specimens studied here) and a specific number for the specimen.

We describe proboscidean fossils from Hayranlı-Haliminhanı, Sivas Basin, providing taxonomic determinations and morphometric comparisons. For dental measurements, we use standard morphometric measurements, including maximum length and width of tooth crown, maximum height of (unworn) tooth crown, number of lophs/lophids and hypsodonty index, calculated as: HI = (maximum crown height/width) × 100 (Göhlich, 1998; Saarinen & Lister, 2023; and references therein). The postcranial measurements mostly follow the conventions of Göhlich (1998) and Koenigswald et al. (2022). For the lunar (os carpi intermedium), we use an additional measurement of minimum height, in addition to the conventional measurement of maximum height (Göhlich, 1998). This is done because of uncertainty of the preservation of the maximum height of the lunar specimen from Hayranlı-Haliminhanı. We measure the lunar minimum height from the cranial side of the bone (similarly to the maximum height), from the lowest point near the sagittal axis of the bone (from the bottom of the saddle-shaped proximal (radius) articular surface to the distal articular surface). Because the lunar minimum height has not been recorded by most authors, we measured it from published photos of comparative specimens in some cases, such as for *Zygolophodon turicensis* from Czujan's sand pit, Czech Republic (Březina, 2014), *Mammut borsoni* from Kaltensundheim, Germany (Koenigswald et al., 2022), and *Choerolophodon pentelici* from Akkaşdaği, Türkiye (Tassy, 2005). We compared dental and lunar morphometrics from Hayranlı-Haliminhanı with other Late Miocene proboscideans and mammutids in diagrams. For the lunar specimens, we also present outline drawings for comparison between taxa, as well as calculated height/width ratios.

We discuss the biochronological, taxonomic, and paleoenvironmental implications of the proboscidean finds from Hayranlı-Haliminhanı.

Institutional Abbreviations—AK, Akkaşdağˇi fossil collection, Natural History Museum of Ankara, Türkiye; **BA**, Baza-1 fossil collection, Archaeological Museum of Granada, Spain; **BSP**, Bayerische Staatssammlung für Paläontologie, Munich, Germany; **Hay**, Hayranlı-Haliminhanı fossil collection, Ahi Evran University, Kirshehir, Türkiye; **HMV**, Hezheng Paleozoological Museum, Hezheng, China; **HNHM**, Hungarian Natural History Museum, Budapest, Hungary; **ISM**, Illinois State Museum, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **KTBA**, Avdan fossil collection, Geological Engineering Department of Pamukkale University, Türkiye; **MNHN**, Muséum national d'histoire naturelle, Paris, France; **MZM**, Moravian Museum, Brno, Czech Republic; **NHMS**, Naturhistorisches Museum Schleusingen, Germany; **PA**, Paleontological museum of Athens, Greece; **PMMS**, Palaeontological Museum of Mytilinii, Samos Island, Greece; **PMU**, Paleontological Museum of Uppsala, Sweden; **SSC RAS**, Southern Scientific Centre of the Russian Academy of Sciences, Rostov-on-Don, Russia; **TK**, Türkiye fossil collection, Museum

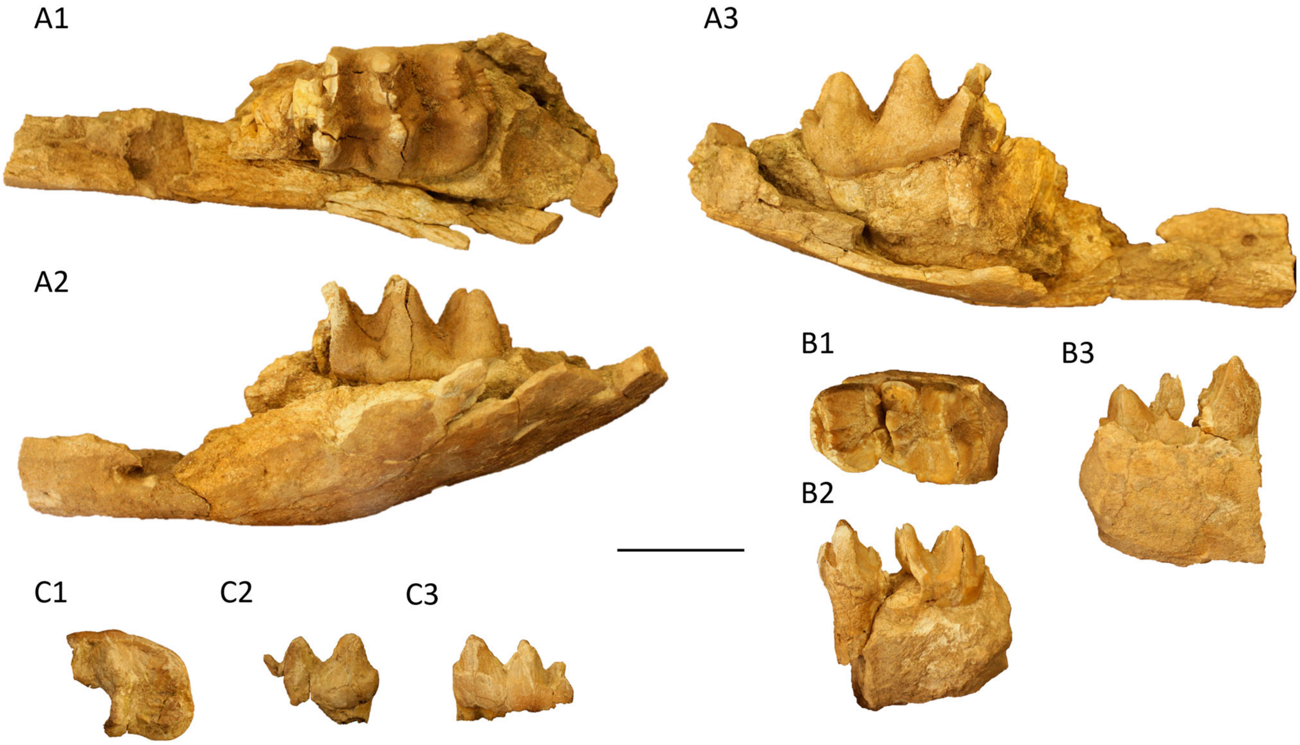

FIGURE 2. Dental specimens of "*Mammut*" cf. "M." *obliquelophus* from Hayranlı-Haliminhanı (Sivas). **A1**–**3**: Left hemimandible fragment with m1 (58-Hay-2/46) in occlusal, **A1**, left lateral, **A2**, and right lateral, **A3** views. **B1**–**3**: left dp4 in mandible fragment (58-Hay-14/53), in occlusal **B1**, left lateral, **B2**, and right lateral, **B3** views. **C1**–**3**: posterior fragment of left DP4 (58-Hay-2/22) in occlusal, **C1**, right lateral, **C2**, and left lateral, **C3** views. Scale bar equals 50 mm.

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SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
PROBOSCIDEA Illiger, 1811
ELEPHANTIMORPHA Tassy and Shoshani 1997, in Shoshani et al., 1998
MAMMUTIDA Tassy and Shoshani 1997, in Shoshani et al., 1998
MAMMUTIDAE Hay, 1922
MAMMUT Blumenbach, 1799
"*MAMMUT*" cf. "*M.*" *OBLIQUELOPHUS* (Mucha, 1980)

Locality—Hayranlı-Haliminhanı, Türkiye.

Type Species (of Genus)—*Mammut americanum* (Kerr, 1792).

Type Locality (of Genus)—Big-Bone Lick, Kentucky, U.S.A.

Type Specimen (of Genus)—m3 dext, MNHN-1643.

Diagnosis (of Genus)—Following Tobien (1996): Large-sized, derived mammutids with moderately to strongly shortened mandibular symphysis and reduced or absent lower tusks. Zygodonty of the molars is well developed, without conules. Intermediate molars are trilophodont, M3/m3 is tetralophodont, with a well-developed posterior cingulum. Upper tusks lack enamel band. The cranium has a shortened basicranium.

Material—m1 (sin.) in mandible fragment (58-Hay-2/46); dp4 (sin.) in mandible fragment (58-Hay-14/53); DP4 (sin.) (58-Hay-2/22).

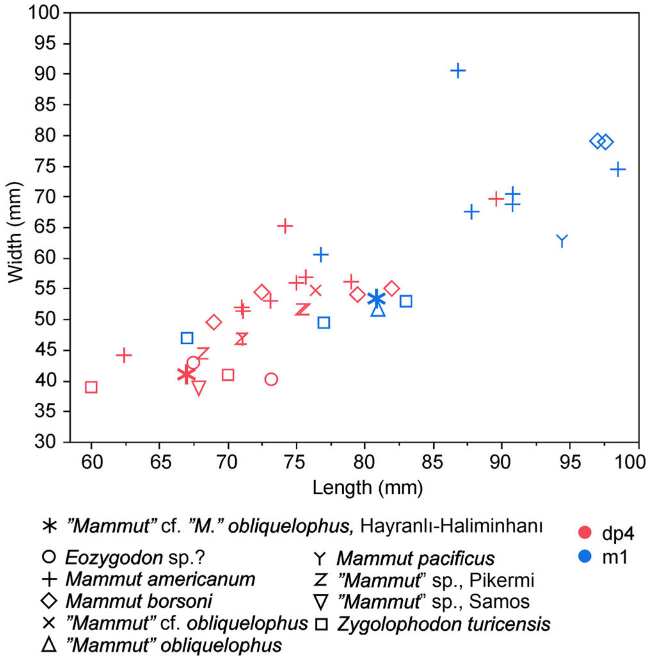

FIGURE 3. Comparison of maximum lengths and widths (in mm) of dp4 and m1 specimens of *Eozygodon*, *Zygolophodon turicensis*, and species of the genus *Mammut*, including the specimens from Hayranlı-Haliminhanı. Data used for this figure are summarized in Table 2 with references.

TABLE 2. Measurements of the dental specimens of “*Mammut*” cf. “*M.*” *obliquelophus* from Hayranlı-Haliminhanı (Sivas), and comparative specimens from other mammutids. **Abbreviations**: **H**, maximum height (of unworn tooth) (mm); **HI**, hypsodonty index, calculated as (H/W) × 100; **L**, maximum length (mm); **(L)**, left; **NL**, number of lophs/lophids (where x refers to talonids); **(R)**, right; **W**, maximum width (mm). **References**: **1**, this study; **2**, Zhang and Wang (2021); **3**, Green and Hulbert (2005); **4**, Dooley et al. (2019); **5**, Tobien et al. (1988); **6**, Ros-Montoya et al. (2017); **7**, Hopwood (1935); **8**, Konidaris (2013); **9**, Wang et al. (2017); **10**, Cahuzac and Tassy (1999); **11**, Tassy (1983); **12**, Konidaris and Koufos (2009, 2013); **13**, Tassy (1977); **14**, Lehmann (1950); **15**, Erten and Koralay (2020); **16**, Titov and Tesakov (2013); **17**, Schlesinger (1917).

Species (+reference nr.)	Locality	Country/ State	Spec.-nr.	tooth	L	W	H	HI	NL
Mammut cf. *M. obliquelophus* (1)	Hayranlı-Haliminhanı	Türkiye	58-Hay-2/46	m1 (L)	80.9	53.3	40.2	75.4	3x
Mammut cf. *M. obliquelophus* (1)	Hayranlı-Haliminhanı	Türkiye	58-Hay-14/53	dp4 (L)	67	41	32.7	79.8	x3x
Mammut cf. *M. obliquelophus* (1)	Hayranlı-Haliminhanı	Türkiye	58-Hay-2/22	DP4 (L)		[46.7]	31.3	—	[3]
Eozygodon sp.? (2)	Leng-shuigou FM	China	IVPP V3081	dp4 (R)	73.2	40.2	—	—	—
Eozygodon sp.? (2)	Leng-shuigou FM	China	IVPP V3080	dp4 (L)	67.5	42.9	—	—	—
Mammut americanum (3)	—	Florida	min	dp4	62.4	44.2	—	—	—
Mammut americanum (3)	—	Florida	mean	dp4	71.1	51.4	—	—	—
Mammut americanum (3)	—	Florida	max	dp4	79	56.2	—	—	—
Mammut americanum (3)	—	Florida	min	DP4	65.4	57	—	—	—
Mammut americanum (3)	—	Florida	mean	DP4	71.9	60.5	—	—	—
Mammut americanum (3)	—	Florida	max	DP4	76.5	64.1	—	—	—
Mammut americanum (4)	—	Arizona	mean	dp4	75	56	—	—	—
Mammut americanum (4)	—	Colorado	mean	dp4	75.68	56.92	—	—	—
Mammut americanum (4)	—	Florida	mean	dp4	73.1	53.06	—	—	—
Mammut americanum (4)	—	Kentucky	mean	dp4	89.6	69.7	—	—	—
Mammut americanum (4)	—	Ohio	mean	dp4	74.17	65.27	—	—	—
Mammut americanum (4)	—	Virginia	mean	dp4	71	52	—	—	—
Mammut americanum (4)	—	Colorado	mean	m1	90.79	68.8	—	—	—
Mammut americanum (4)	—	Florida	mean	m1	86.8	90.6	—	—	—
Mammut americanum (4)	—	Indiana	mean	m1	98.5	74.5	—	—	—
Mammut americanum (4)	—	Ohio	mean	m1	87.8	67.6	—	—	—
Mammut americanum (4)	—	Virginia	mean	m1	90.8	70.48	—	—	—
Mammut americanum (4)	—	Washington	mean	m1	76.78	60.6	—	—	—
Mammut borsoni (5)	—	China	PMU-M1886	dp4 (R)	69	49.5	—	—	—
Mammut borsoni (5)	—	China	PMU-M1888	dp4 (R)	79.5	54	—	—	—
Mammut borsoni (5)	—	China	PMU-M1881	dp4 (L)	82	55	—	—	—
Mammut borsoni (5)	—	China	PMU-M1887	dp4 (L)	72.5	54.4	—	—	—
Mammut borsoni (6)	Baza 1	Spain	BA-1 2000 O11 No. 4B	m1 (R)	97.04	79.04	—	—	—
Mammut borsoni (6)	Baza 1	Spain	BA-1 2000 O11 No. 4A	m1 (L)	97.63	78.86	—	—	—
Mammut cf. *M. obliquelophus* (2)	—	China	IVPP V23943	dp4 (R)	76.44	54.68	—	—	—
Mammut cf. *M. obliquelophus* (7)	—	China	PMU-M1880	dp4 (L)	80	—	—	—	—
Mammut pacificus (4)	—	California	mean	dp4	71.1	46.93	—	—	—
Mammut pacificus (4)	—	California	mean	m1	94.45	62.86	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (8)	Pikermi	Greece	min	dp4	68.2	44.4	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (8)	Pikermi	Greece	mean	dp4	71	46.8	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (8)	Pikermi	Greece	max	dp4	75.4	51.6	—	—	—
Mammut sp. (*M*. obliquelophus)?, Pikermi (8)	Pikermi	Greece	min	DP4	62.5	49.8	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (8)	Pikermi	Greece	mean	DP4	70.7	53.8	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (8)	Pikermi	Greece	max	DP4	76	58.3	—	—	—
Mammut cf. *M. obliquelophus* (9)	Linxia Basin	China	HMV 1428	DP4 (L)	82	65	—	—	—
Mammut cf. *M. obliquelophus* (9)	Linxia Basin	China	HMV 1428	DP4 (L)	79.5	65	—	—	—
Mammut cf. *M. obliquelophus* (9)	Linxia Basin	China	HMV 0009	DP4 (L)	75	61.5	—	—	—
Zygolophodon turicensis (10)	Escalans	France	no nr.?	DP4 (R)	58.7	42.4	—	—	—
Zygolophodon metachinjiensis (11)	Chinji, Siwaliks	Pakistan	BSP 1625	DP4 (L)	63.4	44	—	—	—
Mammut sp. (*M. obliquelophus*)?, Pikermi (12)	Pikermi	Greece	MNHN-PIK-3613	dp4 (R)	75.6	51.6	—	—	—
Mammut sp. (*M. obliquelophus*)?, Samos (12)	Mytilinii-1	Greece	PMMS-53	dp4 (R)	67.9	38.8	—	—	—
Zygolophodon turicensis (13)	Simorre	France	MNHN-Si 11	dp4 (L)	70	41	—	—	—
Zygolophodon turicensis (14)	Indersdorf bei Dachau	Germany	BSP 1916-I-1	dp4 (R)	60	39	—	—	—
Zygolophodon turicensis (15)	Advan	Türkiye	KTBA 1001	m1 (L)	67	47	—	—	—
Mammut obliquelophus (16)	Morskaya 2	Russia	SSC RAS M-2/63	m1 (R)	81	51.6	—	—	—
Zygolophodon turicensis (17)	Mistelbach	Austria	plate 21, fig. 6	m1 (L)	83	53	—	—	—
Zygolophodon turicensis (14)	Indersdorf bei Dachau	Germany	BSP 1916-I-1	m1 (R)	77	49.5	—	—	—

DESCRIPTION AND COMPARISON

The left m1 (58-Hay-2/46) is nearly complete, with the first lophid being fragmentary (Fig. 2A). It has three lophids and a well-developed posterior cingulum consisting of a row of several conelets. The lophids show well-developed zygodonty, with the main cusps and a row of several mesoconelets merged into sharp, wedge-shaped crests. Pretrite crescentoids are present. The interlophid crown base of this specimen is lingually high, resembling *Mammut borsoni* rather than *Zygolophodon turicensis* in this regard (see Tassy, 1985). Morphologically the specimen is similar to dp4 specimens of “*Mammut*” sp. (“*M.*” *obliquelophus*?) from Pikermi, Greece (Gaudry, 1862–1867; Konidaris, 2013; Konidaris & Tsoukala, 2022), but it is larger in dimensions (Fig. 3, Table 2; see also Konidaris, 2013) and has a relatively thick enamel. It is comparable in size to the m1 of “*Mammut*” *obliquelophus* from Morskaya 2, Russia (Titov & Tesakov, 2013), and *Zygolophodon turicensis* from Mistelbach, Austria (Schlesinger, 1917), as well as smallest m1 specimens of *Mammut americanum* (Fig. 3; Table 2). It is slightly larger than the m1 of *Z. turicensis* from Indersdorf, Germany (Fig. 3, Table 2; Lehmann, 1950), and notably longer than a specimen of m1 of *Zygolophodon turicensis* described from Avdan, Kale-Tavas basin, Türkiye (Fig. 3, Table 2; Erten & Koralay, 2020), although it should be noted that the specimen from Avdan is heavily worn. The m1 is attached to a partial hemimandible preserving a part of the symphysis, but the poor preservation of the fragment does not allow much to be said about the morphology of the mandible.

The left dp4 (58-Hay-14/53) is also nearly complete, with the second lophid being fragmentary (Fig. 2B). It is similar in morphology to the specimens of “*Mammut*” sp. (“*M.*” *obliquelophus*?) from Pikermi (Konidaris, 2013; Konidaris & Tsoulaka, 2022) and falls into the smaller end of the size spectrum of dp4 specimens from Pikermi and Samos described by Konidaris and Koufos (2009, 2013) and Konidaris (2013) (Fig. 3, Table 2). It has three lophids with well-developed zygodonty, with narrow crests comprising a row of several small, even-sized mesoconelets and strongly compressed main cusps. In this respect it is similar to other specimens of “*Mammut*” sp. and differs from the dp4 specimens of *Zygolophodon turicensis* from Simorre, France, and Indersdorf, Germany, which have fewer mesoconelets and a more bunodont morphology, as is typical for the genus *Zygolophodon* (see Lehmann, 1950; Tassy, 1977).

The left DP4 (58-Hay-2/22) is incomplete, with a partial second loph and complete third loph preserved (Fig. 2C). It is broadly similar in size and morphology to DP4 specimens of “*Mammut*” sp. from Pikermi and Ravin de Zouaves 5, Greece (Konidaris, 2013), but its incomplete preservation does not allow a full morphometric comparison. As in the other specimens of “*Mammut*” cf. “*M*” *obliquelophus* from Hayranlı-Haliminhanı, the lophs are sharp-crested, comprising an even row of several small, even-sized conelets, corresponding with the specimens of “*Mammut*” cf. “*M.*” *obliquelophus* from Pikermi, Linxia Basin in China and other late Miocene sites (Konidaris, 2013; Konidaris & Tsoulaka, 2022; Wang et al., 2017). In this respect, it differs from the DP4 specimen of *Zygolophodon turicensis* from Escalans, France (Cahuzac & Tassy, 1999), and the DP4 of *Z. metachinjiensis* from Siwaliks (Chinji), Pakistan (Tassy, 1983), which have more clearly separated, more bunodont main cusps.

Remarks

The Late Miocene Eurasian specimens of “*Mammut*” have sometimes been tentatively associated with the common Pliocene European species *Mammut borsoni* (e.g., Koenigswald et al., 2022; Konidaris & Koufos, 2009, 2013), but more recently with the species “*Mammut*” *obliquelophus*, which differs from *M. borsoni* in having a longer mandibular symphysis and larger mandibular tusks (Konidaris et al., 2024; Konidaris & Tsoukala, 2020, 2022; Markov, 2008; Wang et al., 2017). Markov (2008) noted that a comparatively longirostrine specimen of “*Mammut*” described by Kubiak (1972) from Balta sands, Ukraine, was incorrectly assigned into the dubious taxon “*Mammut praetypicum*,” which was originally described from Păgaia, Romania by Schlesinger (1922), and should be considered to represent “*M.*” *obliquelophus* instead. Tassy (1985) and Tobien (1996) noted that the differences in the dental characterisics of *Mammut borsoni* compared to *Zygolophodon turicensis* include well-developed zygodonty without conules and lingually high crown at the base of the interlophids. The Late Miocene “*M.*” *obliquelophus* shares these characteristics with *M. borsoni*, and these traits are present also in the specimens from Hayranlı-Haliminhanı. Due to the morphological and morphometric similarity of the Hayranlı-Haliminhanı with the “*Mammut*” sp. material from Pikermi (Gaudry, 1862–1867; Konidaris, 2013; Konidaris & Tsoukala, 2022) and the m1 in a mandible from Morskaya 2, Russia, assigned to “*M.*” *obliquelophus* by Titov and Tesakov (2013), we assign the mammutid material from Hayranlı-Haliminhanı as “*Mammut*” cf. “*M.*” *obliquelophus.*

Postcranial Specimens of Proboscidea from Hayranlı-Haliminhanı

cf. “*MAMMUT*” *OBLIQUELOPHUS*

The left lunar specimen of a proboscidean (58-Hay-2/118) is sub-complete, caudally somewhat fractured and medially-proximally abraded in part. In terms of morphometrics it is close to specimens of *Zygolophodon turicensis* from Czujan’s sand pit, Czech Republic (Březina, 2014), and *Mammut americanum* from Buesching Site, Indiana (measured from 3D scan at UMORF, University of Michigan, https://umorf.ummp.lsa.umich.edu/wp/specimen-data/?Model_ID=1037) (Figs. 4, 5, Table 3). Although these specimens are smaller than the lunar of *Mammut borsoni* from Kaltensundheim, Germany (Koenigswald et al., 2022), they share with it a comparatively narrow morphology, in comparison to the common Late Miocene Mediterranean and Western Asian gomphothere taxa, *Choerolophodon pentelici* and *Konobelodon atticus* (Fig. 5). This difference is largely due to the cranially widened morphology of the gomphothere lunars (see also Tassy, 2005), in comparison to the mammutid specimens. However, there is variation in this regard within the mammutids and the gomphotheres. For example, the lunar specimen identified as *Zygolophodon turicensis* by Březina (2014) seems less derived in this respect than *M. borsoni* and *M. americanum*, while the morphology of the lunar from Hayranlı-Haliminhanı seems intermediate between *Z. turicensis* and the *Mammut borsoni* specimen from Kaltensundheim (Fig. 5). The deinotheriid lunar specimen PA3973/91 (*Deinotherium proavum*) of similar stratigraphic age to Hayranlı-Haliminhanı from Pikermi, Greece, described by Konidaris et al. (2017) (maximum width: 198.3 mm, maximum height: 114 mm, maximum depth: 151 mm), is wider than its depth (in contrast to the mammutid specimens, see Table 3) and it is much larger in dimensions than the specimen from Hayranlı-Haliminhanı, in fact being larger than any of the comparative elephantimorph specimens included here (although approached in dimensions by *K. atticus* from Pestzentlörincz, Hungary (Schlesinger, 1922)). Due to the morphology comparable to mammutid lunars and the morphometric similarities to the specimens of *Zygolophodon turicensis* and *Mammut americanum*, we tentatively assign the lunar from Hayranlı-Haliminhanı with the same taxon as the dental specimens from this locality, “*Mammut*” cf. “*M.*” *obliquelophus.*

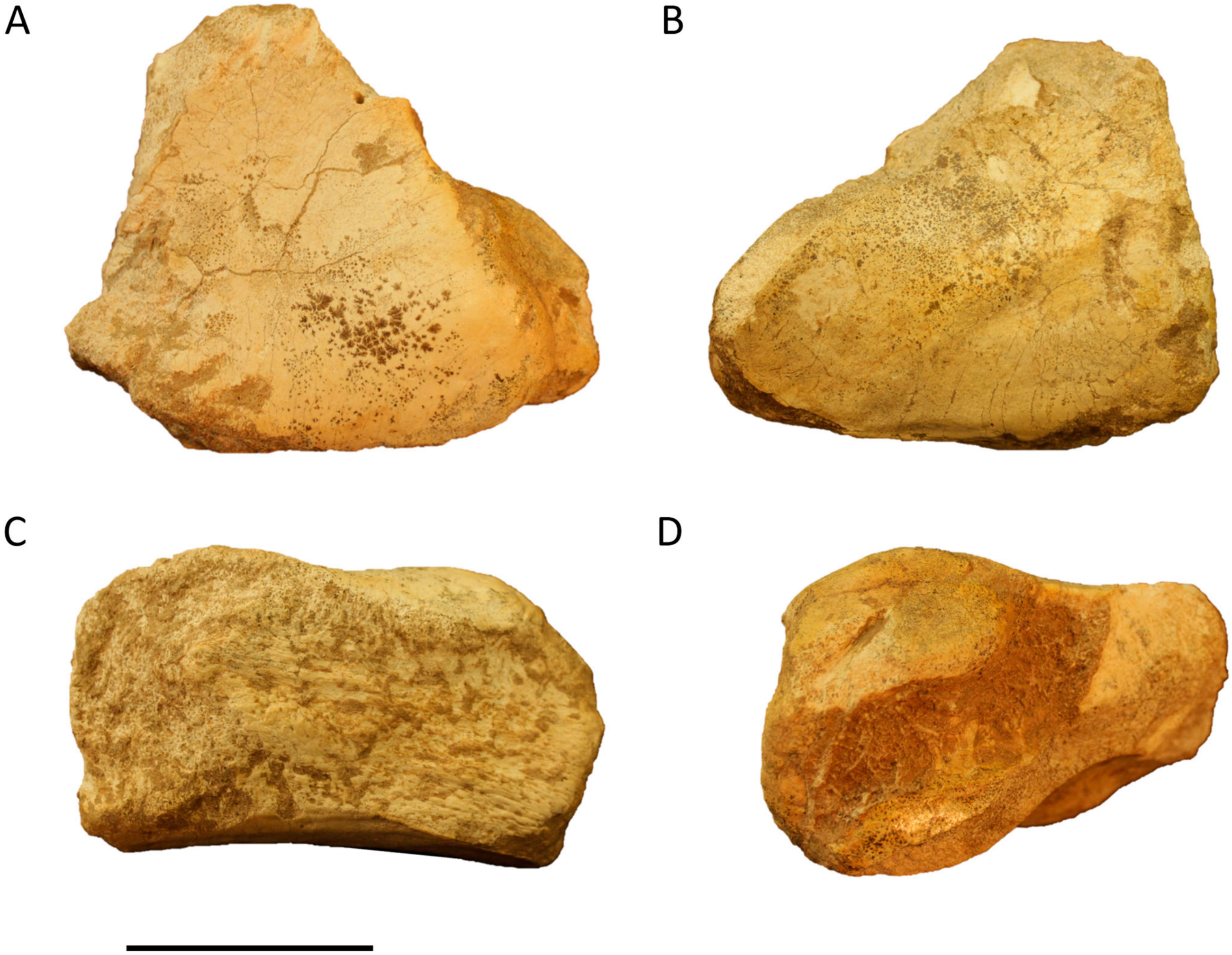

FIGURE 4. Left lunar of cf. "*Mammut*" *obliquelophus* from Hayranlı-Haliminhanı (58-Hay-2/118), in proximal, **A**, distal, **B**, cranial, **C**, and left lateral, **D** view. Scale bar equals 50 mm.

ELEPHANTIMORPHA indet.

A distal femur fragment 58-Hay-2/118 (Fig. 6A) is medially almost complete, preserving the complete medial epicondyle of the distal trochlea. The medial condyle is quite prominent, elongate and oval in shape, representing elephantoid rather than deinotheriid morphology (see Harris, 1978). It resembles the morphology of *Zygolophodon turicensis* from Czujan's sand pit, Czech Republic (Březina, 2014). Thus, its affinity with the same mammutid taxon represented by the dental material and lunar from Hayranlı-Haliminhanı is possible, but we consider it inconclusive due to the incomplete state of the specimen. In morphometrics the femur falls between specimens of *Zygolophodon turicensis* from Czujan's sand pit, Czech Republic (Březina, 2014) and *Mammut borsoni* from Kaltensundheim, Germany (Koenigswald et al., 2022) (Table 4).

PROBOSCIDEA indet.

A proximal fragment of right MC IV (58-Hay-2/163, Fig. 6B) is very large in size, with a maximum proximal width of ca. 120 mm, but its incomplete state does not allow for a more precise taxonomic identification than that of a large proboscidean.

DISCUSSION

Paleoecological Implications of the Mammutid Proboscidean from Hayranlı-Haliminhanı

We note the presence of a derived Late Miocene mammutid proboscidean "*Mammut*" cf. "*M.*" *obliquelophus* in Hayranlı-Haliminhanı, which has not been reported from this site previously. Based on our revision, we present an updated list of fossil mammals from Hayranlı-Haliminhanı (Table 1), with the addition of "*Mammut*" cf. "*M.*" *obliquelophus*. We base the identification as "*Mammut*" cf. "*M.*" *obliquelophus* on the morphological traits of dp4 and m1 specimens, as well as the similarity of their size to other specimens of "*M.*" *obliquelophus* and other Late Miocene members of the genus "*Mammut*" in Europe and Western Asia. On the other hand, we were unable to confirm the presence of other proboscidean taxa in the proboscidean fossil material stored at the paleontological collections at the Ahi Evran University, Kirsehir, although *Choerolophodon* sp. has been reported earlier from Hayranlı (e.g., Meijers et al., 2022).

The similarity of the dental specimens of "*Mammut*" cf. "*M.*" *obliquelophus* from Hayranlı-Haliminhanı with those from the classic Late Miocene site of Pikermi, Greece (MN12; see Koufos, 2013), suggests a broadly similar age for the locality. Based on the bovids and the suid *Microstonyx*, this site has previously been assigned into MN11 or MN12 (Bibi & Gülek, 2008;

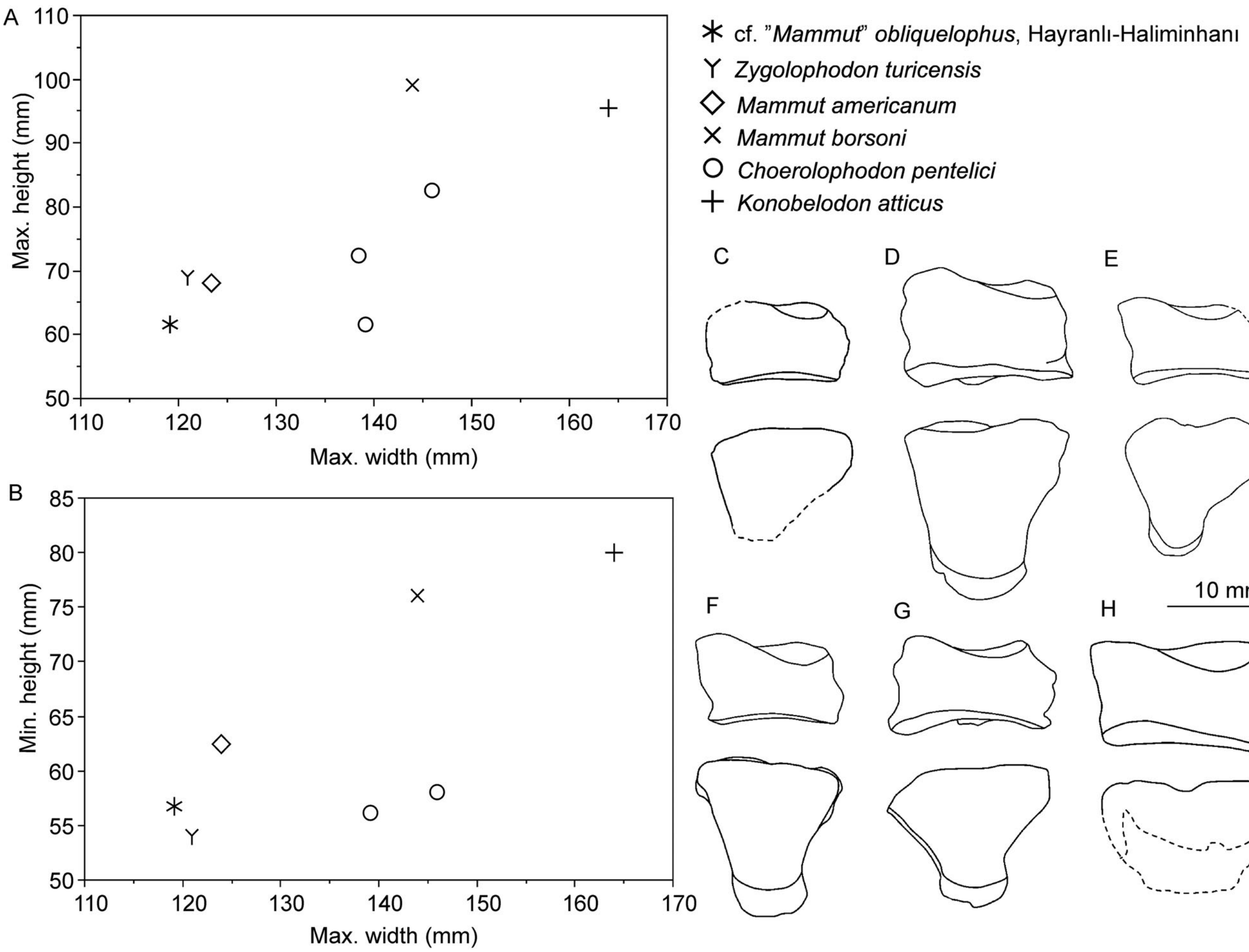

FIGURE 5. **A**, **B**: proboscidean lunar measurements from Hayranlı-Haliminhanı and comparative specimens of mammutid proboscideans, *Choerolophodon pentelici* and *Konobelodon atticus.* **A**, maximum height–maximum width, **B**, minimum height–maximum width. Data used for this figure are summarized in Table 3 with references. **C**–**H**: outline drawings of the Hayranlı-Haliminhanı lunar specimen and comparative proboscidean lunars in cranial (top image) and distal (bottom image) views. **C**, cf. *Mammut obliquelophus,* lunare (sin.), Hayranlı-Haliminhanı (58-Hay-2/118), **D**, *Mammut borsoni*, lunare (sin.), Kaltensundheim (Koenigswald et al., 2022), **E**, *Zygolophodon turicensis*, lunare (sin.), Czujan's sand pit (Březina, 2014), **F**, *Mammut americanum,* lunare (sin.), Buesching, Indiana (ISM 71.3.261; link to 3D scan: https://umorf.ummp.lsa.umich.edu/wp/wp-content/3d/viewer.html?name=B_L_LUN), **G**, *Choerolophodon pentelici*, lunare (original dext, reversed here for comparison), Akkaşdaği (Tassy, 2005), **H**, *Konobelodon atticus* ("*Mastodon grandincisivus*"), lunare (original dext. reversed here for comparison), Pestzentlörincz (examined by JS, originally published by Schlesinger [1922]). Dashed lines in the outline drawings indicate incomplete or worn areas. Scale bar equals 100 mm.

TABLE 3. Lunar measurements of proboscideans from Hayranlı-Haliminhanı and comparative mammutid and gomphothere taxa. **Abbreviations**: **D**, maximum depth (mm); **H (max.)**, maximum height (mm); **H (min.)**, minimum height (mm); **L**, left; **R**, right; **Spec-nr.,** specimen number; **W**, maximum width (mm). **References**: **1**, this study; **2**, Tassy (2005); **3**, own measurements; Gaziry (1976); **4**, own measurements, Schlesinger, (1922); **5**, Koenigswald et al. (2022); **6**, Březina (2014); **7**, UMORF, https://umorf.ummp.lsa.umich.edu; **8**, Konidaris et al. (2017).

Taxon (+reference nr.)	Spec-nr.	Locality	Country/State	Material	W	D	H (max.)	H (min.)	% max. H/W	% min. H/W
cf. "*Mammut*" *obliquelophus* (1)	58-Hay-2/118	Hayranli	Türkiye	lunar (L)	119.2		[61.5]	56.7	52	48
Choerolophodon pentelici (2)	AK4-93	Akkaşdaği	Türkiye	Lunar (R)	146	125.3	82.5	58	57	40
Choerolophodon pentelici (2)	AK6-89	Akkaşdaği	Türkiye	lunar (R)	138.5	122.6	72.3		52	
Choerolophodon pentelici (3)	TK 1830	Garkin	Türkiye	lunar (L)	139.2	121.4	61.5	56.1	44	40
Konobelodon atticus (4)	HNHN-V.79.34	Peszentlörincz	Hungary	lunar (R.)	164		95.5	80	58	49
Mammut borsoni (5)	NHMS-MTe 810/20	Kaltensundheim	Germany	lunar (R)	144	166	99	76	69	53
Zygolophodon turicensis (6)	MZM 7627	Czujan's sand pit	Czech Republic	lunar (L)	121	120	69	54	57	45
Mammut americanum (7)	ISM 71.3.261	Buesching Site	Indiana	lunar (L)	124	131	68	62.4	55	50
Deinotherium proavum (8)	PA3973/91	Pikermi	Greece	lunar (L)	198.3	151	114		57.5	

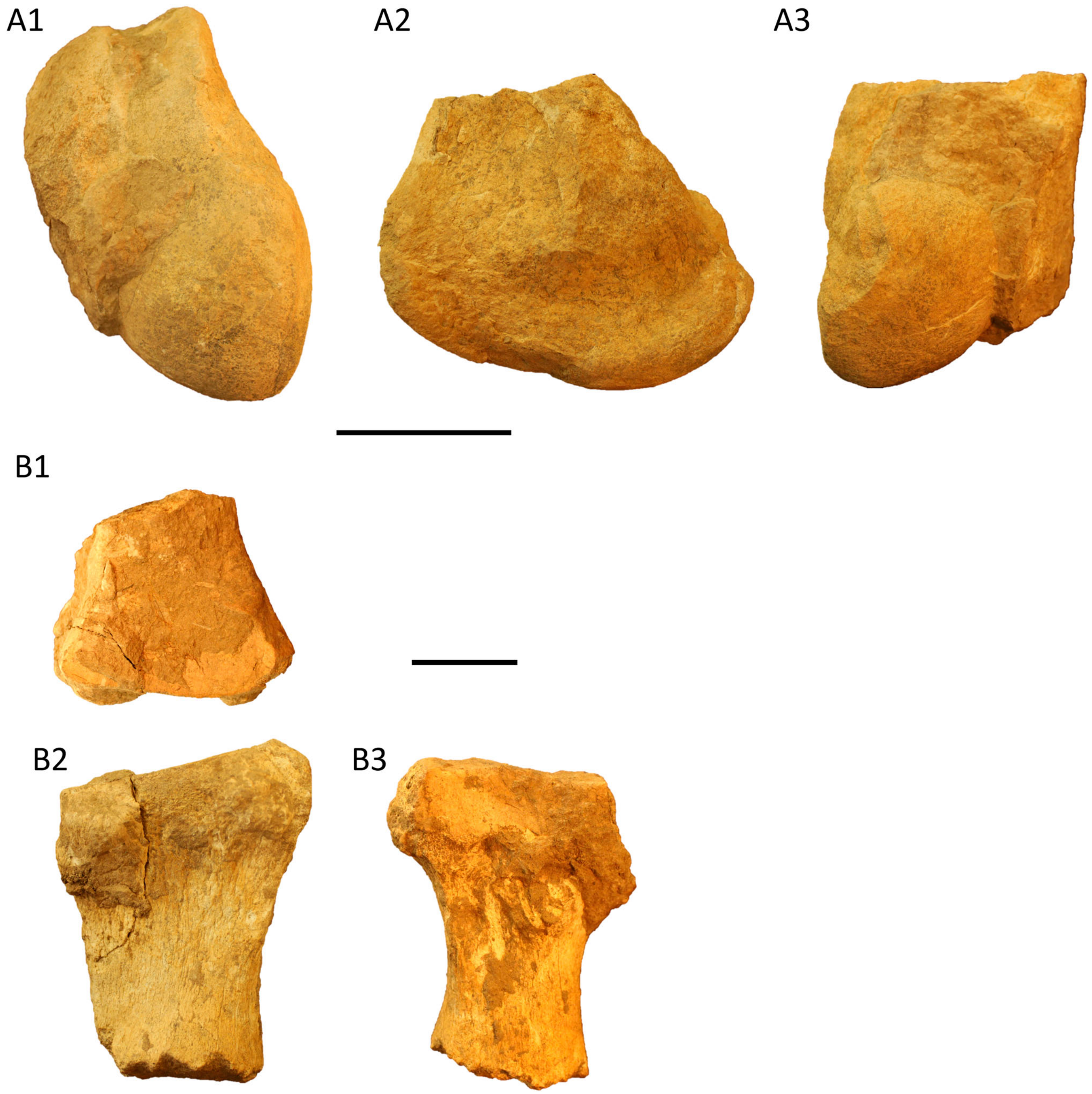

FIGURE 6. **A**, distal fragment of right femur of Elephantimorpha indet. from Hayranlı-Haliminhanı, in distal, **A1**, left lateral, **A2**, and caudal, **A3**, views. **B**, proximal fragment of right MCIV of Proboscidea indet. from Hayranlı-Haliminhanı (58-Hay-2/163) in proximal, **B1**, cranial, **B2**, and left lateral, **B3** views. Proximal width = 119.6 mm. Diaphysis least depth = 67.8 mm. Scale bar equals 100 mm in **A** and 50 mm in **B**.

Made et al., 2013), while the revised chronology of Meijers et al. (2022) refined the age between 8 and 6.5 Ma, further confirming the chronological association with Pikermi and other MN12 localities. “*Mammut*” is relatively rare in the Late Miocene fossil record from Anatolia, especially compared with the very common gomphotheriid taxa *Choerolophodon* and *Konobelodon* (Konidaris et al., 2014, 2016), and its presence in Hayranlı-Haliminhanı is likely related to paleoenvironmental conditions in the Sivas Basin during the MN11-MN12. So far, “*Mammut*” (“*M.*” *obliquelophus*?) has only been reported from the locality of Sazak, in the Late Miocene fossil record of Türkiye (Konidaris et al., 2022), and perhaps from Tokmacık, where the material was originally described as “*Zygolophodon*” by Yilmaz Usta et al. (2020), although affinity with “*Mammut*” was considered more likely by Konidaris et al. (2022) based on Turolian age of the site.

According to paleodietary analyses, the mammutids consistently retained browsing or at least browse-dominated diets throughout their evolutionary history, as shown for example for the Early Miocene *Eozygodon morotoensis* (Saarinen & Lister, 2023), the Middle Miocene *Zygolophodon turicensis* (Loponen, 2020), the Pliocene *Mammut borsoni* (Haiduc et al., 2018; Rivals & Lister, 2016; Saarinen & Lister, 2016), and the Pleistocene *Mammut americanum* (e.g., Cammidge et al., 2020; Green et al., 2005, 2017; Newsom & Mihlbachler, 2006; Rivals

TABLE 4. Femur measurements from Hayranlı-Haliminhanı, with comparative measurements of mammutids. **Abbreviations**: **Distal max D**, distal maximum depth; **medial cond. H**, medial condyle height; **medial cond. W**, medial condyle width. **References**: **1**, this study; **2**, Březina (2014); **3**, Koenigswald et al. (2022); **4**, UMORF, https://umorf.ummp.lsa.umich.edu.

Taxon (+reference nr.)	Specimen nr.	Locality	Country	Element	distal max. D	medial cond. H	medial cond.W
Elephanti morpha indet. (1)	58-Hay-2/118	Hayranlı-Haliminhanı	Türkiye	femur (dext.), distal fragment	255	166	102
Zygolophodon turicensis (2)	MZM Ot 7652&7655	Czujan's sand pit	Czeckh Republic	combined femur specimens	172	121	90
Mammut borsoni (3)	NHMS-MTe 810/8	Kaltensund heim	Germany	femur (sin.)	298	169	125
Mammut americanum (4)	ISM 71.3.261	Buesching	Indiana	femur (sin.)	228	127	105

et al., 2012, 2019). Moreover, feeding on predominantly woody browse, such as leaves of coniferous and deciduous trees, bark, and fruit has been mostly suggested (e.g., Green et al., 2005, 2017; Newsom & Mihlbachler, 2006), although Cammidge et al. (2020) found indication of more generalized, browse-dominated but mixed diet, sometimes including seasonal intake of grasses, for *Mammut americanum*. Saarinen and Liu (2024) argued that the presence of "*Mammut*" sp. in the classic Late Miocene locality of Pikermi, Greece, reflects a more wooded paleoenvironment in Pikermi compared with the more open and grassier paleoenvironment of Maragheh, Iran, where "*Mammut*" is absent, despite having an otherwise similar proboscidean fauna. Recently, "*Mammut*" cf. "*M.*" *obliquelophus* was described from Abkhareh village in Varzeghan region in Iran (Yaghoubi et al., 2024), about 150 km north from Maragheh. It is thus not directly associated with the Maragheh faunal assemblage, and the paleoenvironmental conditions there could have been different. Yaghoubi et al. (2024) interpreted the paleoenvironment in Abkhareh to have been "open woodland," with prominent presence of the giant browsing deinothere *Deinotherium proavum*. As a generalized paleoecological interpretation, the presence of "*Mammut*" cf. "*M.*" *obliquelophus* in Hayranlı-Haliminhanı can with relative confidence be taken to indicate the presence of browse resources and probably prominent woody vegetation in the paleoenvironment. This supports the previous paleoenvironmental evaluations for Hayranlı-Haliminhanı, especially those of Bibi and Güleç (2008) based on bovid taxa and Kaya and Kaymakçı (2013) based on the mean ordinated hypsodonty value of large herbivorous mammals from this locality, which suggest a woodland- or shrubland-dominated, rather than grassland-dominated paleoenvironment.

Postcranial Morphology of the Hayranlı-Haliminhanı Mammutid and other Mammutid Proboscideans

Morphometric comparisons of the lunar bone of cf. "*Mammut*" *obliquelophus* from Hayranlı-Haliminhanı (58-Hay-2/118) allow for some tentative interpretations on its postcranial ecomorphology. It is broadly similar in size and proportions to the specimens of *Zygolophodon turicensis* from Czujan's sand pit, Czech Republic (Březina, 2014), and *Mammut americanum* from Buesching Site, Indiana (ISM 71.3.261), and notably smaller than the specimen of *M. borsoni* from Kaltensundheim (NHMS-MTe 810/8 [Koenigswald et al., 2022]). The ratio of maximum lunar height to maximum lunar width is higher in *M. borsoni* compared with *Z. turicensis* and *M. americanum*, and the specimen from Hayranlı-Haliminhanı is similar to the latter two rather than *M. borsoni* in this respect. However, it should be noted that because of the somewhat abraded proximal-medial surface, the preserved height of the Hayranlı-Haliminhanı lunar may not represent quite the complete maximum height of the bone. In fact, in terms of minimum height to maximum width ratio, the Hayranlı-Haliminhanı specimen is intermediate between *Z. turicensis* and *M. borsoni* (Table 3).

Koenigswald et al. (2022) noted that the forelimb bones of *M. borsoni* from Kaltensundheim share most prominent similarities with *M. americanum* from Buesching site rather than with the more plesiomorphic *Z. turicensis* from Czujan's sand pit. As far as can be observed from the lunar specimen from Hayranlı-Haliminhanı, it is more similar in proportions to the specimens of *Mammut* than to *Zygolophodon turicensis*. This supports the interpretation of Koenigswald et al. (2022) whose results indicate affinity of the "*Mammut borsoni* group," including Late Miocene Eurasian mammutids, with the genus *Mammut*. However, the differences in size and morphometric details compared with *M. borsoni* from Kaltensundheim tentatively support that the Late Miocene Eurasian mammutids (cf. *M. obliquelophus*) were distinct from the larger and more derived Pliocene *M. borsoni*, although size alone should not be taken as a trait to distinguish between proboscidean taxa due to the typically pronounced sexual dimorphism and individual variation in proboscidean size.

ACKNOWLEDGMENTS

We thank the Research Council of Finland (projects nr. 315691 and 340775) for funding this work. We owe special thanks to the director of the excavations in Sivas Basin, Prof. Dr. E. Güleç from Ankara University. We thank the reviewers G. Konidaris and W. Sanders for their insightful and constructive comments, which helped us improve this manuscript.

AUTHOR CONTRIBUTIONS

JS, AT, and ES collected the data. JS performed the morphometric and morphological comparisons. All authors participated in planning and preparing the manuscript.

DATA AVAILABILITY STATEMENT

All data used in this study are listed in the tables in this article.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

ORCID

Juha Saarinen http://orcid.org/0000-0003-1351-4652
Ali Taş http://orcid.org/0000-0002-2066-6075
Elçin Şener http://orcid.org/0000-0002-4127-0766
Ahmet Cem Erkman http://orcid.org/0000-0003-3382-1019

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Handling Editor: Luke Holbrook.