

TUFANBEYLİ: NEW LOWER PLIOCENE MAMMAL-YIELDING LOCALITY AND FIRST RECORD OF “*MAMMUT*” *BORSONI* FROM TURKEY

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Abstract. At the crossroads between Africa, Asia, and Europe, Turkey occupies a prominent position regarding terrestrial mammal interchanges. In stark contrast with a wealth of Late Miocene fossil record, the Early Pliocene interval was virtually undocumented for large mammals in Turkey so far, which made it impossible to characterise their biogeographical affinities in the concerned time interval. In this study, we present the first record of the mammutid proboscidean “*Mammut*” *borsoni* in Turkey, found in association with the rhinocerotid *Pliorhinus megarhinus*, in Lower Pliocene lignite beams at the Tufanbeyli Thermal Power Plant Lignite Operation site, Adana. “*Mammut*” *borsoni* spans the Pliocene–Early Pleistocene interval in Eurasia while *Pliorhinus megarhinus* is a conspicuous element of uppermost Miocene–Pliocene faunas in Western Eurasia and Turkey. This megamammal assemblage represents an important advance in our knowledge of the large mammal faunas of the Early Pliocene of Asia Minor, further attesting to close biogeographic affinities between Anatolia and other circum-Mediterranean regions just after the end-Miocene salinity crisis.

INTRODUCTION

The Miocene/Pliocene transition is a key event for the terrestrial vertebrate faunal successions in Eurasia, because of the important changes in climatic parameters and palaeoenvironment af-

ter the end of the Messinian Salinity Crisis (MSC; e.g. Koufos et al. 2005; Koufos & Vasileiadou 2015; Raffi et al. 2020). Although Upper Miocene mammal fossils are well documented in the Eastern Mediterranean region, the mammalian fossil record is poorly known for Early Pliocene times. From the viewpoint of mammal biogeography, Anatolia occupies a central position between Africa, Asia and Europe. Unfortunately, most Early Pliocene Anato-

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Fig. 1 - Geographical location of Tufanbeyli, Adana Province, Turkey (Modified from Google Earth).

lian records are from micromammals (e.g. van den Hoek Ostende et al. 2015; Şen et al. 2017, 2018) and only a couple of localities have yielded large mammals in Turkey (e.g., Çalta 2 and KaleTepe-3; Şen 1998; Albayrak 2017). In this context, the newly found locality of Tufanbeyli, located at the Tufanbeyli Thermal Power Plant Lignite Operation site, in the Tufanbeyli district of Adana (Fig. 1) is of first interest. There, mammutid proboscidean and rhinocerotid remains were found from the Lower Pliocene lignites of the Ahmetçik Formation.

Mammutids first occurred in Africa in Oligocene times. By the late Early Miocene, they dispersed into Eurasia and the New World (Tobien 1996; Sanders et al. 2010; Koenigswald et al. 2022). Mammutids are morphologically conservative and they did not diversify much until their extinction in the Late Pleistocene. During the late Early Miocene, mammutids dispersed across the Bering land bridge to North America, where they ended up with *Mammut americanum* (Kerr, 1792). The latter, from the Early Pleistocene of North America, is the type species of the genus *Mammut* Blumenbach, 1799. The earliest mammutid species in Europe, *Zygodolophodon turicensis* (Schinz, 1824), appeared during the Burdigalian about 18–17 Ma (MN3b) and persisted until early Tortonian times (MN10; Tassy 1985, 1990; Göhlich 2010). The latest Eurasian mammutid, “*Mammut*” *borsoni* (Hays, 1834), persisted in Europe until the earliest Pleistocene (MNQ17; Koenigswald et al. 2022). The remains

of mammutids in Europe are very rare and mostly consist of isolated molars, with the exception of the more complete records from Milia (Greece) and Kaltensundheim (Germany). Unfortunately, cranial morphology remains almost entirely unknown. As a consequence, the phylogenetic relationships of mammutids are still under debate (Tassy 1996; Koenigswald 2016). In particular, there are differing opinions regarding the species included within *Mammut*, especially concerning Eurasian specimens and the generic assignment of “*M.*” *borsoni*. The genus name *Mammut* is formally tied to the North American species *M. americanum*, and European representatives cannot be confidently assigned to the same genus. Therefore, following Markov (2008), the name of this genus is used within quotation marks in this study (see discussion in Markov 2008; Koenigswald & Göhlich 2019; Koenigswald et al. 2022, 2023).

The mammutid record from Turkey was so far restricted to Miocene localities, with *Zygodolophodon* sp. from Tokmacık (Yılmaz Usta et al. 2019, 2020) which is considered as “*Mammut*” in Konidaris et al. (2023), *Z. turicensis* from Akçahisar, Çatakbağyaka (Sickenberg et al. 1975), and Avdan (Erten & Koralay 2020), and “*Mammut*” sp. (“*M*” cf. *oblique-lobus* (Mucha, 1980)) from Sazak (Konidaris et al. 2023).

Here, we describe the mammal remains discovered in the Lower Pliocene lignites of Tufanbeyli, which are attributable to a mammutid pro-

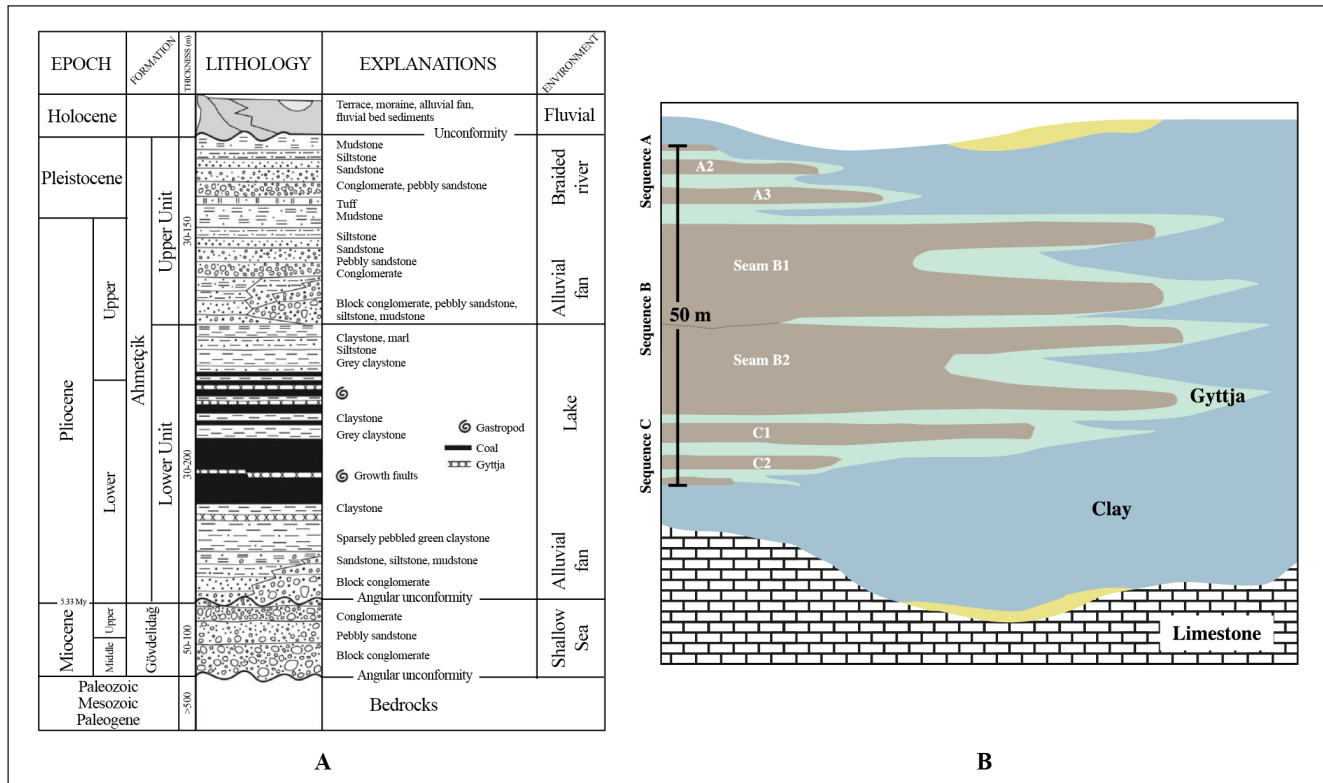


Fig. 2 - A) Stratigraphical section of Tufanbeyli (Yusufoğlu 2017); B) schematic cross section and megaherbivore-yielding Lower Pliocene lignite seams at Tufanbeyli, Adana, Turkey (Vattenffal 2012).

boscidean and a rhinocerotid, and discuss their biochronological and biogeographical implications.

GEOLOGICAL SETTING

Fossils from Tufanbeyli were recovered during fieldwork in 2015, 2020, and 2022 at the lignite mine of the Tufanbeyli Thermal Power Plant, situated between the villages of Yamanlı, Kayarcık, and Taşpınar in the Tufanbeyli district of Adana (Fig. 1). The specimens derive from the lower unit of the Ahmetçik Formation, which is dated to the Early Pliocene (Yusufoğlu 2017).

The basement of the Tufanbeyli Basin consists of Paleozoic and Mesozoic carbonates (Fig. 2A; Metin et al. 1982). The overlying Eocene (Lutetian) succession includes limestones, sandstones, conglomerates, and mudstones. Terrestrial conditions developed during the Oligocene–Middle Miocene, associated with the final closure of the Neo-Tethys. In the Early Miocene, strike-slip, dip-slip, and thrust faulting shaped the basin, initiating a new depositional phase. From the Early Pliocene onwards, humid subtropical conditions enhanced fluvial erosion

and promoted the accumulation of fluvial and shallow-lacustrine sediments, locally exceeding 100 m in thickness. The youngest stratigraphic units comprise Pliocene and Quaternary clastics.

The basin fill is represented by the Pliocene–Quaternary Ahmetçik Formation, consisting of coal-bearing lacustrine deposits at the base and tephra-interbedded fluvial sediments at the top (Yusufoğlu 2022). Lacustrine facies dominate the basin center, while fluvial facies prevail along the margins; both show lateral and vertical transitions. The succession begins with fluvial conglomerates reworked from basement rocks, overlain by marls and claystones, followed by a thick lignite horizon. Up-section, gyttja, lignitic gyttja, and fossiliferous layers with mollusk shells occur.

This interval is overlain by ~50–60 m of clay-rich gyttja with lignite streaks, organized into three seam sequences (C, B, A from oldest to youngest), each including several seams (Fig. 2B). The uppermost succession consists of claystones and poorly consolidated mudstones, whereas fluvial facies are represented by conglomerates and sandstones (Cicioğlu 2001).

Species	Locality	Country	Reference
<i>Zygodolophodon turicensis</i>	Malartic	France	Tassy (1977)
	Simorre	France	Tassy (1977)
	Rajégats	Rajégats	Tassy (1985)
	Montastruc-sur-Baise	France	Göhlich (1998)
	Freising	Germany	Lehmann (1950)
	Tutzing	Germany	Lehmann (1950)
	Bitola	North Macedonia	Garevski et al. (2012)
" <i>Mammut</i> " <i>obliqueolophus</i>	Ahmatovo	Bulgaria	Nikolov and Kovačev (1966)
	Puiești	Romania	Konidaris et al. (2024)
" <i>Mammut</i> " <i>borsoni</i>	Baza-1	Spain	Ros-Montoya (2010)
	Kisláng	Hungary	Mihály Gasparik (pers. comm.)
	Alt-Lichtenwarth (1)	Austria	Thenius 1978
	Milia (2)	Greece	Tsoukala&Mol 2016
	Vialette (3)	France	Lortet & Chantre 1878; Koenigswald et al. 2022
	Kaltensundheim (4)	Germany	Koenigswald et al. 2022
	Sülzfeld (5)	Germany	Koenigswald et al. 2022
	Hajnáčka (6)	Slovakia	Schlesinger 1922
	Nova Vieska (7)	Slovakia	Koenigswald et al. 2022
	Strekov (8)	Slovakia	Holec 1985
	Wörth am Rhein (9)	Germany	Koenigswald et al. 2022
	Zalaszentiván (10)	Hungary	Mihály Gasparik (pers. comm.)
	Bács-Bodrog megye (11)	Hungary	Mihály Gasparik (pers. comm.)
	Hidvég (12)	Hungary	Mihály Gasparik (pers. comm.)
	Vác környéke (13)	Hungary	Mihály Gasparik (pers. comm.)
	Söjtör (14)	Hungary	Mihály Gasparik (pers. comm.)
	Usztató (15)	Hungary	Mihály Gasparik (pers. comm.)
	Ajánáskő (16)	Hungary	Mihály Gasparik (pers. comm.)
	Ócsa (17)	Hungary	Gasparik 2010

Tab. 1 - Mammutid molars selected for comparative analysis (1-17, the numbers of the localities in fig. 5).

The evolution of the basin has been controlled by strike-slip faulting related to the neotectonic regime, active from the Early Pliocene to the present (Bedi et al. 2017).

MATERIALS AND METHODS

All specimens were prepared, identified and permanently deposited in the MTA Natural History Museum (Ankara, Turkey).

Upper and lower teeth are indicated by uppercase and lowercase letters, respectively. In the case of mammutids, terminology follows Tobien (1975, 1996) for teeth and Smuts & Bezuidenhout (1993, 1994) and Göhlich (1998) for postcranial remains, while the measurements of teeth and bones were taken according to Göhlich (1998) with digital calipers and recorded to the nearest 0.1 mm. Comparative data were obtained from the existing literature (Table 1). For rhinocerotids, dental terminology follows Heissig (1969, 1972: pl. 13) and Antoine (2002), and postcranial terminology follows Antoine et al. (2010), while measurements follow the protocol of Guérin (1980).

Measurements are provided in mm except when explicitly noted otherwise (H, height; L, length). Hypsodonty index (HI) is the height/anteroposterior length ratio. The Neogene geological time scale and European Land Mammal Ages (Hilgen et al. 2012; Raffi et al. 2020) are used as references for the stratigraphical framework.

SYSTEMATIC PALEONTOLOGY

Order **Proboscidea** Illiger, 1811

Family **Mammutidae** Hay, 1922

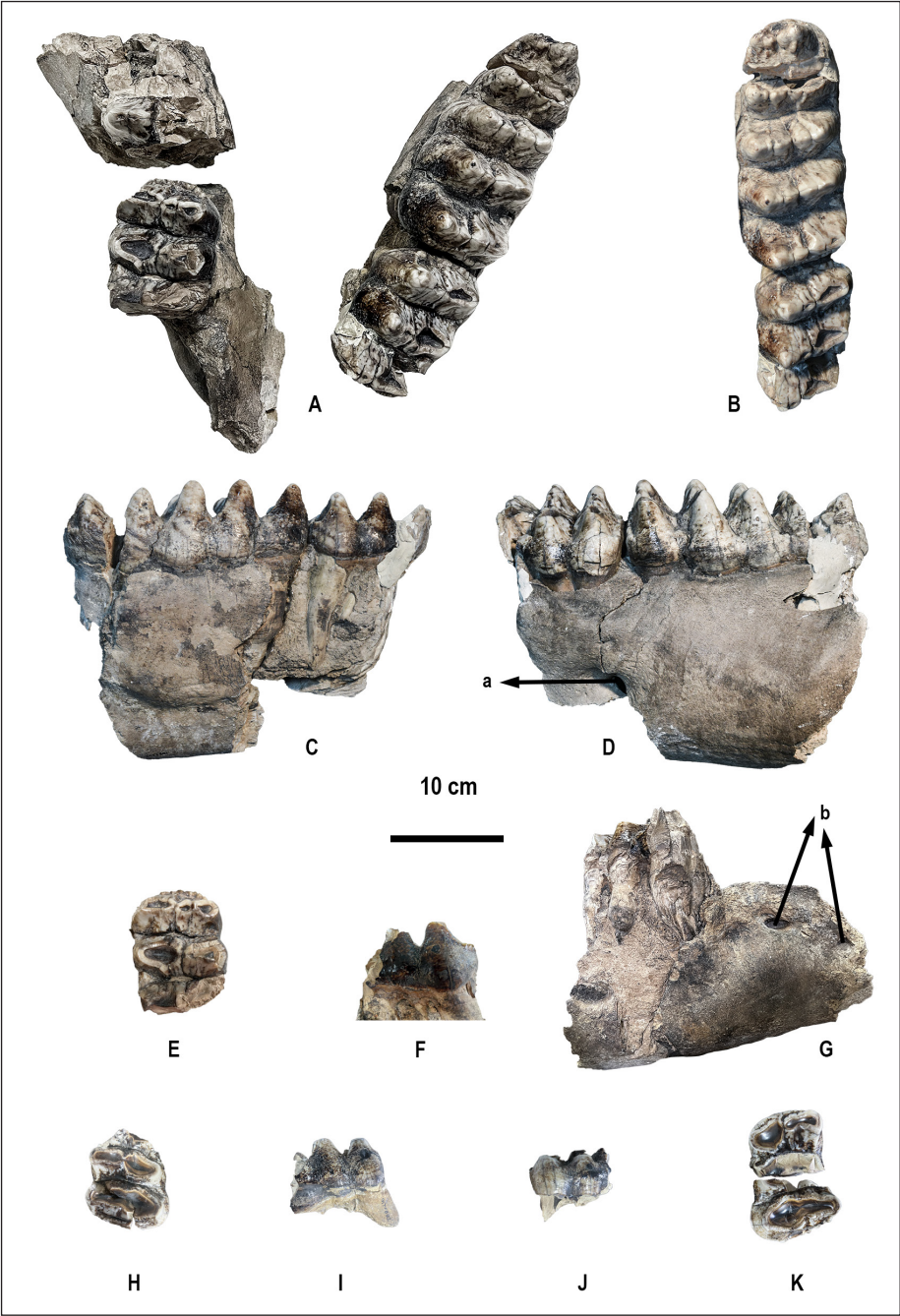
Genus *Mammut* Blumenbach, 1799

"*Mammut*" *borsoni* (Hays, 1834)

Material: Mandible with m2s and m3s (01TFB01), left m2 (01TFB02), right m2 (01TFB03), upper incisor (01TFB04) right unciform (01TFB05), right scapula (01TFB06), right humerus (01TFB07), right femur (01TFB08), right metacarpal (01TFB09).

Description. 01TFB01 (Fig. 3A-G, Tab. 2) is a mandibular fragment with left m2 and m3, right m2 and very small fragment of m3. The mandible comprises both corpuses but the symphysis and

Fig. 3 - “*Mammul*” *borsoni* from Pliocene deposits of Tufanbeyli, Adana, Turkey. A-G) partial mandible with left and right m2s and m3s (01TFB01) in A, occlusal view; B, occlusal view of left m2 and m3; C, lingual view of left m2 and m3; D, buccal view of left m2 and m3; E, occlusal view of right m2; F, lingual view of right m2; G, buccal view of right m2.; H-J) right m2 (01TFB02) in H, occlusal; I, lingual; J, buccal view; K) left m2 (01TFB03), occlusal view; J) fragment of upper tusk (01TFB04). Abbreviations: a, posterior mental foramen b, anterior mental foramen.



Tab. 2 - Measurements of molar teeth of “*Mammul*” *borsoni*. Measures in square brackets are estimates of original values. Abbreviations: L, length; W, width (1-4 are the number of the lophids); H, height. All measurements are in mm.

Specimen	L	Max. W.	W1	W2	W3	W4	H
01TFB01 (m2 / L)	120.8	95.9	[82.4]	94.5	95.9	-	65.9
01TFB01 (m2 / R)	[120.0]	91.3	[81.7]	[91.3]	[91.2]	-	[63.5]
01TFB01 (m3 / R)	216.7	105	100.6	105	100.4	[85.3]	74.5
01TFB02 (m2 / R)	[112.0]	-	90.1	85.6	-	-	-
01TFB03 (m2 / L)	-	-	92.6	-	77.3	-	-

both rami are broken. The m1s were shed before the animal’s death, because the bone surface in front of the right m2 is rough.

Both m2s have three lophids plus posterior cingula and are moderately worn. Median sulci are

distinct and shifted labially. The transverse valleys between lophids are unblocked without any conules. The posterior cingula have crenulations and connect with the 3rd pretrites. The zygodont crests are most visible on the 3rd posttrite half-lophids. On the labi-

Specimen	L (along outer curve)	L (along the inner curve)	Circum. I	Circum. II	Circum. III
01TFB04	119	120	16	38	46

Tab. 3 - Measurements of tusk of “*Mammul borsoni*”. Abbreviations: Circum, circumference. Circum. I is taken from the tip, II is from 60 cm from the tip, III is taken from the root side. All measurements are in cm.

al sides of the transverse valleys, there are small cingula. The left m2 (Fig. 3B-D) is almost complete with small broken parts on the posterior side of the 1st pretrite and lingual side of the 1st posttrite. The 1st anterior crescentoid connects with the anterior cingulum. The posttrite half-lophids are made up with a main cusp and one mesoconelet. The mesoconelets are lower and narrower than the main cusps. Most of the 1st lophid, the tip of the 2nd posttrite and the labial side of the 3rd pretrite of the right m2 are broken (Fig. 3A, E, F). In general, the features are almost the same as the left m2, although the posttrites of right m2 are worn slightly more than the left ones, which express the mode of mastication of this individual. A similar asymmetry is seen in the Kaltensundheim's m2s (Koenigswald et al. 2022).

The left m3 (Fig. 3B-D) has four lophids and a talonid and is almost complete with only a small broken part on the posterior half of the 4th lophid. It is slightly worn only on the anterior and posterior slopes and the tips of the 1st and 2nd pretrites. The pretrite half-lophids consist of a main cone and one mesoconelet. There are one to two mesoconelets on the posttrites. The talonid is developed with one abaxial large tubercule on both the labial and the lingual sides and several smaller tubercules on adaxial side. The median sulcus is distinct and shifted labially and the vertical valleys are open without any conules. The 1st pretrite is connected with the anterior cingulum. Zygodont crests are visible on all posttrite half-lophids. A labial cingulum is present in all pretrite exits of the transverse valleys. An enamel ridge runs down in medial direction on the anterior slopes of the first and the second pretrites. These are the facets formed during the first phase of mastication. In mammutids, during this phase of chewing, the bolus is compressed by closure of the lower jaw mainly in an orthal direction and the lophids of the upper and the lophids of the lower molars intercalate. This phase is very important when the crests of the molars are not blunted and the dentine core is not exposed yet by progressive wear (Laub 1996; Koenigswald 2016; Koenigswald et al. 2022).

The right m3 (Fig. 3A) comprises only a very small fragment of second pretrite. The main cone and the mesoconelet are slightly worn.

Although the mandible is not complete, some features of the corpus can be identified. The posterior mental foramen (PMF) (Fig. 3D) can be seen on the left side of the mandible and anterior mental foramina (AMF) (Fig. 3G) on the right side. Although the ventral part of the corpus is broken, a very large PMF can be identified on the left side positioned below the posterior lophid of the m2, almost in the middle of the corpus. There are two AMFs. Both are at the level of the symphysis and close to the dorsal border of the corpus. The one at the posterior is larger and located just below the bony part in front of the right m2. The anterior AMF is smaller. The mandibular canal can be seen on the right corpus. It is small and displaced posteriorly to the tooth row and lingually to the corpus.

01TFB02 (Fig. 3H-J, Tab. 2) is a fragment of right m2 including the first and second lophids, while third lophid is broken. Tooth is in advanced stage of wear. The anterior cingulum is crenulated. Zygodont crests are visible on both posttrites. A crenulated labial cingulum is seen on the labial side of the transverse valleys. 01TFB03 (Fig. 3K, Tab. 1) is the left m2. It has the first and the third lophid whereas the second lophid is broken. The tooth is in advanced stage of wear given that the first pretrite and posttrite half-lophids are fused. The posterior cingulum is more crenulated on the lingual side and connects with the third pretrite. The anterior cingulum is crenulated and connects with the first pretrite. As 01TFB02 and 01TFB03 were found together at the same place in the field and the stages of wear are nearly the same, they most probably belong to the same individual.

01TFB04 (Fig. 4, Tab. 3) is a fragment of an upper tusk. It is broken from the root and very near the tip. It is dorsally (upwardly) curved without any twist. It has a circular cross section and becomes more oval at the tip. The pulp cavity is closed. There is no enamel band. The tusk and the mandible (01TFB01) belong to the same individual.

01TFB06 (Fig. 5A, B, Tab. 4) is a fragment of a right scapula. It has the glenoid cavity and collum. As this bone is fragmentary and the most describable parts are broken, no detailed identifications could be made.

Specimen	Wc	Wgc
01TFB06	223.5	132.0

Tab. 4 - Measurements of scapula of “*Mammul*” *borsoni*. Abbreviations: Wc, width of collum; Wgc, width of glenoid fossa. All measurements are in mm.

Fig. 4 - “*Mammul*” *borsoni*, fragment of upper tusk (01TFB04) from Tufanbeyli, Adana, Turkey.

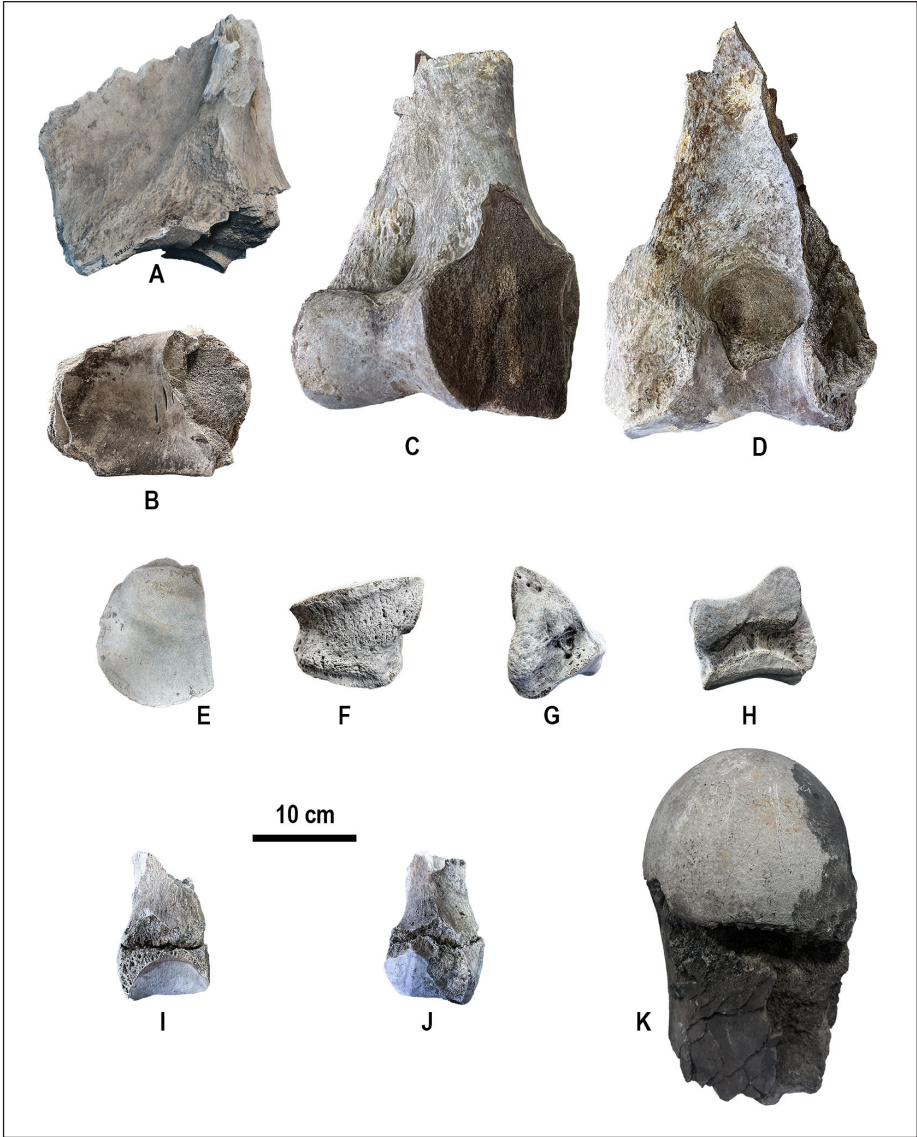
01TFB07 (Fig. 5C, D) is the distal part of a right humerus. The distal epiphysis is fused. The epicondylus lateralis is broken. On the cranial side,

the medial part of the *fossa radialis* is shallow and wide, while the lateral part is small and very deep. On the caudal side, the *fossa olecrani* is large, deep and elliptical. As the bone is broken, only the distal width over the trochlea could be measured (238.8 mm).

01TFB05 (Fig. 5E-H, Tab. 5) is the right unciform (hamatum, carpal [C] IV) with a flat and



Fig. 5 - “*Mammul*” *borsoni* from Tufanbeyli, Adana, Turkey. A-B) right scapula fragment (01TFB06) in A, dorsal; B, distal view; C-D) right humerus fragment (01TFB07) in C, anterior; D, posterior view; E-H) right unciform (01TFB05) in E, dorsal; F, anterior; G, posterior; H, medial view; I-J) right met-carpal (01TFB09) in I, anterior; J, posterior; K, right femur fragment (01TFB08).



	01TFB05
GH	119.1
Hdo	79.7
GD	138.9
GW	125.9
Ddg	146.2
WFp	123
DFp	116.8
HpFm	54.4
DdFm	109.1
WIFd	44.2
DIFd	92.6
WFd	74.1
DFd	104.6
WmFd	35.3
DmFd	105.4

Tab. 5 - Measurements of unciform of “*Mammul*” *borsoni*. Abbreviations: DdFm, depth of proximal medial facet for magnum; Ddg, diagonal width; DFd, depth of distal facet for McIV; DdFm, depth of distal medial facet for McIII; DFp, depth of proximal facet for lunatum and cuneiform; DIFd, depth of lateral distal facet for McV; DmFd, depth of medial distal facet for McIII; GD, greatest depth; GH, greatest height; GW, greatest width; Hdo, dorsal height; HpFm, height of proximal medial facet for magnum; WIFd, width of distal facet for McIV; WFp, width of proximal facet for lunatum and cuneiform; WIFd, width of lateral distal facet for McV; WmFd, width of medial distal facet for McIII. All measurements are in mm.

humerus and unciform were found together at the same place and the stages of epiphyseal fusion are compatible with each other, they presumably belong to the same individual.

01TFB09 (Fig. 5I, J, Tab. 6) is a right metacarpal, probably the third one (McIII), with only its distal half preserved. The distal epiphysis is not fused.

high medial side which is strongly lowering laterally. The posterior side is rugose and triangular in shape with peaks. The proximal surface is almost entirely covered by the articular facet for cuneiform and almost flat anteriorly whereas the posterior part is markedly convex lateromedially and domes towards the palmomedial corner, which is the highest point of the bone. On the distal side there are three articular surfaces for metacarpals (Mc) III, IV and V. On the medial side there are two articular facets for the magnum (CIII), which are closer to each other anteriorly and diverge posteriorly. The proximal facet is larger and higher than the distal one and also noticeably higher at the posterior part and highest at the most posterior point. Both facets are weakly convex in the middle. As the scapula,

Although most part of the shaft is broken, longitudinal crest can be seen on the posterior side. There are protuberances for ligaments on the lateral and medial sides of the distal end of the shaft.

01TFB08 (Fig. 5K) is a fragment of a right femur that consists of the caput and part of the colum. The caput is not fused.

Remarks and Comparisons. The molars of mammutids are distinguished by zygodont cheek teeth, which are characterized by mesoconules lower than the principal conules, mesiodistal narrowing of half-loph(id)s to form transverse crests, presence of posttrite zygodont crests and absence of accessory conules (Tobien 1975, 1996). All these features are functional in vertical shearing (Tobien 1996; Sanders et al. 2010). The typical zygodont characters of Tufanbeyli's molars allow the identification of the teeth as a mammutid.

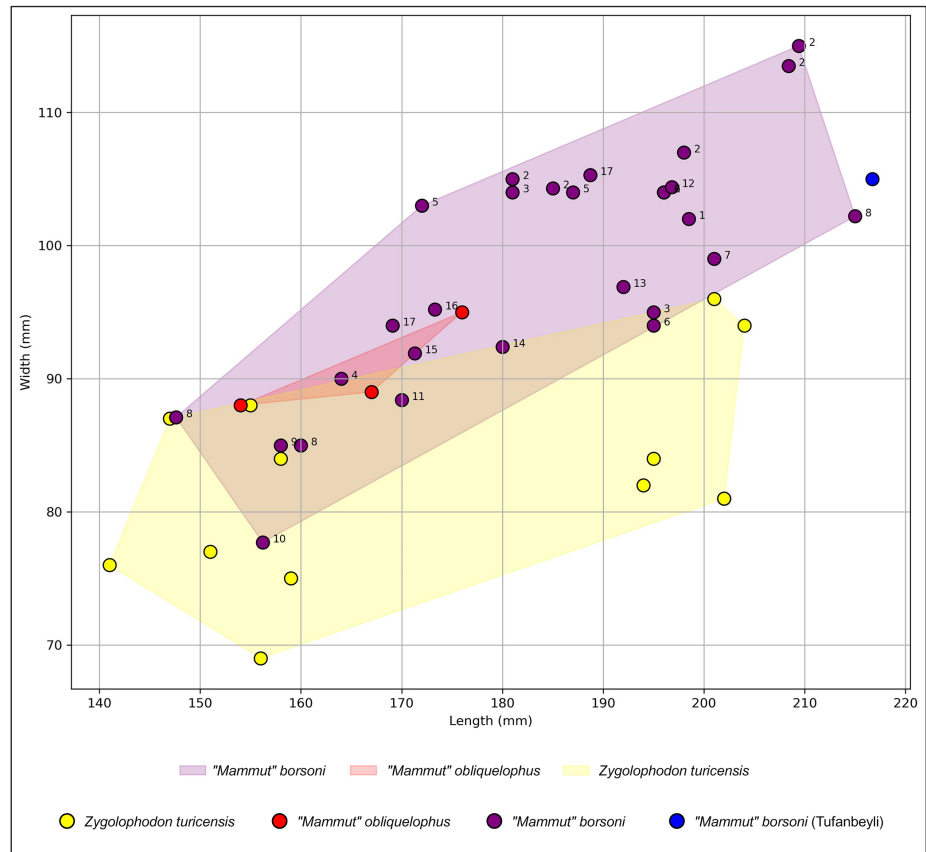
In Europe, two genera of mammutids are documented: *Zygolophodon* and “*Mammul*”. Species of the less derived genus, *Zygolophodon*, display more pronounced bunodont characteristics, with moderately developed pretrite conules that almost block the transverse valleys, and lower crowns in the interlophids. Their upper tusks are curved downward and bear an enamel band on the outer side. In contrast, representatives of the more derived genus, “*Mammul*”, possess strongly developed zygodont cheek teeth due to the absence of conules obstructing the transverse valleys, along with reduced crescentoids, weakened cingula on the m2 and m3, and relatively higher crowns at the base of the interlophids. The upper tusks are straight or curved upward and they lack enamel (Konidaris & Tsoukala 2020; Koenigswald et al. 2022; Konidaris et al. 2024). A well-expressed zygodonty—characterized by the absence of crescentoids and additional conules—along with the high crown at the base of the interlophids and the upward-curved, enamel-less upper tusk, supports the attribution of the Tufanbeyli specimens to “*Mammul*”.

In Eurasia, two species of “*Mammul*” are recorded: the Late Miocene “*Mammul*” *obliqueolophus* and the Pliocene “*M.*” *borsoni*. Both species exhibit nearly identical cheek tooth morphology (Markov 2008;

Specimen	Wd	Dd	WTr
01TFB09	87.7	85.8	73.9

Tab. 6 - Measurements of metacarpal of “*Mammul*” *borsoni*. Abbreviations: Wd, max. distal width; Dd, max. distal depth; WTr, max. width of trochlea. All measurements are in mm.

Fig. 6 - Metric comparison and bivariate plot of length vs. width for m3 of *Zygolophodon turicensis*, “*Mammut*” *obliquephus* and “*Mammut*” *borsoni* from Tufanbeyli and selected localities. For the comparative sample, see Table 1.



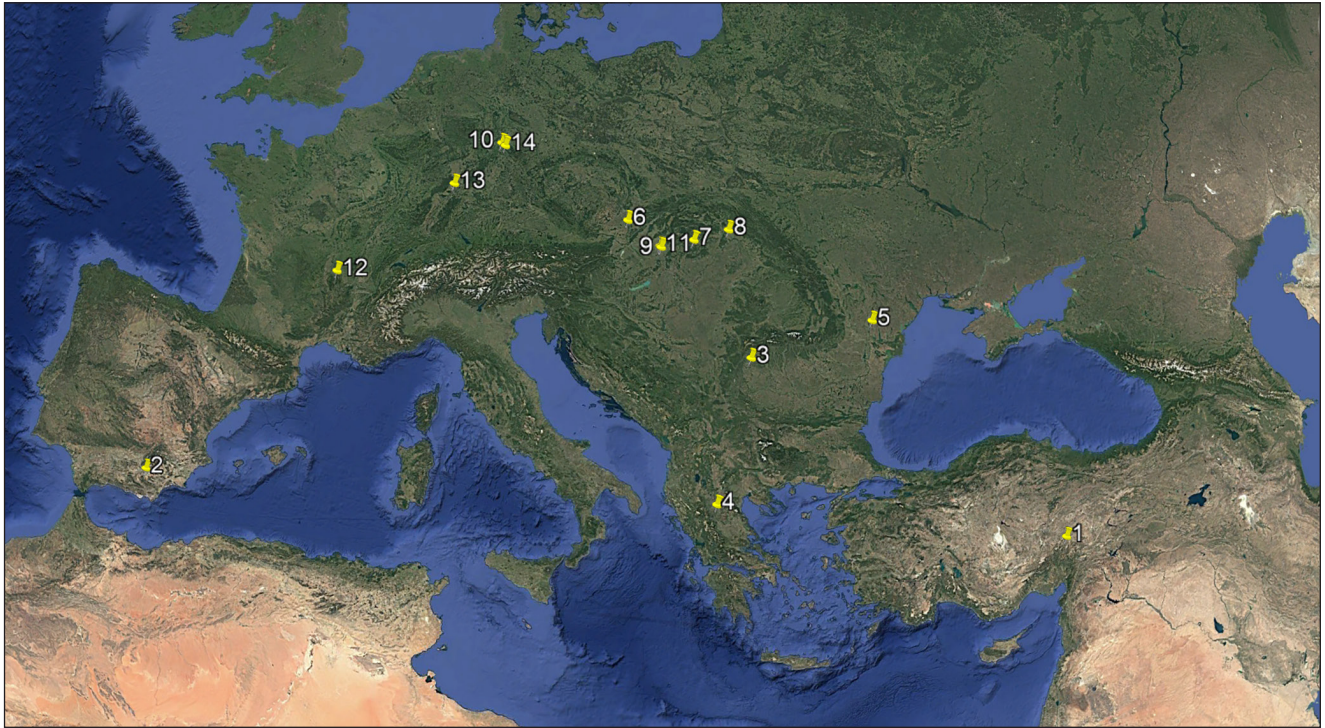


Fig. 7 - Selected Pliocene and Lower Pleistocene localities with “*Mammuth*” *borsoni* in Europe and Anatolia. 1) Tufanbeyli; 2) Baza-1; 3) Husnicioara; 4) Milia; 5) Otman Hill; 6) Alt-Lichtenwarth; 7) Hajnáčka; 8) Kuzmice; 9) Nova Vieska; 10) Kaltensundheim; 11) Strekov; 12) Viallette; 13) Wörth am Rhein; 14) Sülzfeld. Data from Ros-Montoya et al. (2017), Codrea and Diaconu (2007), Tsoukala (2000), Tsoukala and Mol (2016), Obada (2014), Thenius (1978), Schlesinger (1918), Fejfar (1964), Čerňanský (2006), Holec (1996), Koenigswald et al. (2022), Lortet & Chantre (1878), Lacombe et al. (2008). Satellite image from Google Earth.

left m2s (01TFB02, 01TFB03) belong to a second one, while the scapula (01TFB06), the humerus (01TFB07) and the unciform (01TFB05) may belong to a third one. The femur probably belongs to a fourth individual as the fossilization and the stage of epiphyseal fusion are different from those of other specimens.

The PMF and AMF of Tufanbeyli “*M.*” *borsoni* (01TFB01) are well developed as usually seen in non-elephantid elephantoids (Ferretti & Debruyne 2011). The location and the size of the PMF is the same as in Kaltensundheim and Milia’s “*M.*” *borsoni*. In Viallette’s “*M.*” *borsoni*, the PMF is as large as others but

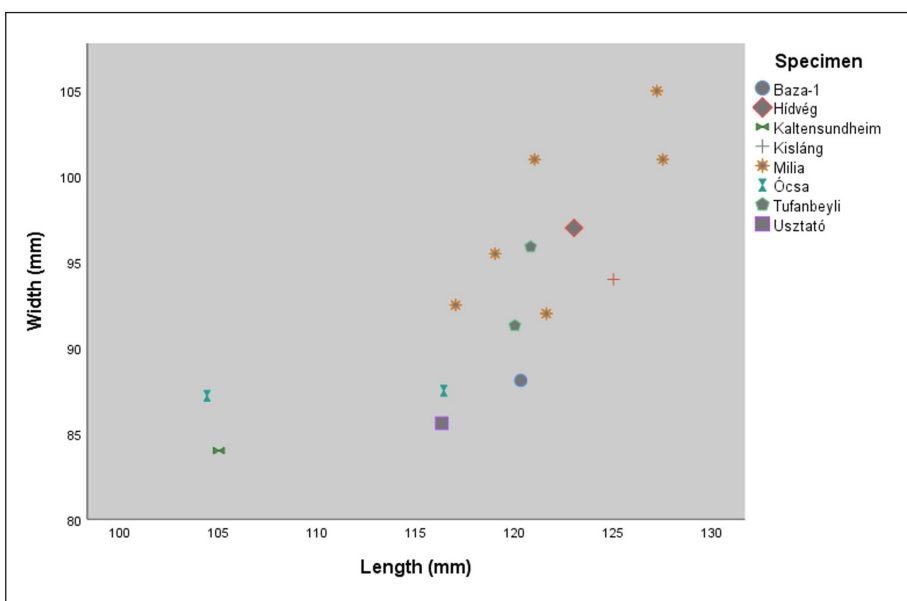


Fig. 8 - Scatter diagram comparing the length and width of m2 of “*Mammuth*” *borsoni* from European sites and Tufanbeyli.

positioned more anteriorly, below the first lophid of m2 (Osborn 1936, fig. 150). A single AMF is present in the “*M.*” *borsoni* specimens from Kaltensundheim and Viallette. In the former, it is positioned below the bony area in front of the m2, while in the latter it is located very anteriorly on the symphysis (Osborn 1936; Koenigswald et al. 2022). Therefore, the number of PMF in the Tufanbeyli “*M.*” *borsoni* mandible is higher.

The humerus from Tufanbeyli has a deeper sagittal sulcus, which separates the trochlea humeri, a significantly deeper fossa radialis and a wider fossa olecrani than in the Kaltensundheim’s and Buesching’s mastodon. On the caudal side, the medial epicondyle is more robust and so the fossa radialis is shifted laterally with respect to the Buesching’s mastodon.

The unciform from Tufanbeyli displays some differences from the Kaltensundheim and Milia specimens. The anterior edge of the proximal surface of the Tufanbeyli’s unciform is more circular in shape. The tubercle at the posterior side is narrower than the others. On the medial side, the distance between the two facets for the magnum of the Tufanbeyli specimen is wider than in the specimens from Kaltensundheim and Milia. Especially in the Kaltensundheim specimen, two facets are almost in contact anteriorly whereas there is a distance at this point in the Tufanbeyli specimen. The distal facet for the McIV is distinctly wider in Tufanbeyli specimen. In comparison with the Buesching mastodon (*M. americanum*), the dorso-medial edge of the unciform is flat in the Tufanbeyli specimen and, on the contrary, it is slightly concave toward the anterior in the Buesching mastodon. On the medial side, the distal facet for the magnum extends nearly the entire length of the medial surface. On the contrary, it is almost half the length in Buesching mastodon.

Due to the very limited availability of post-cranial remains for comparison, it proves difficult to assess if the slight post-cranial differences observed between the Tufanbeyli, Kaltensundheim and Milia mammutids fall within or beyond intraspecific variation.

The femur (01TFB08) belongs to a young individual, as the caput is not fused. According to Hodgson et al. (2008), the proximal epiphysis of the femur fuses between the ages of 25 and 32 in females and after the age of 29 in males of *M. americanum*. Therefore, this individual was probably younger than 25 years old.

Order **Perissodactyla** Owen, 1848

Family Rhinocerotidae Gray, 1821

Genus *Pliorhinus* Pandolfi et al., 2021

Pliorhinus megarhinus (de Christol, 1834)

Material: Left maxillary fragment with P4-M2 (01TFB16), left M3 fragment (01TFB11), left p3 (01TFB10), right m3 (01TFB12), proximal phalanx of a right fourth metatarsal (01TFB14).

Description. On all dental specimens available, enamel is thick (up to ~2 mm), with a wrinkled and corrugated aspect. Teeth are moderately high crowned (HI = 1.16 on the unworn p3). There is neither cement preserved (except at places, on the ectoloph of the upper series 01TFB16), nor any trace of enamel linear hypoplasia.

The most complete and diagnostic specimen is a left maxillary fragment with a P4-M2 series (01TFB16) (Fig. 9A-C). Unfortunately, no cranial feature is preserved and the P4 is damaged anterolabially. The P4 and M1 are worn whereas the M2 is moderately worn. There are no enamel foldings. The lingual roots are separate, with the antero-lingual one being much more developed than the postero-lingual one. The labial cingulum is faint on the P4 and M1, and absent from the M2. On P4, the crochet is hardly discernable, due to wear. The metaloph is complete, without a constriction. It forms a dihedron, with the hypocone being posterior to the metacone. The postfossette is restricted to a small and narrow circular pit. A lingual cingulum is visible, restricted to the antero-lingual angle of the tooth and to the opening of the lingual valley. There is neither antecrochet nor crista or medifossette. The protocone is not constricted. The protocone and the hypocone are connected, forming a lingual bridge with wear. On M1-M2, there is no marked antecrochet, and the crochet is simple and sharp, sagittally oriented. There is no crista or medifossette, but a short and sharp fold in the anterolabial angle of the medial valley of the M2. A faint lingual cingulum is visible in the opening of the valley. The protocone is very thick lingually, as thick on M1 as on M2, without a constriction. The paracone fold is strong but restricted to the apical half of the crown and vanishing towards the neck. The parastyle is short but sharp, anteriorly oriented. There is no metacone fold. The metastyle is long and the metaloph is quite long with respect to the protoloph. The posterior part of the ectoloph is concave in occlusal view.

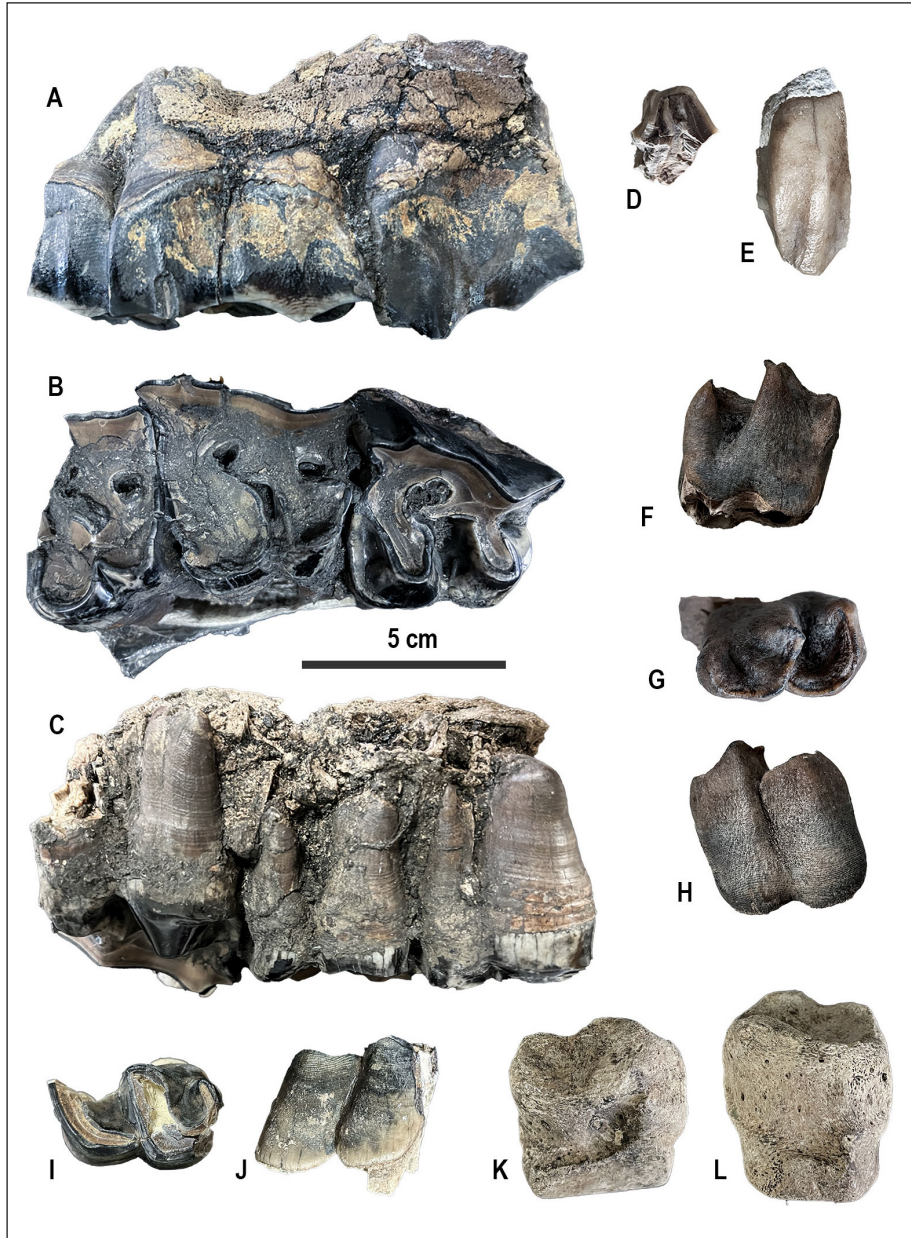


Fig. 9 - *Pliorhinus megarhinus* from Pliocene deposits of Tufanbeyli, Adana, Turkey. A-C) left maxillary fragment with P4-M2 (01TFB16) in A, buccal; B, occlusal; C, lingual view; D-E) left M3 fragment (01TFB11) in D, occlusal; E, lingual; F-H) left p3 (01TFB10) in F, buccal; G, occlusal; H, lingual view; I-J) right m3 (01TFB12) in I, occlusal; J, lingual view; K-L) first phalanx of a right fourth metatarsal (01TFB14) in K, anterior; L, posterior view.

The posterior cingulum is restricted to the entrance of the postfossette and very low. The postfossette becomes particularly narrow with wear. The metaloph is continuous, without a constricted hypocone, at least on the M2 (this area is not visible, covered by matrix, on the M1). The lingual valley is open lingually, much more broadly on M2 than on M1. There is no lingual groove on the protocone of M1 and M2. A very smooth mesostyle is visible on the M2 (absent from the M1). The antecrochet and the hypocone are close but not connected or fused.

An upper cheek tooth fragment (01TFB11) (Fig. 9D, E) is identified as a left M3, due to the acute angle ($\sim 55^\circ$) between the anterior and the labial walls in occlusal view (i.e., pointing to a triangular occlusal

outline). Only the anterolabial part is preserved. It is moderately worn. The parastyle is short and the paracone fold is thick at the top of the crown, and vanishing close to the neck. There is no labial cingulum, but a strong anterior cingulum is partly preserved, ~ 15 mm from the neck.

01TFB10 (Fig. 9F-H) is a fully unworn left p3 ($L=38.5$, $H=44.5$). It has smooth and rounded outlines, both in occlusal and labial views. The enamel displays horizontal incremental lines. There is no lingual or labial cingulum. The anterior and posterior cingula are faint. No vertical rugosities are visible on the ectolophid. The ectolophid groove is shallow, almost vanishing towards the neck, and oblique upward and frontward. The trigonid is higher than the

talonid. In occlusal view, the trigonid and the talonid are rounded. The trigonid forms an obtuse dihedron, with the metaconid being posterior to the protoconid. The posterior wall of the tooth (hypolophid) is transversally oriented. The paraconid is developed, transversally oriented, and not bifurcated. There is a bulbous protoconid fold. The metaconid and the entoconid would be somehow constricted with wear. The lingual opening of the posterior valley is V-shaped in lingual view.

01TFB12 (Fig. 9I, J) is a right m3, with a broken entoconid (preserved antero-posterior $L = \sim 48$). The preserved part is restricted to the trigonid. It is moderately worn, belonging to a young adult ($H = 35.5$). The enamel shows infra-millimetric incremental lines, roughly horizontal. The trigonid valley is much shorter than the talonid valley. In occlusal view, the trigonid is angular, the ectolophid groove is deep (right angle), the metalophid and hypolophid form a $\sim 105^\circ$ dihedron, and the hypolophid is oblique ($\sim 45^\circ$ with the antero-posterior line). In labial view, the ectolophid groove is sigmoid and reaching the neck. In occlusal view, the paralophid is thin and transversely oriented, with a strong wear-facet on its anterior wall. The metaconid is constricted anteriorly and flat lingually. In lingual view, the opening of the trigonid valley is V-shaped and the opening of the anterior valley is much shallower than that of the posterior valley. The anterior cingulum is faint and restricted to a small horizontal ridge, further short transversally. There are neither lingual nor labial cingula. The posterior cingulum is restricted to a narrow and smooth spur, located in the lingual half of the hypolophid.

A proximal lateral phalanx is the only postcranial rhinocerotid element preserved at Tufanbeyli (01TFB14) (Fig. 9K, L). This bone is markedly elevated and exhibits an approximately isometric shape, with proportions resembling a cube. In dorsal view, the biconcave proximal surface (fovea articularis) is partly hidden by a fragment of bone, probably belonging to the distal articulation of the corresponding metapodial. The dorsal outline is heart-shaped, with a shallow posterior groove. The fovea articularis has a similar outline, but with a straight posterior edge. The axial side is marked by a strong dorsal oblique ridge. There is no abaxial counterpart to it. The dorsodistal ridge is very strong, running all over the anterior surface. The plantar ridge is thick and overhanging a deep plantar groove. The distal facet, for

the second phalanx, is flat transversally and smoothly convex antero-posteriorly, with an acuminate abaxial posterior tip. Comparison with the phalanges of extant *Ceratotherium simum* enables its identification as the right proximal phalanx of the fourth metatarsal, given its heart-shaped dorsal outline and acuminate plantar facet.

Comparisons. Comparisons were made with Pliocene–Pleistocene rhinocerotids from the circum-Mediterranean area. All of them belong to the Rhinocerotina, i.e. the clade encompassing all living rhinoceroses (Geraads et al. 2021; Pandolfi et al. 2021; Antoine et al. 2025).

The dimensions of the Tufanbeyli rhinocerotid remains widely exceed those of specimens assigned to the Late Middle Miocene–Holocene *Dicerorhinus* (see Guérin 1980 for *Dicerorhinus sumatrensis*; Antoine et al. 2022). Moreover, in terms of morphology, they are distinct from the latter in having a long metaloph, a concave posterior half of the ectoloph, a low and interrupted posterior cingulum, and a V-shaped lingual opening of the posterior valley on M1–M2 (Pandolfi et al. 2021; Antoine et al. 2022). They differ from the Late Miocene–Late Pliocene representatives of *Dibopius* in possessing a lingual bridge on P4 and a concave posterior half of the ectoloph on M1–M2 (Pandolfi et al. 2020, 2021). Finally, an assignment to the latest Miocene–Early Pleistocene *Stephanorhinus* can also be ruled out, as the Tufanbeyli rhinocerotid does not have a medifossette on P4, but a strong paracone fold on M1–M2, an angular trigonid on the lower cheek teeth, and an oblique hypolophid on lower molars (Fortelius et al. 1993; Lacombe & Mörs 2008; Pandolfi et al. 2017, 2021).

Conversely, the described remains display several diagnostic traits of the latest Miocene–Late Pliocene *Pliorhinus* species, such as the constriction of the protocone usually absent from P3–P4, the posterior part of the ectoloph concave on M1–M2, or the angular trigonid on lower cheek teeth (Pandolfi et al. 2021). The Late Pliocene *Pliorhinus miguelsfonti* (Guérin & Santafé-Llopis 1978) is diagnosed by dental features such as wrinkled enamel, a protocone always present on M1–M2, a postfossette wide on upper premolars, a protocone and a hypocone always separated on P4, and a labial cingulum always absent on upper molars. All these characters are lacking in the Tufanbeyli rhinocerotid, which discounts an assignment to this species. On the other hand, the specimens here described have a lingual bridge but

		P4	M1	M2	p3	p4
<i>Pliorhinus</i>	L	-	50.8	52.6	34.3	43.2
<i>megarhinus</i>	Want	-	61.8	60.0	20.8	30.6
(Tufanbeyli)	Wpost	55.6	53.8	45.8	23.5	-
	H	-	30.8	41.4	38.8	34.6
<i>Pliorhinus megarhinus</i>	L	43-57 [29] 47.26	47.5-64 [24] 55.56	50.5-65.5 [24] 60.21	35-47 [34] 40.36	37.5-48 [31] 43.56
(other localities)	Want	52.5-67 [41] 58.56	54-70 [32] 62.38	57-73 [38] 65.71	-	-
	Wpost	-	-	-	22-31.5 [41] 26.71	27.5-38 [39] 31.63
	H	50 [1]	52 [1]	53-56.5 [3] 55	40-43 [4] 41.75	44.5 [1]
<i>Pliorhinus miguelsafonti</i>	L	-	55.5 [1]	56.5 [1]		36-36.5 [2] 36.25
	Want	-	60			-
	Wpost	-	57			25-28.5 [2] 26.75
	H	-	-		44.5	-
<i>Stephanorhinus etruscus</i>	L	37-49 [13] 41.89	41-54 [16] 48.59	45.5-57 [13] 50.34	31.5-37.5 [15] 34.63	37-42.5 [15] 39.26
(other localities)	Want	45-63 [25] 54.82	48-60.5 [26] 55.36	48.-65.5 [21] 57.02	-	22-31 [15] 27.46
	Wpost	-	-	-	21.5-29 [19] 23.55	-
	H	-	54 [1]	52.5 [1]	-	35-41.5 [2] 38.25

Tab. 7 - Dental dimensions of *Pliorhinus megarhinus* (Mammalia, Perissodactyla) from Tufanbeyli, Pliocene, Turkey and other localities (Guérin, 1980). Comparison with dental dimensions of *Pliorhinus miguelsafonti* from Layna, Spain (type locality; Guérin, 1980). Size ranges matching the Tufanbeyli specimens are bold-typed. Number of specimens is detailed between square brackets and *Stephanorhinus etruscus* from various localities (Guérin, 1980). Abbreviations: ant, anterior; H, height (of unworn teeth for other localities, if available); L, length; post, posterior; W, width. All measurements are in mm.

no antecrochet on P4, which are two diagnostic features of *Pliorhinus megarhinus* (de Christol, 1834) from the latest Miocene–Early Pliocene of the Western Mediterranean (see Pandolfi et al. 2015, 2021). Other characters, such as the presence of a labial cingulum on P4–M2, the absence of a crista and a medifossette from M1–M2, and the absence of a lingual cingulum from the lower molars are compatible with the variability range of *P. megarhinus* (see Pandolfi et al. 2021). The dental dimensions of the Tufanbeyli material further match this taxonomic assignment (Tab. 7; e.g., Guérin et al. 1969; Guérin & Santafé-Llopis 1978; Pandolfi et al. 2015, 2021). The presence of an anterior constriction on the M1 hypocone, considered as diagnostic of *P. megarhinus* by Pandolfi et al. (2021), cannot be assessed on the P4–M1 series from Tufanbeyli. In any event, this constriction is also absent from at least four M1 and M2 from the type locality of *P. megarhinus* ('Sables de Montpellier'). Some other peculiar features of *P. megarhinus* are retrieved on the Tufanbeyli specimens, such as the short enamel process at the anterolabial corner of the median valley of M2 and the bulbous protoconid fold on p3.

DISCUSSION

This bispecific assemblage, further restricted to two megaherbivores, does not allow us to provide

a refined age for Tufanbeyli. Nevertheless, some elements can be discussed in terms of biochronology, particularly on the basis of occurrence-based databases, such as Rhino Resource Center database (Geraads et al. 2021) and the NOW database (The NOW Community 2024; Tab. S1).

Both taxa are conspicuous elements of Pliocene assemblages from Europe and the Eastern Mediterranean (e.g., Geraads et al. 2021). "*Mammuth borsoni*" reached its peak occurrence during the Pliocene (Tobien 1996; Tsoukala & Mol 2016; Koenigswald et al. 2022), whereas the acme of *Pliorhinus megarhinus* spans the Early Pliocene (MN14–MN15; Fig. 10; Pandolfi et al. 2015, 2021). "*Mammuth borsoni*" is known from the Ruscinian to early Villafranchian (MN14–MN16) of Europe and Asia. Its presence during the middle Villafranchian (MNQ17) in Europe, however, remains uncertain based on the current fossil record (Konidaris & Tsoukala 2022). Moreover, the taxonomic revision of *Pliorhinus* by Pandolfi et al. (2021), based on direct examination of the type and referred material of both species, raised some doubts about the persistence of *P. megarhinus* in the Late Pliocene, as it seems to be replaced by its sister taxon *P. miguelsafonti*, at least in all localities where the concerned material could be revised properly. As a consequence, even in the absence of associated micromammals likely to refine its biochronological age, Tufanbeyli is considered to have

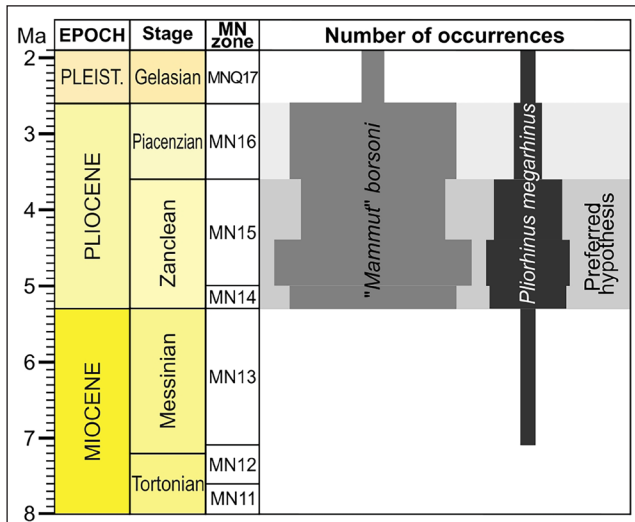


Fig. 10 - Stratigraphical ranges and number of occurrences of “*Mammut*” *borsoni* and *Pliorhinus megarhinus*. Occurrences and ages are based on NOW Community database (2024) and on Geraads et al. (2021), respectively.

an Early Pliocene age (Zanclean, MN14–MN15; Fig. 8) (Yusufoğlu 2022).

In Anatolia, *P. megarhinus* had been previously described at Çalta 2 (MN15; Guérin & Şen 1998) and listed at Gülyazı (MN16; Sickenberg et al. 1975). Both localities have yielded diverse mammalian assemblages, with ~30 taxa in each. The big-nosed rhino counts among the three taxa shared at the species level between these localities. The material from Gülyazı could not be analyzed for the current work, so its referral to *P. megarhinus* cannot be confirmed. In any event, Tufanbeyli represents one of the very few occurrences of this large rhinocerotine in Anatolia.

In Europe, “*M.*” *borsoni* is often found in association with the gomphotheriid *Anancus arvernensis*, notably at several localities of the Triversa Faunal Unit in Italy, such as Umbria, Piedmont and Santa Croce (Azzaroli 1983; Argenti 2004; Masini & Sala 2007; Petronio et al. 2011), as well as at Sülzfeld (Kahlke et al. 1984), Milia (Tsoukala & Mol 2016), Viallette (Lacombat et al. 2008) and Kisláng and Ócsa (Gasparik 2010). In Turkey, *A. arvernensis* has been identified at several Pliocene localities, such as Gülyazı (MN16b) and Yukarısöğütözü (MN17) (Sickenberg et al. 1975; Gaziry 1976; Saraç 2003; Mayda et al. 2014;). However, no proboscidean remains have been uncovered at Çalta 2 (MN15).

The present study documents one of the easternmost occurrences of “*M.*” *borsoni* in the circum-Mediterranean region and the first record

from Asia Minor. This finding further supports the close biogeographical affinities between Anatolia and other circum-Mediterranean regions following the end of the MSC, by Early Pliocene times.

CONCLUSION

The Eastern Mediterranean region suffers from a lack of available fossiliferous localities dating back to the Pliocene, and more specifically documenting the Ruscinian stage (Early Pliocene). The situation is even more pronounced in Anatolia, especially when it comes to large mammals. Accordingly, the discovery of an assemblage comprising the huge mammutid “*M.*” *borsoni* and the large two-horned rhinocerotine *P. megarhinus* at Tufanbeyli represents an important advancement in our knowledge of the large mammal faunas of the Early Pliocene of Asia Minor. This eastern occurrence of “*M.*” *borsoni* further attests to close biogeographical affinities between Anatolia and other circum-Mediterranean regions after the end of the MSC.

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