

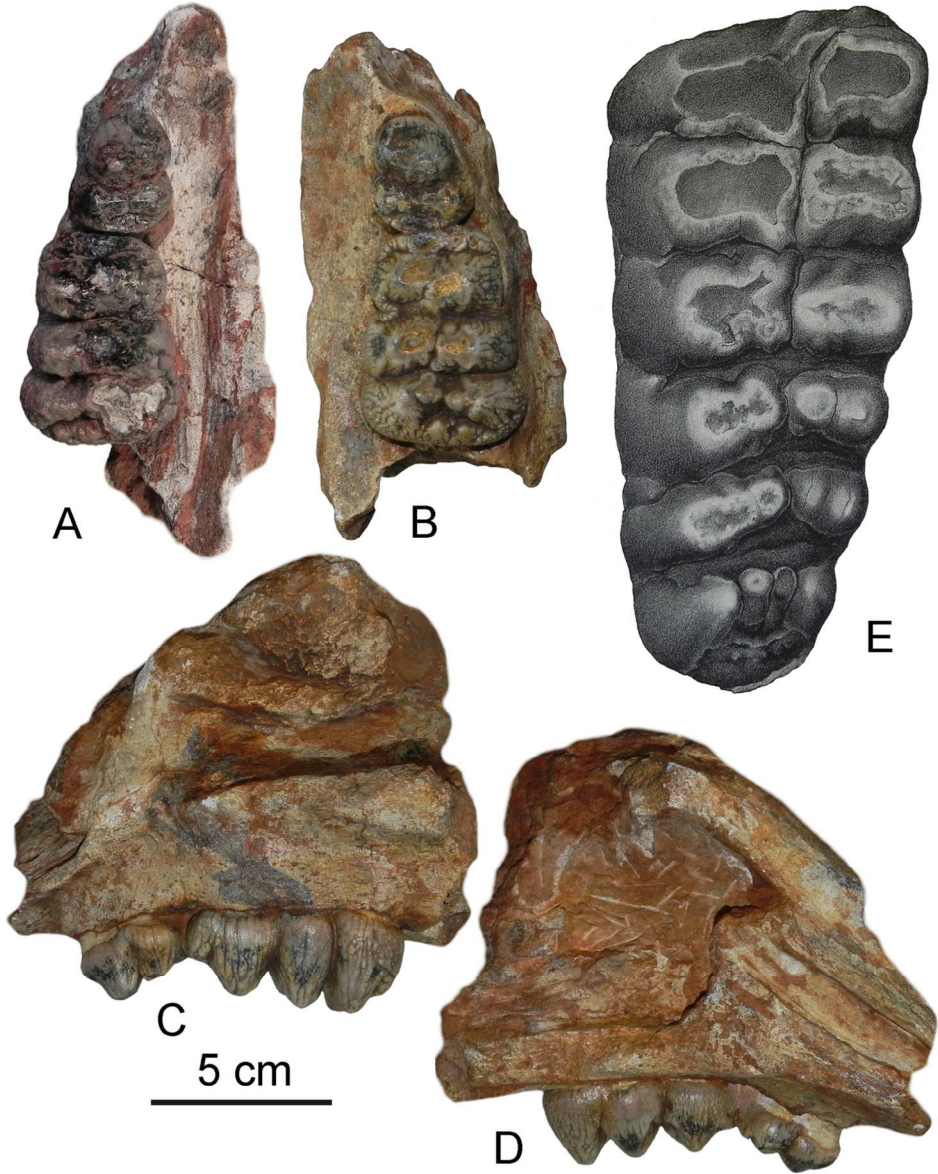
The Eurasian occurrence of the shovel-tusker *Konobelodon* (Mammalia, Proboscidea) as illuminated by its presence in the late Miocene of Pikermi (Greece)

Journal:	<i>Journal of Vertebrate Paleontology</i>
Manuscript ID:	JVP-2013-0131.R2
Manuscript Type:	Article
Date Submitted by the Author:	15-Nov-2013
Complete List of Authors:	Konidaris, George; Aristotle University of Thessaloniki, Geology Roussiakis, Socrates; University of Athens, Historical Geology and Paleontology Theodorou, George; University of Athens, Historical Geology and Paleontology Koufos, George; Aristotle University of Thessaloniki, Geology
Key Words:	Proboscidea, Greece, <i>Konobelodon</i> , late Miocene, taxonomy, biostratigraphy, paleogeography

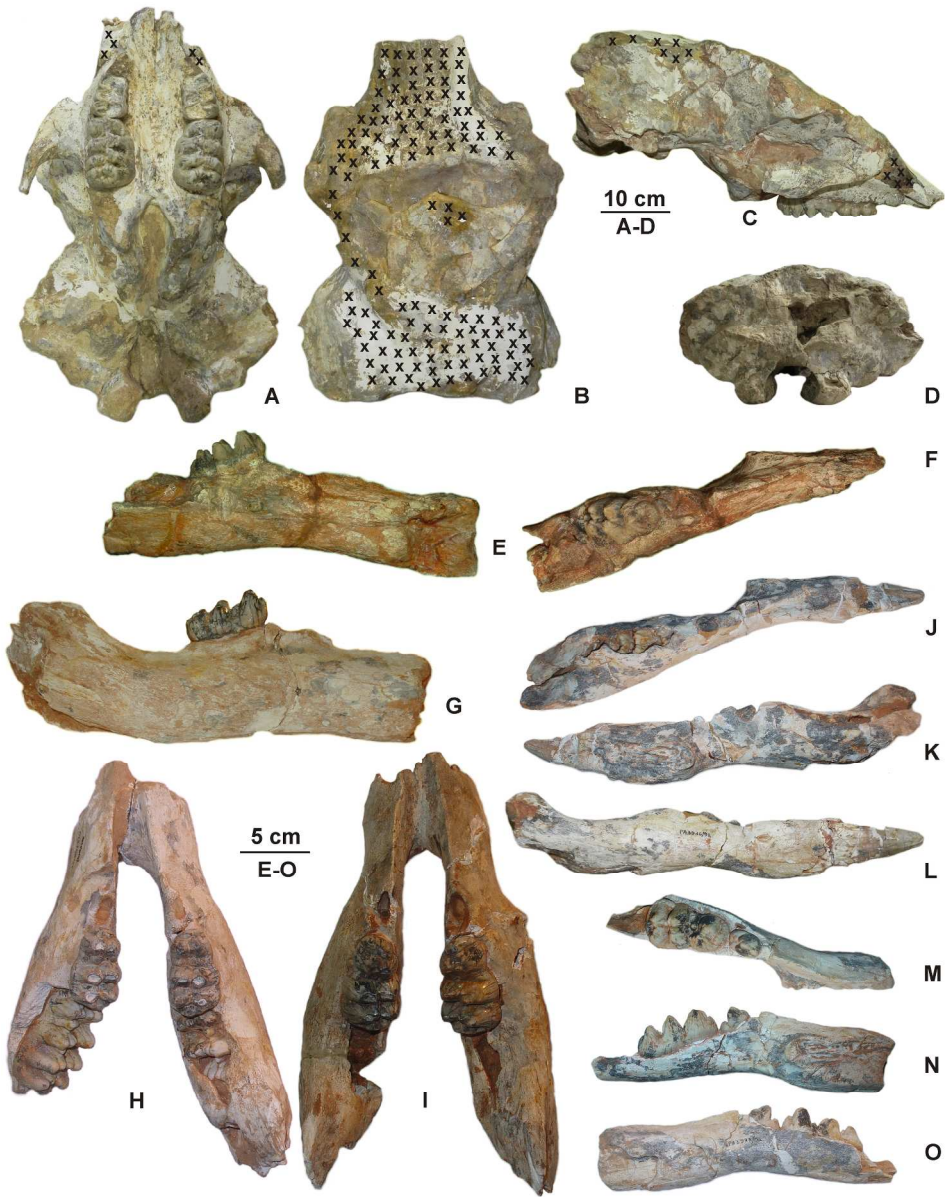
SCHOLARONE™
Manuscripts



180x177mm (300 x 300 DPI)



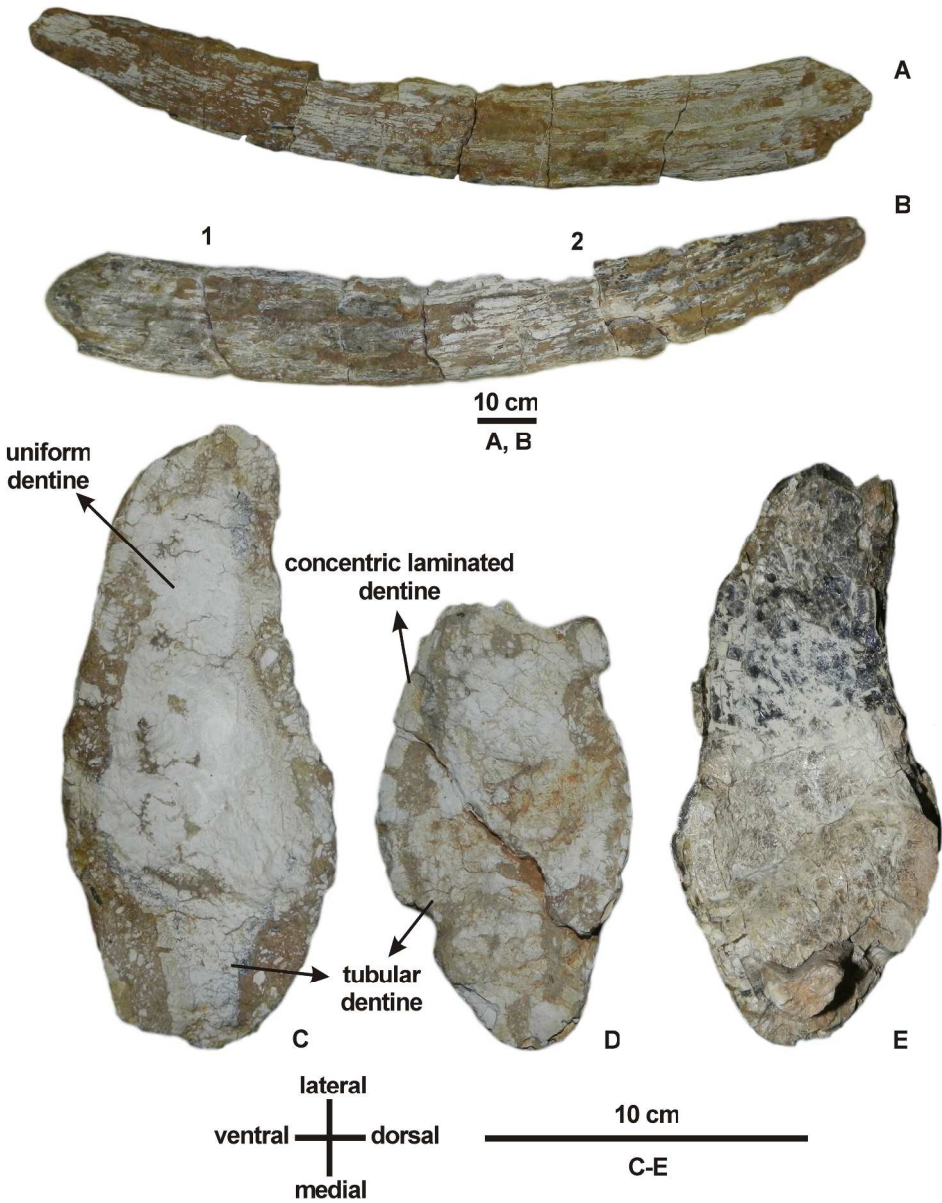
114x145mm (300 x 300 DPI)



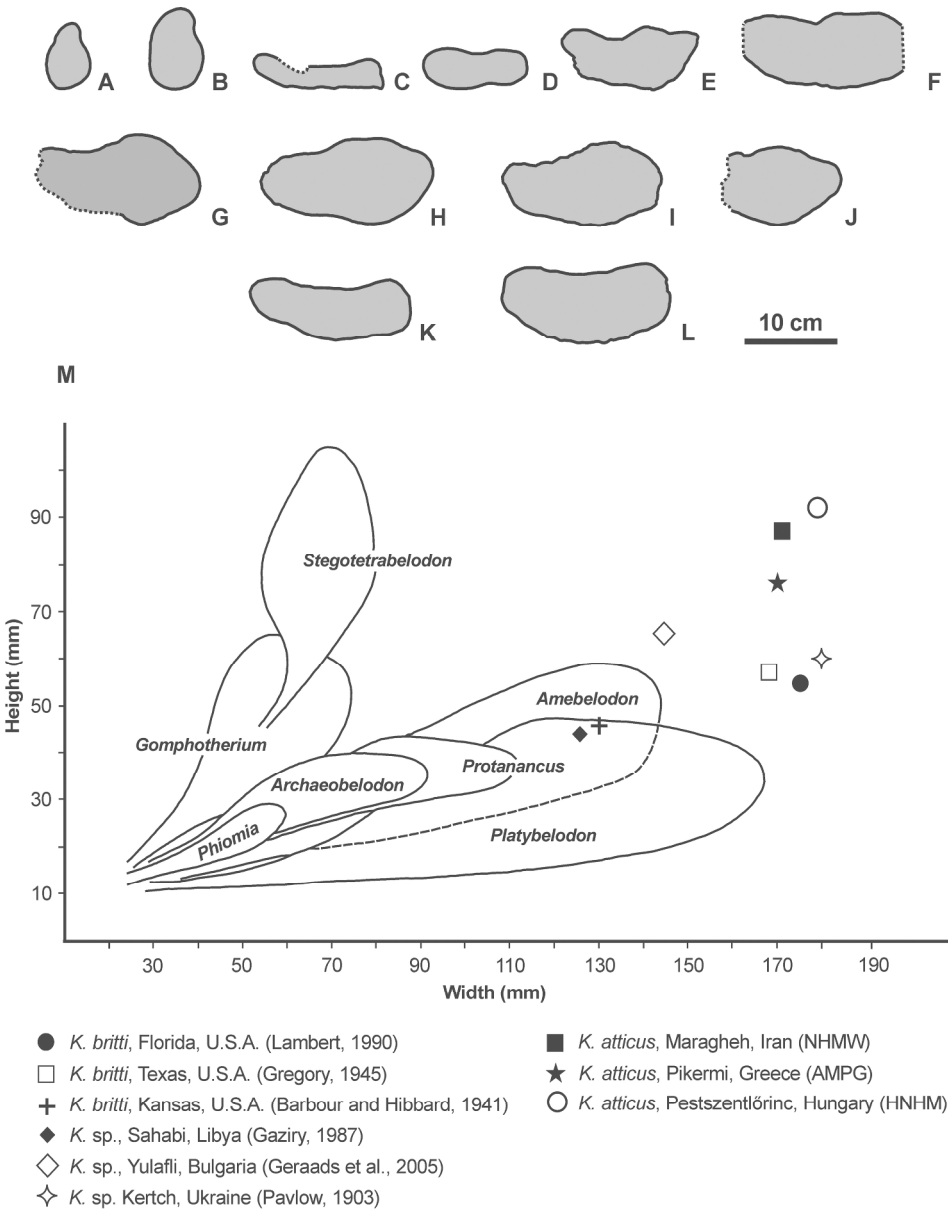
232x296mm (300 x 300 DPI)



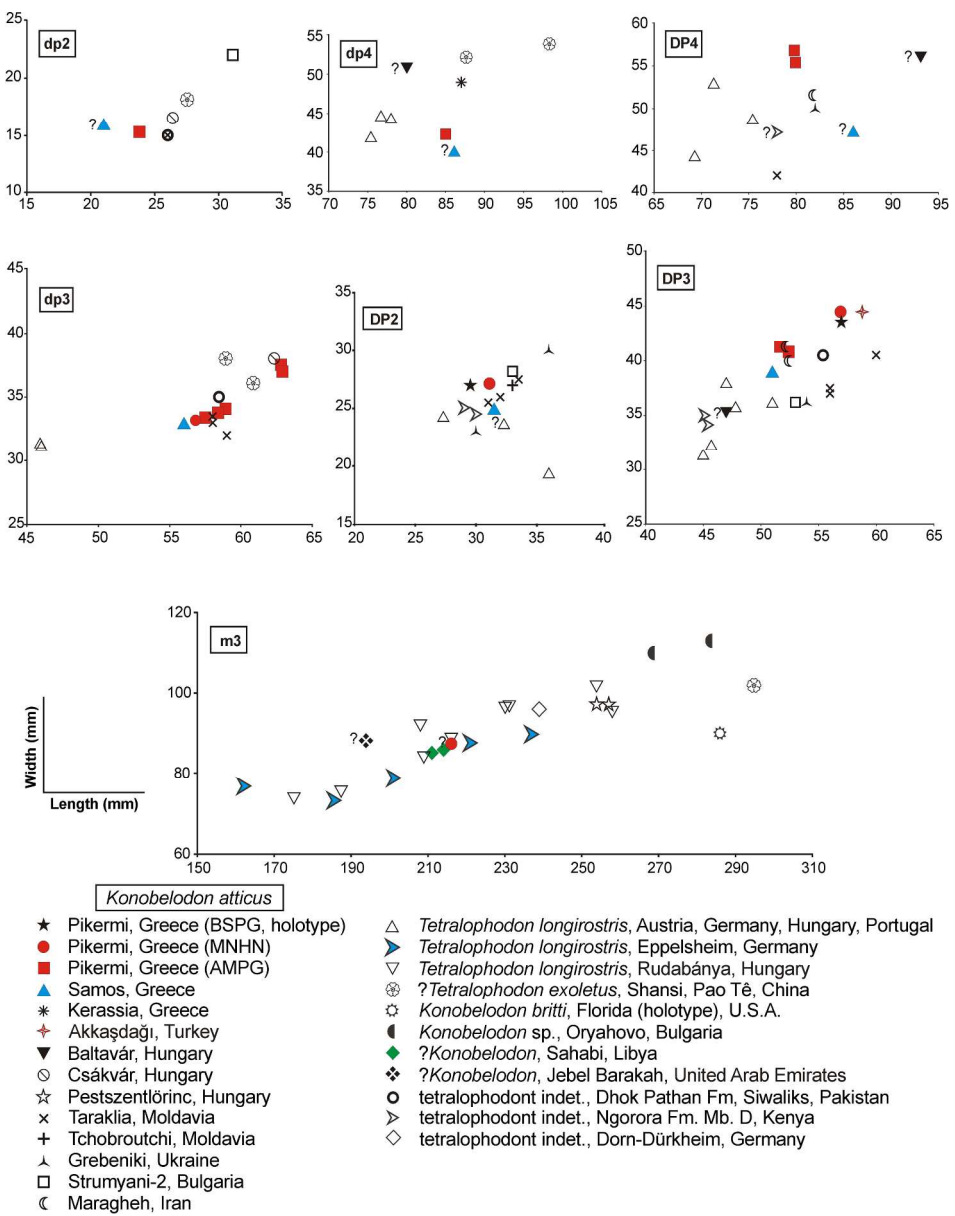
232x296mm (300 x 300 DPI)



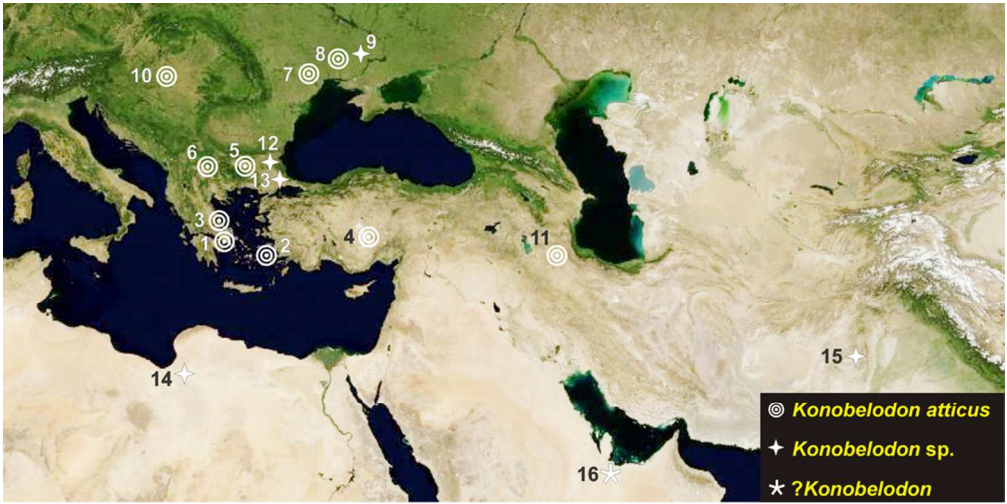
232x296mm (300 x 300 DPI)



232x296mm (300 x 300 DPI)



232x296mm (300 x 300 DPI)



91x45mm (300 x 300 DPI)

TABLE 1. Cranial and mandibular measurements (in mm) of *Konobelodon atticus* from Pikermi (AMPG). The numbers in the first column correspond to the measurements used by Tassy (1996b:figs. 11.1, 11.2). Measurements in parentheses represent the greatest measureable value of the parameter.

	Skull	Mandibles			
	PA3933/91	PA3935/91	PA3708/91	PA3936/91	PA3937/91
1	(500)	(290)	(290)	(299)	(217)
2	240	(58)	(58)	—	(82)
3	—	177	186	—	—
4	—	(230)	(240)	—	—
5	—	(165)	—	—	—
6	330	163	—	—	—
7	160	53	60	53	—
8	—	30	37	26	21
9	—	85	—	—	—
10	200	(72)	—	—	—
11	220	86	—	—	—
12	(500)	(72)	—	—	—
13	300	31	—	—	—
14	120	21	—	—	—
15	145	36	—	—	—
16	280	68	73	44	45
17	90	57	60	—	—

18	—	57	62	41	45
TABLE 1. (Continued)					
19	(285)	(55)	(67)	—	—
20	58	—	—	—	—
21	75	—	—	—	—
22	155	—	—	—	—
23	70	—	—	—	—
24	—	105	110	—	—
25	140				
26	350				
29	50				
30	75				
31	185				
32	245				
34	150				

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

TABLE 2. Dental measurements (in mm) of *Konobelodon atticus* from Pikermi (AMPG, BSPG, MNHN). **Abbreviations:** **L**, length; **W**, width; **H**, height; **HI**, hypsodonty index ($H \times 100/W$); **C**, circumference. Measurements in parentheses represent the greatest measureable value of the parameter.

Specimen	Tooth		L	W	H	HI	C	Remarks
AMPG PA3929/91	i1	right	100	44.6	16.7		33.0	
AMPG PA3936/91	i1	right	(87)	24.2	12.2			30 mm from tip
idem	idem	idem		37.0	13.5			cross section at symphysis
AMPG PA3937/91	i1	left	—	32.0	11.3			cross section at symphysis
AMPG PA1972/61	i1	right	1400					
idem	idem	idem		170	76		410	1st cross-section: 320 mm from base
idem	idem	idem		159	73		400	2nd cross-section: 540 mm from base
idem	idem	idem		(153)	75		(380)	3rd cross-section: 670 mm from base
idem	idem	idem		(126)	80		(340)	4th cross-section: 950 mm from base
idem	idem	idem		(138)	73		(350)	5th cross-section: 1100 mm from base
AMPG PA3937/91	dp2	left	23.8	15.3	16.0	104.6		
MNHN PIK-1704	dp3	right	56.8	33.2	24.9	75.0		
AMPG PA3708/91	dp3	right	58.4	33.8	22.8	67.5		

idem dp3 left 57.5 33.4 24.6 73.7

TABLE 2. (Continued)

AMPG PA3935/91	dp3	right	62.9	37.0	26.0	70.3
idem	dp3	left	62.8	37.5	27	72.0
AMPG PA3937/91	dp3	left	58.9	34.1	25.5	74.8
AMPG PA3708/91	dp4	left	85.0	42.3	41.0	96.9
BSPG AS II 182	DP2	left	29.5	27.0	17.0	63.0
MNHN PIK-1704	DP2	right	31.1	27.2	18.8	69.1
BSPG AS II 182	DP3	left	57.0	43.6	27.0	61.9
MNHN PIK-1704	DP3	right	56.9	44.5	29.2	65.6
AMPG PA3933/91	DP3	right	52.4	40.8	—	—
idem	DP3	left	51.7	41.3	—	—
AMPG PA3933/91	DP4	right	79.8	56.8	35.5	62.5
idem	DP4	left	79.9	55.4	37.0	66.8

The Eurasian occurrence of the shovel-tusker *Konobelodon* (Mammalia, Proboscidea)
as illuminated by its presence in the late Miocene of Pikermi (Greece)

GEORGE E. KONIDARIS,^{*1} SOCRATES J. ROUSSIAKIS,² GEORGE E.
THEODOROU,² and GEORGE D. KOUFOS¹

¹Aristotle University of Thessaloniki, Department of Geology, Laboratory of Geology
and Paleontology, 54124 Thessaloniki, Greece, geo.konidaris@gmail.com;
koufos@geo.auth.gr;

²National and Kapodistrian University of Athens, Faculty of Geology and
Geoenvironment, Department of Historical Geology and Paleontology,
Panepistimiopolis, 15784 Athens, Greece; srousiak@geol.uoa.gr;
gtheodor@geol.uoa.gr

*Corresponding author.

Formatted: Not Superscript/ Subscript

RH: KONIDARIS ET AL.—THE EURASIAN OCCURRENCE OF
KONOBELODON

1
2
3
4
5
6 ABSTRACT—Presented here are the tetralophodont proboscidean remains from the
7
8 late Miocene locality Pikermi (Attica, Greece). The study of the Pikermi
9
10 tetralophodonts and their comparison with other relevant specimens revealed that the
11
12 late Miocene species ‘*Tetralophodon*’ *atticus* and ‘*Mastodon*’ *grandincisivus* are
13
14 synonymous. The morphological characters of the Pikermi specimens, as well as of
15
16 those attributed to ‘*Mastodon*’ *grandincisivus*, are consistent with the North American
17
18 shovel-tusker *Amebelodon* (*Konobelodon*). However, an upgrading of *Konobelodon* at
19
20 generic rank is deemed appropriate. The observed differences between the type
21
22 species *Konobelodon britti* and the Pikermi tetralophodont indicate that the latter
23
24 belongs to a distinct species, *Konobelodon atticus*. This species encompasses the
25
26 Turolian tetralophodont shovel-tusked from eastern Europe–western Asia. The
27
28 paleogeographic distribution and biostratigraphy of *Konobelodon atticus* are
29
30 discussed, as well as the evolution and the possible migrational scenarios of
31
32 *Konobelodon*.

INTRODUCTION

The fossiliferous locality of Pikermi, near Athens (Fig. 1), became known in the 19th century, when a rich fauna was discovered and described (Wagner, 1839; Roth and Wagner, 1854; Gaudry, 1862–67). Several excavations carried out in Pikermi (mainly during the 19th and early 20th century) yielded an abundance of fossils, dispersed in several European museums and institutes. This has marked ~~out~~ Pikermi as one of the most famous late Miocene localities of Eurasia. The Pikermi fauna includes a great number of mammalian taxa, as well as some reptiles and birds. However, its age remains unclear because the various Pikermian museum collections are mixed. Early authors noticed that the fossils in Pikermi were collected along a ravine in two or three locally occurring stratigraphic levels from multiple quarries (Gaudry, 1855:896, 1862–67:14; Woodward, 1901:482–483; Abel, 1922:fig. 132). Unfortunately, the exact stratigraphic provenance of the specimens ~~unearthed~~ is not specified in the relevant museum collections or publications. Consequently, the faunal content of each fossiliferous level is unknown and most Pikermian museum collections do not represent a taxonomically and chronologically homogeneous fauna. As already mentioned by Theodorou et al. (2010), the old Pikermian museum collections could represent a rather homogeneous paleocommunity only if the sedimentation and fossil accumulation had been rapid, lasting a few thousand years. Despite these impediments, the Pikermi fauna collectively is correlated to the end of the middle Turolian with an age of ~7.1 Ma (Koufos, 2006, 2009 and ref. cited). Since 2008, paleontological excavations in Pikermi, carried out by the University of Athens, led to the discovery of the new site “Pikermi Valley-1”, 500 m east-southeast of the classical Pikermi locality, as well as of various other fossiliferous sites in the Pikermi

ravine (Theodorou et al., 2010). Further research in these new sites will certainly generate more data and help to clarify the local biostratigraphy.

The Pikermi locality has yielded quite a few proboscidian -specimens. A recent revision of the Pikermi proboscideans by Konidaris (2013) suggests the presence of *Deinotherium gigantissimum* Stefanescu, 1892 (= *Deinotherium proavum*), ‘*Mammut*’ sp., *Choerolophodon pentelici* (Gaudry and Lartet, 1856), as well as the presence of a tetralophodont elephantoid. The latter was referred under various names; most commonly as *Tetralophodon atticus* (Wagner, 1857). The main aim of this article is to describe, compare, and discuss the taxonomy and paleogeography of this tetralophodont proboscidean from Pikermi.

MATERIAL AND METHODS

The material studied here includes the Pikermian collections housed at AMPG, BSPG and MNHN. Comparative material has been studied at HGI, HNHN, MNHN, NHMW, NMNH and SU. For the description of the skull and mandibular specimens we generally use comparative anatomical terminology, following Barone (1999) and I.C.V.G.A.N. (2005), opting for the English equivalents of the Latin terms. In dental terminology we follow Tassy (1996a). We use the uppercase letters DP and M to indicate the upper deciduous premolars and molars, respectively, and the lowercase letters dp and m to indicate the corresponding lower teeth. For the cranial and mandibular measurements we follow Tassy (1996b). For the cheek teeth, the dimensions measured are the maximal mesiodistal diameter (length) and the maximal labiolingual diameter (width), as well as the maximal height of the crown. For the tusks, we measured the maximal length from the base to the tip in straight line. At

Formatted: Indent: First line: 0.2"

various cross-sections across each tusk’s length, we also measured the dorsoventral diameter (height), the mediolateral diameter (width) and the circumference. We took the measurements with calipers or, in the case of large measurements, with measuring tape. All measurements are given in mm. ~~For~~ incomplete or inadequately preserved specimens, we provide measurements in parentheses to indicate the greatest measurable value of a parameter. Measurements are given in Table 1 and Table 2.

Institutional Abbreviations—**AMPG**, Athens Museum of Paleontology and Geology, Athens (Greece); **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, München (Germany); **HGI**, Hungarian Geological Institute, Budapest (Hungary); **HNHM**, Hungarian Natural History Museum, Budapest (Hungary); **MNHN**, Muséum National d’Histoire Naturelle, Paris (France); **NHMW**, Naturhistorisches Museum Wien (Austria); **NMNH**, National Museum of Natural History, Sofia (Bulgaria); **SU**, Paleontological Museum of the Sofia University (Bulgaria).

Anatomical Abbreviations—**apocc2**, anterior posttrite central conule of the second lophid; **aprcc1, 2, 3**, anterior pretrite central conule of the first, second, third loph(id), respectively; **ppocc1, 2**, posterior posttrite central conule of the first and second loph, respectively; **pprcc1, 2**, posterior pretrite central conule of the first and second lophid, respectively.

SYSTEMATIC PALEONTOLOGY

Order PROBOSCIDEA Illiger, 1811

Superfamily ELEPHANTOIDEA Gray, 1821

Family GOMPHOTHERIIDAE Hay, 1922

Subfamily AMEBELODONTINAE Barbour, 1927

Genus *KONOBELODON* Lambert, 1990

Diagnosis—Tetralophodont second molar; third molars with six well-developed lophids; permanent lower tusks with tubular internal dentine; dentinal tubes with distinctive morphology, relatively narrow, structurally distinct near proximal end of the tusk, expanding and tending to merge towards distal end (Lambert, 1990).

Type Species—*Konobelodon britti* Lambert, 1990, Moss Acres Racetrack site, Florida, U.S.A.

KONOBELODON ATTICUS (Wagner, 1857)

(Figs. 2–5)

Mastodon atticus Wagner, 1857:140, pl. 5, fig. 16.*Mastodon longirostris* Kaup, 1832: Lartet, 1859:497.*Mastodon pentelici* Gaudry and Lartet, 1856: Gaudry, 1862–67:142, pl. 23, figs. 2–4.*Mastodon longirostris* Kaup, 1832: Vacek, 1877:32, pl. 7, figs. 1, 1a.*Mastodon longirostris* Kaup, 1832: Pavlow, 1914a:35, pl. 7, figs. 1, 2.*Mastodon pentelici* Gaudry and Lartet, 1856: Pavlow, 1914a:36, pl. 7, fig. 3.*Mastodon longirostris* Kaup, 1832: Pavlow, 1914b:184, pl. 8, figs. 15, 15a.

Mastodon longirostris Kaup, 1832: Khomenko, 1914:43, pl. 1, figs. 11–14.

Mastodon (Bunolophodon) longirostre Kaup, 1832: Schlesinger, 1917:77, pl. 11, fig. 1, 2; pl. 14, fig. 4.

Mastodon (Bunolophodon) grandincisivum Schlesinger, 1917:119, pl. 34, figs. 1, 2.

Mastodon (Bunolophodon) grandincisivus Schlesinger, 1917: Schlesinger, 1922:7, pl. 2, figs. 1–3; pl. 3, figs. 1–7; pl. 4, figs. 1–3; pl. 5, figs. 2–5; pl. 6, fig. 1.

Mastodon (Bunolophodon) longirostris Kaup, 1832: Schlesinger, 1922:45, pl. 8, figs. 2–9.

Mastodon pentelici Gaudry and Lartet, 1856: Mecquenem, 1924:137, pl. 1, figs. 6, 9.

Mastodon longirostris Kaup, 1832: Riabinin, 1929:115, pl. 6, fig. 2; pl. 11, figs. 1–2.

Turicius atticus (Wagner, 1857): Osborn, 1936:220, fig. 164.

Tetralophodon grandincisivus (Schlesinger, 1917): Osborn, 1936:360, figs. 317, 321.

Mastodon longirostris Kaup, 1832: Simionescu and Barbu, 1939:1, pl. 1, figs. 1–6.

Mastodon longirostris Kaup, 1832: Burchak-Abramovich, 1940:28, figs. 1, 3, 4.

Mastodon longirostris Kaup, 1832: Lehmann, 1950:208, pl. 22, fig. 108.

Bunolophodon longirostris (Kaup, 1832): Garevski, 1976:25, figs. 1, 2.

Stegotetrabelodon grandincisivus (Schlesinger, 1917): Tobien, 1978:177.

Amebelodontidae gen. indet. *grandincisivus* Schlesinger, 1917: Tassy, 1985: 560, fig. 228.

Tetralophodon atticus (Wagner, 1857): Tassy, 1985:742, figs. 181g, 293a, b.

Tetralophodon longirostris (Kaup, 1832): Korotkevich, 1988:pl. 25, fig. 1.

Tetralophodon cf. *longirostris* (Kaup, 1832): Theodorou, Athanassiou, Roussiakis, and Iliopoulos, 2003:523.

Stegotetrabelodon grandincisivus (Schlesinger, 1917): Kovachev, 2004:169, pl. 1, figs. 1–3; pl. 2, figs. 1, 2.

“*Tetralophodon*” *atticus* (Wagner, 1857): Tassy, 2005:711, fig. 7.

?*Tetralophodon atticus* (Wagner, 1857): Geraads, Spassov, Hristova, Markov, and Tzankov: 2011:455, fig. 3a–c.

Holotype—Part of left maxilla preserving the DP2–DP3, BSPG AS II 182 (Fig. 2B–D).

Type Locality—Pikermi, Attica, Greece.

Age—Middle Turolian, MN 12 (late Miocene).

Diagnosis—Amebelodontine with tetralophodont intermediate molars and trilophodont dp3/DP3. Third deciduous upper premolar with enlarged third loph and posttrite-pretrite connection in both transverse valleys. Intermediate molars and m3/M3 with trefoil patterns in pretrite half-loph(id)s, which diminish towards the distal part of the tooth; weaker posttrite trefoils in anterior half-loph(id)s; possible presence of accessory cusplets; relatively high loph(id)s. Third lower molar with six lophids. Third upper molar with five lophs. Possible alternating contact in posterior loph(id)s of molars. Cementodonty. Adult lower tusks very large in size; protruding beyond the rostrum; bearing longitudinal furrows dorsally and ventrally; with flattened cross-section, thin concentric laminated dentine layer externally and tubular dentine internally. Upper adult tusks large, lacking enamel band. Anterior zygomatic process strong, situated ventrally at the dentary level. Rostral margin of choanae just behind dentition. Orbital fossa situated above last molar in function. Nasal cavity wide. Occipital low and wide. Mandible with long and high symphysis.

Differential Diagnosis—Differs from the type species *Konobelodon britti* Lambert, 1990, by the presence of an external laminated dentine layer in the lower tusks and by the tetralophodont structure in the DP4.

Referred Specimens—Juvenile skull preserving the DP3–DP4 of both sides, AMPG PA3933/91; right maxilla with DP2–DP3, MNHN PIK-1704a; right mandible with dp3, MNHN PIK-1704b; partial mandible preserving the dp3 of both sides, AMPG PA3935/91; partial mandible preserving the dp3–dp4 of both sides, AMPG PA3708/91; right mandibular fragment preserving the juvenile permanent lower tusk (i1) and the dp2–dp3, AMPG PA3936/91; left mandibular fragment preserving part of the juvenile permanent lower tusk (i1) and the dp2–dp3, AMPG PA3937/91; right adult lower tusk (i1), AMPG PA1972/61; right juvenile permanent lower tusk (i1), AMPG PA3929/91. The specimens MNHN PIK-1704a and MNHN PIK-1704b probably belong to the same individual (Gaudry, 1862–67:146).

Description

All studied cranial and mandibular Pikermi specimens (AMPG, BSPG, MNHN) represent juvenile individuals. All available cheek teeth are deciduous. Following Tassy (1987) and Delmer (2009), we consider the available lower tusks to be permanent (i1), representing either ontogenetically juvenile or adult individuals.

Skull—The only available skull from Pikermi (AMPG PA3933/91) is that of a juvenile individual (Fig. 3A–D). It lacks parts of the maxillary and premaxillary bones, and the rostral part of the nasal area. The zygomatic arches are partially preserved. The dorsal part of the skull, especially the nasal and parietal area, is partly restored with plaster. The occipital is low and wide with protruded exoccipitals (Fig. 3D). The occipital condyles are strong and the foramen magnum large. The basicranium is poorly preserved. The choanae are wide and deep; their rostral margin terminates at the level of the distal border of DP4 (Fig. 3A). The nasal cavity is well defined, wide and deep. The orbital fossa is above the DP4 and the infraorbital

foramen opens above the DP3. The anterior zygomatic process is strong and wide, expanding from the level of the distal half of DP3 to the mesial half of DP4. The parietal area is wide and flat.

Mandible—The available mandibular specimens do not preserve the rami. The specimens AMPG PA3708/91 and AMPG PA3935/91 preserve adequately the mandibular angle, which seems to be obtuse (Fig. 3G). In all specimens (Fig. 3E–O) the symphysis is robust (even in specimens representing very young individuals, e.g., Fig. 3J–O), high (the height is equal or slightly smaller than that of the mandibular corpus) and slightly deflected ventrally and outward. In AMPG PA3936/91 and AMPG PA3937/91 the mental foramen is ~35 mm in front of the dp2.

Upper Deciduous Dentition—The DP2 consists of two lophs; the second one is the widest (Fig. 2A–D). It has strong mesiolingual and distal cingula, as well as a weak lingual one. The paracone is the strongest cusp. The lophs are separated by an open transverse valley. The second loph consists of the hypocone, the metacone and the mesoconelets; the half-lophs are separated by a median sulcus.

The DP3 consists of three lophs; the third one is the widest (Figs. 2A–D, 4P). The lophs are divided by a median sulcus into half-lophs. The mesial cingulum consists of a series of cusplets and is connected to the first pretrite half-loph. The first and second pretrite half-lophs are located slightly mesially relative to the posttrite ones, especially in the first loph. The ppoc1 and aprcc2 in the first transverse valley are connected, and so are the ppoc2 and aprcc3 in the second transverse valley. The third pretrite and posttrite half-lophs are opposite each other. The enamel is rugose.

The DP4 consists of four lophs (Fig. 4Q). The lophs are quite high and the crown in the interlophs is higher lingually. The mesial lophs are partially worn and the dentine is exposed. The first and second pretrite half-lophs have a trefoil pattern.

Posttrite, the main cusps are accompanied by two–three mesoconelets and the transverse valleys are open. The third posttrite half-loph bears three–four mesoconelets. In the left DP4 of AMPG PA3933/91 these are equally high and aligned, whereas in the right DP4 of the same specimen they decrease in height and are directed distally to connect to the fourth pretrite half-loph. The fourth loph is simple and curved slightly convex mesially. The enamel is rugose.

Lower Deciduous Dentition—The dp2 consists of two lophids; the mesial one is clearly higher than the distal one (Figs. 3M–O, 4K). There is a weak mesial cingulum, consisting of two cusplets; the stronger one is appressed on the protoconid and the weaker one on the metaconid. The protoconid and metaconid are almost equal in height and appressed to each other; their apices are well-distinguished and have each of them a posterior central conule. The transverse valley is open. The entoconid and hypoconid are clearly separated; the latter has an equally high posterior central conule, which is connected to the distal cingulum. The distal cingulum consists of two cusplets located in the middle of the distal margin of the tooth.

The dp3 consists of three lophids and is wider in its distal part (Fig. 4L–O). The mesial cingulum consists of a series of cusplets, which decrease in size towards the labial side; in the more worn specimens only the stronger lingual cusplets are visible. The first lophid is oriented in a mesiolabial to distolingual direction and bears anterior and posterior pretrite and posttrite central conules appressed to the main cuspids. In the first transverse valley of AMPG PA3708/91, PA3936/91 and PA3937/91 there is a low but strong pretrite cusplet, which can be considered a central conule (Fig. 4N, O); the right dp3 of AMPG PA3708/91, in particular, also has a posttrite conule (Figs. 3H, 4O). In specimens AMPG PA3935/91 and MNHN PIK-1704b the pprcc1 and apocc2 are connected (Fig. 4L, M). Unlike the first lophid, the second has mesiolingual to

distolabial direction. In the second transverse valley the pprcc2 and aprcc3 are connected. The stronger cusplets of the distal cingulum are located in the middle. The distal cingulum continues along the labial wall of the third lophid and reaches the second transverse valley. The enamel is rugose.

The dp4 AMPG PA3708/91 is totally unworn; it was not erupted, but part of the mandibular bone was removed to reveal its morphology. It consists of four rather high lophids and has mesial and distal cingula (Figs. 3H, 4R–T). The mesial cingulum consists of a series of cusplets; the three stronger ones are located in the middle. The main cusps of each lophid are almost opposite each other. The posttrite half-lophids bear one strong mesoconelet. The pretrite half-lophids bear two mesoconelets; the more labial one is the strongest. The first half-lophid is slightly more complicated with accessory cusplets and rugose enamel. The transverse valleys are lingually open. In the first and second transverse valley there is a very weak aprcc and a strong pprcc, which close these valleys labially; the pprcc1 is stronger than the pprcc2. The third transverse valley has no central conules. The mesoconelets of the fourth lophid are set mesially relative to the main cusps. The distal cingulum consists of three cusplets.

Lower Permanent Tusks—The juvenile permanent lower tusks (Fig. 4A–J) are flattened and bear a very thin enamel layer with longitudinal furrows dorsally and ventrally. A series of buds is developed on the mesiolateral side of AMPG PA3936/91 and AMPG PA3929/91, which are better observable in the latter (Fig. 4A–C, H–J). The emerging lower tusk of AMPG PA3936/91 belongs to a very young individual; however, it is strong and with oblique mediolateral axis (Fig. 3J–L). The cross-section is flattened pyriform in AMPG PA3929/91, whereas in AMPG PA3936/91 and AMPG PA3937/91 it is convex ventrally and concave dorsally. The core of the tusk consists of dentinal tubules, which are clearly visible in AMPG PA3929/91 (Fig. 4G).

The adult lower tusk AMPG PA1972/61 lacks a small part of its tip and the external dentine layer in several parts along it (Fig. 5A–D). It is dorsoventrally flattened with pyriform cross-section, it curves slightly outwards and it bears a longitudinal dorsal concavity. The tusk consists of a core of uniform or tubular dentine, which is surrounded by a thin layer of concentric laminated dentine. In the basal part of the tusk the dentine is mainly uniform, whereas toward the apical part it becomes gradually more tubular (Fig. 5C–D).

COMPARISONS

Tetralophodons were early recognized in Pikermi when Wagner (1857) described them as ‘*Mastodon atticus* G. & L.’. Note that, Wagner (1857) attributed ‘*Mastodon atticus*’ to Gaudry and Lartet (1856), but, as noted by Gaudry (1862–67:142 footnote), the only bunodont proboscidean referred by Gaudry and Lartet (1856:273) was the trilophodont ‘*Mastodon*’ *pentelicus*, a species that was later attributed to *Choerolophodon*. Subsequently, Lartet (1859) transferred the Pikermi tetralophodons to ‘*Mastodon*’ *longirostris* (= *Tetralophodon longirostris*). Gaudry (1862–67) included all bunodont proboscideans from Pikermi (tri- and tetralophodons) to ‘*Mastodon*’ *pentelici*. A few years later, Vacek (1877:32, pl. 7) attributed a third molar from Pikermi to ‘*Mastodon*’ *longirostris*, although in the corresponding plate it was figured as ‘*Mastodon*’ *atticus*. This tooth was later transferred to ‘*Stegotetralodon grandincisivus*’ by Tobien (1978). The tetralophodont material of Wagner (1857) and Gaudry (1862–67), as well as that described by the latter author as ‘*Mastodon turicensis*’, was included in the zygodont taxon ‘*Turicius atticus*’ by Osborn (1936). More recently, Tassy (1985) referred the tetralophodons of Pikermi to

Tetralophodon atticus, although he subsequently questioned this generic attribution (Tassy, 2005). Tetralophodons are also known from the late Miocene of Samos Island (Greece) and they are referred either to '*Tetralophodon longirostris*' or to '*Stegotetralophodon grandincisivus*' (Lehmann, 1950; Solounias, 1981; Bernor et al. 1996). Recently, Konidaris and Koufos (2013) mentioned the possible presence of '*Tetralophodon*' *atticus* in the old Samos material. Therefore, it is obvious that the taxonomy of the tetralophodons is problematic; various authors have provided various different taxonomic interpretations. This has partly resulted from the fact that early collections do not provide any or adequate stratigraphic information for the provenance of the material; the relative material is mostly fragmentary and scarce and the specimens are distributed in many museums and institutes all over the world, which does not facilitate their study.

The single adult lower tusk from Pikermi differs from *Tetralophodon* in that it is definitely larger in size, with a flattened cross-section and an internal structure with dentinal rods (Fig. 6A, B, I, J). Therefore, the Pikermi tetralophodont material is clearly different from *Tetralophodon*. Moreover, compared to the type species *T. longirostris*, the deciduous premolars from Pikermi are larger in size (Fig. 7), the DP3 bears an enlarged third loph with marked second entoflexus, as well as a well-expressed ectoflexus (Figs. 2A–B, 4P) and the available mandibles have a longer and higher symphysis (Fig. 3E–O) in regard to the mandibles of *T. longirostris* of similar ontogenetic age described by Vacek (1877:pl. 1, fig.1; pl. 2, fig. 1) and Klähn (1931:pl. 1, fig. 1).

The strong and well-developed mandibular symphysis and the strong, flattened and shovel-like lower tusks from Pikermi indicate that they belong to an amebelodon (Tobien, 1973; Göhlich, 1999). The amebelodons (the name consists of three Greek

words: ἄμη = shovel, βέλος = arrow and οδούς = tooth) is a group of bunodont, predominant trilophodont gomphotheres, commonly called ‘shovel-tuskers’ (Göhlich, 1999). They are considered either a separate family, Amebelodontidae, or a subfamily of the Gomphotheriidae, Amebelodontinae (Tassy, 1996c; Shoshani, 1996); the second view was recently followed (Shoshani and Tassy, 2005; Sanders et al. 2010). Based on the internal structure of the lower tusks, two groups of amebelodontines can be distinguished: one with only concentric laminated dentine and another with presence of tubular dentine (dentinal rods). The former includes the genera *Progomphotherium*, *Archaeobelodon*, *Afromastodon*, *Protanancus*, *Amebelodon* and *Serbelodon*, and the latter only the genus *Platybelodon* (Tassy, 1986, 1996c; Sanders et al., 2010). The lower tusks from Pikermi with the tubular internal dentine structure belong to the second group. However, they differ from *Platybelodon* in that they have a less dorsoventrally flattened cross-section and less expressed tubular dentine structure (Osborn and Granger, 1931; Maglio, 1969; Gaziry, 1976) (Fig. 6C, I, J). The compression index ($\text{height} \times 100 \div \text{width}$) is ~ 47 in the studied adult tusk versus 16–34 in *Platybelodon* (Guan, 1996).

Another elephantoid, the tetralophodont ‘*Mastodon*’ *grandincisivus* is also included in the amebelodonts, due to the shape and structure of the lower tusks (Tassy, 1985, 1999, 2005). ‘*Mastodon*’ *grandincisivus* is known from eastern Europe (Bulgaria, Hungary, Ukraine), western Asia (Turkey, Iran) and from Siwaliks, Pakistan (Pavlow, 1903; Schlesinger, 1922; Bakalov and Nikolov, 1962; Tassy, 1983a, 1999; Geraads et al., 2005; Markov, 2008). The species *Amebelodon cyrenaicus* Gaziry, 1987 from Sahabi (Libya) is considered a junior synonym of ‘*Mastodon*’ *grandincisivus* (Tassy, 1999, 2003). The holotype of ‘*Mastodon*’ *grandincisivus* is from Maragheh (Iran) and corresponds to a large and dorsoventrally

flattened lower tusk fragment with pyriform cross-section, tubular internal dentine structure and thin concentric laminated dentine layer peripherally (Fig. 5E). These features are fully consistent with those of the Pikermi adult lower tusk (AMPG PA1972/61). Mecquenem (1924) described some deciduous teeth from Maragheh as ‘*Mastodon pentelici*’; however, the presence of three lophs in the DP3s (MNHN MAR-930, 935) and four in the DP4 (MNHN MAR-4009) suggests a tetralophodont form with similarities to ‘*Tetralophodon*’ *atticus*. Thus, these specimens were subsequently included to this latter species by Markov (2008). Nevertheless, the existence of *T. atticus* in Maragheh was recognized quite early, earlier even than the definition of the holotype of ‘*Mastodon*’ *grandincisivus*. Kittl (1886) referred a specimen from Maragheh to ‘*Mastodon*’ sp. Schlesinger (1917:98) mentioned that this specimen was labelled ‘*Mastodon atticus* Wagn.²²’; despite this, he referred it to ‘*Mastodon* (*Bunolophodon*) *longirostre*’. A rich sample from Pestszentlörinc (Hungary), including upper and lower tusks, mandibular fragments, and third upper and lower molars (HNHM V.79.34), was determined as ‘*Mastodon grandincisivus*’ by Schlesinger (1922). The lower tusks of the Hungarian material (length = 1.5 m) have similar morphology to that from Pikermi. Likewise, the Oryahovo material (Bulgaria, SU) reported as ‘*Tetralophodon grandincisivus*’ by Bakalov and Nikolov (1962) presents close morphology to that from Pikermi. Tusks and molars reported as ‘*Mastodon* cf. *longirostris*’ from Kertch (Ukraine) were also attributed to ‘*Mastodon grandincisivus*’ by Schlesinger (1922). Recently, Geraads et al. (2005) described a lower tusk fragment and a M2 from Yulafli (Turkey) as ‘*Amebelodon grandincisivus*’.

Lower tusks with similar morphology are also known from North America. Large-sized and dorsoventrally flattened tusks with tubular internal dentine structure are described from Florida (U.S.A.) as *Amebelodon* (*Konobelodon*) *britti* by Lambert

Formatted: Font: Italic

Formatted: Left

(1990). The latter author included in this species the material described by Osborn and Granger (1931:fig. 26), Barbour and Hibbard (1941:figs. 15–19) and Gregory (1945:fig. 1, pl. 46). He also considered that the Sahabi ‘*Amebelodon cyrenaicus*’ described by Gaziry (1987) belongs to the same genus/subgenus. However, neither Gaziry (1987) nor Lambert (1990) compared their material with ‘*Mastodon grandincisivus*’, despite the fact that Tassy (1985) had already mentioned the possible relationships of this taxon with American forms.

The diagnostic features of *Konobelodon* are the tetralophodont second molars, the tubular internal dentine structure of the lower tusks, and the presence of six well-developed lophids in m3. The dentinal tubules are separated by considerable intervals of smooth dentine near the root of the tusk and they become more closely spaced towards the tip (Gregory, 1945). The large-sized, dorsoventrally flattened and dorsally grooved lower tusk from Pikermi has tubular internal dentine that merges near its basal part and tends to be more tubular towards the apical part. All these features suggest that the lower tusk from Pikermi is similar to that of *Konobelodon* and could be attributed to this taxon (Fig. 5). However, the tetralophodont structure in all intermediate molars (dp4/DP4, m1/M1, m2/M2) distinguish the Pikermi sample from *Amebelodon (Konobelodon) britti*, the type species of the subgenus, which according to Lambert (1990) has tetralophodont first and second molar but trilophodont DP4. Moreover, *Amebelodon (Konobelodon) britti* is characterized by the absence of laminated dentine in the cortex of the lower tusk (Lambert, 1990) contrary to the presence of lamellar dentine peripherally in the Pikermi tusk. It should be noted, however, that Barbour and Hibbard (1941) mentioned the presence of a thin outer wall of laminated dentine in a pair of tusks from Kansas (U.S.A).

The [upgrading-elevation](#) of *Konobelodon* to generic level was proposed by Gheerbrant and Tassy (2009:tab. 1), albeit without any comments. In our opinion, the tubular internal dentine structure and the tetralophodont intermediate molars of *Konobelodon* clearly distinguish it from *Amebelodon* and confirm its generic status. Moreover, *Konobelodon* differs from *Platybelodon* in the less flattened lower tusks and the large upper tusks, whereas *Platybelodon* presents plate-like lower tusks and reduced in size upper ones.

The allocation of the Pikermi tetralophodon to *Konobelodon* is quite clear. As mentioned above, the Pikermi tetralophodon was referred to '*Tetralophodon*' *atticus*. All described material from Pikermi belongs to juvenile individuals, except for the adult lower tusk studied herein (AMPG PA1972/61) and the third molar described by Vacek (1877). The similarity of '*Mastodon*' *grandincisivus* with the Pikermi tetralophodon is also obvious. Therefore, a comparison of all this material is necessary to identify their relationships. Unlike the juvenile '*Tetralophodon*' *atticus* specimens, those of '*Mastodon*' *grandincisivus* correspond entirely to adult individuals, which makes the comparison difficult.

Comparison of the Skull

The studied skull (AMPG PA3933/91) belongs to a juvenile individual. Two other skulls of similar ontogenetic age are known: one from Maragheh, the type locality of '*Mastodon*' *grandincisivus* (Schlesinger, 1917:pl. 11, figs. 1, 2), and another from an unknown locality of Samos (Lehmann, 1950:pl. 22, fig. 108). The Maragheh skull NHMW 2013/0478/0001 (A 4823) was referred to '*Mastodon*' *grandincisivus* by Tassy (1986), based on the fact that Maragheh is the type locality of this taxon. Note that, the same locality has yielded deciduous cheek teeth attributed to '*Tetralophodon*'

atticus (Mecquenem, 1924; Markov, 2008). The Maragheh skull is similar to the Pikermi skull (dentition, location of the choanae, form and structure of the basicranium and the occipital) and should belong to the same taxon. The Samos skull was recently referred to ‘*Tetralophodon*’ *atticus* by Konidaris and Koufos (2013) and presents clear similarities to the Pikermi one (dentition, location of the anterior zygomatic process and the choanae) and could also belong to the same taxon.

Comparison of the Lower Tusks

As mentioned above, there is an obvious similarity between the studied adult lower tusk from Pikermi and that of *Konobelodon*. The lower tusk of *Tetralophodon* is clearly different from that of Pikermi as it has a more rounded cross-section, no dentinal rods, and is smaller in size (Fig. 6A, B; Steininger, 1965; Tobien, 1978:162; pl. 13; Gasparik, 2005). On the other hand, the Pikermi lower tusk is morphologically and metrically similar to ‘*Mastodon*’ *grandincisivus* from Maragheh and Pestszentlörinc (Figs. 5E, 6G–H, M; Schlesinger, 1922:pl. 2, fig. 3). The permanent lower tusks of young individuals have also flattened cross-section with dentinal rods (Fig. 4D–G); these tusks resemble the adult lower one from Pikermi (AMPG PA1972/61) and should be referred to *Konobelodon*.

Comparison of the Deciduous Dentition

The studied DP3s from Pikermi (Figs. 2A–D, 4P), with their enlarged third loph and well-marked second ectoflexus, are very similar morphologically to the Maragheh and Samos material. Additionally, the AMPG Pikermi DP3s are metrically very close to those from Maragheh and Samos (Fig. 7), which confirms their similarity. The available DP4s show morphological and metrical similarities with the Maragheh and

the Samos material, although the Pikermi DP4 is slightly wider (Fig. 7). Moreover, the Pikermi deciduous upper teeth are morphologically similar to those of ‘*Tetralophodon*’ *atticus* from Akkaşdağı, Turkey (Tassy, 2005), ?*Tetralophodon atticus* from Strumyani-2, Bulgaria (Geraads et al., 2011; NMNH), and to the tetralophodont material from Grebeniki (Ukraine), Taraklia, and Cimişlia (Moldavia) referred to ‘*Tetralophodon*’ *atticus* (Tassy, 1985 and ref. cited; Markov, 2008 and ref. cited). All these specimens show similarities with those of Pikermi and should be ~~included-referred~~ to *Konobelodon*.

The available lower deciduous teeth are more in number and thus their comparison yields better results. The Pikermi dp2 is similar to the material from Csákvár, Hungary (HGI V.11393) and from Taraklia described as ‘*Mastodon longirostris*’ by Khomenko (1914). The dp2 from Strumyani-2 referred to ?*Tetralophodon atticus* exhibits a metaconid that is much lower than the protoconid (Geraads et al., 2011), whereas in the dp2 from Pikermi these two cuspids are almost equal in height. In size the dp2 from Pikermi is similar to those from Taraklia, Csákvár and Samos, but smaller than that from Strumyani-2 (Fig. 7).

The Pikermi dp3s can be divided in two groups. The first group includes the specimens AMPG PA3935/91 and MNHN PIK-1704b. It is characterized by the alternating contact between pprcc1 and apocc2 in the first transverse valley (Fig. 4L, M), and in this respect shows similarities to the material from Csákvár (HGI V.11395) and Baltavár (HGI Ob-328), Hungary (Schlesinger, 1922:pl. 8, fig. 6). The second group includes the specimens AMPG PA3708/91, AMPG PA3936/91 and AMPG PA3937/91. It is characterized by the rather isolated and low, but strong central conule in the first transverse valley (Fig. 4N, O), and shows similarities to the dp3s from Taraklia, Cimişlia and Novaya-Emetovka-Kostev Ovrage (Khomenko, 1914;

Simionescu and Barbu 1939; Korotkevich, 1988). The dp3s of AMPG PA3935/91 have larger dimensions than other Pikermi specimens (Fig. 7), but this is ~~into~~within the expected range of an intraspecific size variation, since the other available Pikermi specimen with similar morphology is smaller in size. In this regard, the distinction of the Pikermi dp3s in two morphological groups is taxonomically insignificant. The dp4 from Pikermi has similar morphology to the dp4s from Cimişlia, Moldova (Simionescu and Barbu, 1939) and Kerassia (Theodorou et al., 2001, 2003); their size is also similar (Fig. 7).

Comparison of the Third Molar

The only known adult molar from Pikermi is that described by Vacek (1877) as ‘*Mastodon longirostris*’ (length × width = (216) × 87.3 mm [second lophid], MNHN cast measurements). It consists of six lophids; the three anterior lophids form pretrite trefoils; posttrite trefoils are weaker and only in the first two lophids; the lophids are rather high; with cement deposits (Fig. 2E). This molar was originally regarded as an M3, which was doubted by Markov and Vergiev (2012) and Konidaris (2013) who considered it an m3. Tobien (1978) attributed this specimen to ‘*Stegotetrabelodon grandincisivus*’, whereas Tassy (1985, 2005) referred it to ‘*Tetralophodon atticus*’, based on its similarities with the deciduous dentition of this species. Its size is smaller than *Konobelodon* from Oryahovo, Bulgaria, and Pestszentlőrinc, Hungary (Fig. 7). However, size differences can be observed in several proboscideans, such as *Gomphotherium angustidens* (Cuvier, 1817) from En Péljouan, France (Tassy, 1996b). The m3 of *Tetralophodon longirostris* from Eppelsheim (Germany) varies significantly in length (162–237 mm), exhibiting a maximum–minimum difference of ~46%; similarly, in *T. longirostris* from Rudabánya (Hungary) the length of m3

exhibits a range of ~47% (Göhlich, 1998; Gasparik, 2005) (Fig. 7). This size variation can be attributed either to sexual dimorphism or to local environmental factors (Tassy, 1996b). The size difference between the largest m3s attributed to ‘*Mastodon*’ *grandincisivus* of Oryahovo (Bulgaria) and the Pikermi m3 is ~31%, smaller than the observable size range of a single species from the same locality.

Besides size, the Pikermi m3 has rather simple occlusal morphology. However, the complexity of the tetralophodont molars varies greatly; e.g., pretrite central conules may be weak or strong, posttrite central conules may be developed or not and alternating contacts may be present or absent (Tassy, 1985:735). The complexity may vary even among the upper and lower molars of the same individual (Hautier et al., 2009). Consequently, the Pikermi m3 could belong to the same species with ‘*Mastodon*’ *grandincisivus* from various European localities, whose m3 presents a more complicated morphological pattern, and all these samples could be referred to *Konobelodon*.

Taxonomic Conclusions

All the above comparisons indicate that the Pikermi tetralophodont material combines characters of ‘*Tetralophodon*’ *atticus*, as regards the deciduous dentition and ‘*Mastodon*’ *grandincisivus*, as regards the size, shape and structure of the lower tusks. These characters co-exist in some Pikermi specimens (AMPG PA3936/91, AMPG PA3937/91), a fact that supports the synonymy of ‘*Tetralophodon*’ *atticus* and ‘*Mastodon*’ *grandincisivus*. This synonymy is also confirmed by the comparison with the tetralophodont samples from other Eurasian localities. On the other hand, the size and structure of the lower tusk from Pikermi and the tetralophodont intermediate molars suggest that this tetralophodon belongs to *Konobelodon*. The species

‘*Mastodon atticus*’ was erected by Wagner (1857) for some tetralophodont material from Pikermi, whereas the species ‘*Mastodon grandincisivus*’ was proposed by Schlesinger (1917, 1922) for some material from Maragheh (Iran) and Pestszentlőrinc (Hungary). *Mastodon* is a generic name no longer in use and *Tetralophodon* is clearly different from the Pikermi sample. The specific name *atticus* has priority over *grandincisivus*, and thus the Pikermi tetralophodon is determined to *Konobelodon atticus* (Wagner, 1857). *Konobelodon atticus* differs from the type species *Konobelodon britti*; the former presents tetralophodonty in all intermediate molars and lower tusks with external concentric laminated dentine layer.

GEOGRAPHIC AND BIOSTRATIGRAPHIC DISTRIBUTION

The known material of *Konobelodon* is relatively scarce and sporadic in biogeographic distribution, which makes it difficult to clarify the origin and relationships of the genus. Contrary to Lambert’s (1990) opinion that *Konobelodon* is related to *Amebelodon*, Tassy (1986, 1999, 2005) suggested that ‘*Mastodon grandincisivus*’ (= *Konobelodon*) is related to *Platybelodon*. In fact, the tubular dentine structure of the lower tusks is a character shared by *Platybelodon* and *Konobelodon*, whereas *Amebelodon* has lower tusks that present only concentric lamellar dentine structure. *Platybelodon danovi*, the type species of the genus, was originally described from Belomechetskaya (Russia), correlated to the early Astaracian, MN 6 (Pickford et al., 2000). This species can be considered rather primitive because of its exclusively trilophodont intermediate molars. The more advanced *Platybelodon* is *P. grangeri*, known from several Chinese localities correlated mainly to the late Astaracian, MN 7+8 (Fortelius, 2013). *Platybelodon*

grangeri attained tetralophodonty in the second molars. Its dp4/DP4 and m1/M1 are trilophodont, but present a prominent talon(id), which can be considered a tendency towards tetralophodonty; its molars are high-crowned and covered by cement (Tobien, 1973; Tobien et al., 1986; Guan, 1996). The tetralophodont *Konobelodon* could have derived from a *P. grangeri* stock during the end of the middle Miocene or the beginning of the late Miocene. *Konobelodon* is also reported from Yulafli (Turkey), which could be considered its earliest occurrence because this locality is correlated to the late Vallesian, MN 10, between 9.4–9.3 Ma (Geraads et al., 2005). However, a European origin of *Konobelodon* seems unlikely, given that advanced *Platybelodon* forms, such as *P. grangeri*, are unknown from western Eurasia. *Konobelodon* appears to have originated from a Central Asian form which migrated to the East and the West. The Yulafli *Konobelodon* probably represents the first immigrants that arrived in Europe during the Vallesian. This hypothesis agrees with the scenario proposed by Kalb et al. (1996), according to which some amebelodons may have crossed back from eastern to western Eurasia and Africa during the Tortonian (~10.5 Ma). The final evolutionary stage of the European clade is *Konobelodon atticus*. The western migration of *Konobelodon* has also a southern clade which entered Africa. If the Sahabi (Libya) shovel-tusker material is indeed homogeneous, which is not certain (Markov, 2008; Sanders, 2008; Sanders et al. 2010), then the Sahabi *Konobelodon* (latest Miocene, ~5.3 Ma) with its tetralophodont m2 and trilophodont m1 corresponds to a local [evolutionary form/taxon](#) derived from the Vallesian immigrant. Another possibility could be that the development of internal tubules in the Sahabi shovel-tusker might have occurred independently as a result of parallelism.

The east migration path led through the Beringian landbridge to America. The genus *Konobelodon* appeared in North America at ~7.0 Ma, where it survived until the end of the Miocene (Lambert, 1990). *Konobelodon* arrived in America at that time (~7.0 Ma) or earlier and the time gap is possibly due to the lack of fossils.

The problem ~~of~~with the above hypothesis is the absence of *Konobelodon* in the eastern Asia. Nonetheless, there are several late Miocene tetralophodont proboscideans from that region which are referred under various specific names, and whose relationships with the European forms are not clearly defined.

As defined herein, *Konobelodon atticus* is known from Pikermi, Samos, Kerassia (Greece), Akkaşdağı (Turkey), Tchobroutchi, Taraklia, Cimişlia (Moldavia), Grebeniki, Novaya Emetovka-Kostev Ovrage (Ukraine), Pestszentlőrinc, Baltavár, Csákvár, Polgárdi (Hungary), several localities in Bulgaria (e.g., Hadjidimovo), Dolni Disan (FYROM) and Maragheh (Iran). Tchobroutchi and Csákvár are dated to the early Turolian (MN 11); Pikermi, Akkaşdağı, Taraklia and Baltavár to the middle Turolian (MN 12); and Polgárdi to the late Turolian (MN 13) (Lungu and Delinschi, 2006; Fortelius, 2013). Consequently, *Konobelodon atticus* can be regarded as a characteristic tetralophodont amebelodontine for the Turolian of eastern Europe and western Asia. The first appearance of *Konobelodon atticus* depends on whether some material of Vallesian age (e.g., Yulaflı, Turkey) belong to this species or not. As a result of this ambiguity, the Yulaflı material is herein attributed to *Konobelodon* sp. The material from Oryahovo (Bulgaria) is also attributed to *Konobelodon* sp., because, as mentioned by Markov (2008), it is an isolated specimen, which can exclude neither a Vallesian age, nor a specific differentiation from *Konobelodon atticus*. The last appearance of the genus is marked at Sahabi, Libya (Lambert, 1990). Tetralophodont material from several other European Turolian localities, e.g.,

Mannersdorf bei Angern, Austria (Schlesinger, 1917) and Dorn-Dürkheim 1, Germany (Gaziry, 1997), may also belong to *Konobelodon*, but this cannot be definitely confirmed at the ~~moment~~present time. The lower tusk DD 4424 from Dorn-Dürkheim 1 described by Gaziry (1997) seems to exhibit features similar to those of *Konobelodon*, but without an illustration or direct study of the specimen, such a generic attribution would be tentative. Consequently, *Konobelodon atticus* is a typical Turolian representative of eastern Europe and western Asia (Fig. 8). Its potential presence in Central Europe needs confirmation, as the available data cannot support this.

CONCLUSIONS

The existence of tetralophodont proboscideans in Pikermi ~~is has been~~ recognized established since the mid 19th century. However, their morphological characters ~~had been~~ were inadequately known and several opinions had been expressed about their taxonomy. Similarly, many other late Miocene Eurasian tetralophodonts were of problematic taxonomic determination and had been referred under various generic and specific names. The study of unpublished specimens from Pikermi (AMPG) and the reinvestigation of the other Pikermi collections suggest that the Pikermi tetralophodont sample, which is characterized by flattened lower tusks with tubular internal dentine structure, represents a shovel-tusker that belongs to the genus *Konobelodon*. The tetralophodont structure of all intermediate molars distinguish the Pikermi sample from the type species *Konobelodon britti*. The Pikermi tetralophodont was described as '*Tetralophodon*' *atticus* and thus it must now be referred to *Konobelodon atticus* (Wagner, 1857). The comparison of the Pikermi tetralophodont

with the eastern European and western Asian tetralophodons that are referred to ‘*Mastodon grandincisivus*’ or ‘*Tetralophodon*’ *atticus* indicates that they are all similar and should be included to the same species: *Konobelodon atticus*. The genus *Konobelodon* probably appeared in eastern Asia and originated from the middle Miocene *Platybelodon grangeri*. Then, at the beginning of the late Miocene it dispersed to the East and West. A branch of the western migration path diverged to the south and entered Africa, where it survived until the end of the Miocene. The eastern immigrants arrived at North America through the Beringian landbridge at ~7.0 Ma or earlier, where they survived until the end of the Miocene. The species *Konobelodon atticus* is well documented at the Turolian of the eastern Europe and western Asia. It might have also been present earlier, at the Vallesian, even though this cannot yet be established beyond doubt.

ACKNOWLEDGMENTS

G.E. Konidaris thanks the following persons for allowing access to collections under their care and offering help during his stay at the various museums and institutions: P. Tassy and S. Sen (MNHN), U. Göhlich (NHMW), G. Rössner (BSPG), G. Markov (NMNH), L. Kordos (HGI), M. Gasparik (HNHM) and M. Ivanov (SU). Financial support was provided by SYNTHESYS (European Union-funded Integrated Activities grant) to G.E.K. for visits to Vienna (AT-TAF-3825) and Budapest (HU-TAF-1683) and to S.J.R. for visit to Vienna (AT-TAF-3283). We are grateful to D. Kostopoulos (University of Thessaloniki) for valuable comments and W. Sanders (University of Michigan) for providing important literature. Editor E. Davis and

reviewers U. Göhlich and W. Sanders made constructive comments and suggestions for improvement of the manuscript.

LITERATURE CITED

- Abel, O., 1922. Lebensbilder aus der Tierwelt der Vorzeit. G. Fischer Verlag, Jena, 643 pp.
- Antunes, M. T., and A. V. Mazo. 1983. Quelques mastodontes miocènes du Portugal. *Ciências da Terra* 7:115–128.
- Bakalov, P., and I. Nikolov. 1962. Les Fossiles de Bulgarie. X. Mammifères Tertiaires. Académie des Sciences de Bulgarie, Sofia, 162 pp.
- Barbour, E. H. 1927. Preliminary notice of a new proboscidean *Amebelodon fricki*, gen. et sp. nov. *Bulletin of the Nebraska State Museum* 13:131–134.
- Barbour, E. H., and C. W. Hibbard. 1941. A shovel-tusked mastodon, *Amebelodon fricki*, from Kansas. *Bulletin of the University of Nebraska State Museum* 2:37–46.
- Barone, R. 1999. Anatomie Comparée des Mammifères Domestiques. Tome I: Ostéologie. Vigot Frères, Paris, 761 pp.
- Bernor, R. L., N. Solounias, C. C. Swisher, and J. A. van Couvering. 1996. The correlation of three classical “Pikermian” mammal faunas—Maragheh, Samos and Pikermi—with the European MN unit system; pp. 137–154 in R. L. Bernor, V. Fahlbusch, and H. W. Mittmann (eds.), *The evolution of Western Eurasian Neogene mammal faunas*. Columbia University Press, New York.

Burchak-Abramovich, N. 1940. Contribution to the Study of the Hipparion fauna of South Ukraine. I. Proboscidea from the Meotic Deposits of the Village Grebenniki, Tiraspol District (Moldavian SSR). AN URSS Geologichnii Zhurnal 7:27–52.

Cuvier, G. 1817. Le règne animal. Déterville, Paris, 540 pp.

Delmer, C. 2009. Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscideans. Acta Palaeontologica Polonica 54:561–580.

Fortelius, M. (coordinator). 2013. Neogene of the Old World Database of Fossil Mammals (NOW). University of Helsinki. Available at www.helsinki.fi/science/now.

Garevski, R. 1976. Weiterer Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Der Mastodonschädel von der Umgebung des Dorfes Dolni Disan (Negotino). Posebno Izdanie Musei Macedonici Scientiarum Naturalium 7:21–26.

Gasparik, M. 2005. Proboscidean remains from the Pannonian of Rudabánya. Palaeontographia Italica 90:181–192.

Gaudry, A. 1855. Sur les premiers résultats de la mission qui lui a été confiée par l'Académie pour l'exploration du gîte fossilifère de Pikermi (Attique). (Extrait d'une lettre de M. A. Gaudry à M. le Secrétaire perpétuel). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 41:894–897.

Gaudry, A., 1862. Animaux Fossiles et Géologie de l'Attique. Savy, Paris, 474 pp.

Gaudry, A., 1867. Animaux Fossiles et Géologie de l'Attique. Atlas. Savy, Paris.

Gaudry, A., and E. Lartet. 1856. Résultats des recherches paléontologiques entreprises dans l'Attique sous les auspices de l'Académie. Comptes Rendus de l'Académie des Sciences, Paris 43:271–274.

- Gaziry, A. W. 1976. Jungtertiäre Mastodonten aus Anatolien (Türkei). *Geologisches Jahrbuch* 22:3–143.
- Gaziry, A. W. 1987. Remains of Proboscidea from the Early Pliocene of Sahabi, Libya; pp. 183–203 in N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. d. Heinzelin and D. D. Boaz (eds.), *Neogene Paleontology and Geology of Sahabi*. A. R. Liss, New York.
- Gaziry, A. W. 1997. Die Mastodonten (Proboscidea, Mammalia) aus Dorn-Dürkheim 1 (Rheinhessen). *Courier Forschungs-Institut Senckenberg* 197:73–115.
- Geraads, D., T. Kaya, and S. Mayda. 2005. Late Miocene large mammals from Yulafli, Thrace region, Turkey, and their biogeographic implications. *Acta Palaeontologica Polonica* 50:523–544.
- Geraads, D., N. Spassov, L. Hristova, G. N. Markov, and T. Tzankov. 2011. Upper Miocene mammals from Strumyani, South—Western Bulgaria. *Geodiversitas* 33:451–484.
- Gheerbrant, E., and P. Tassy. 2009. L'origine et l'évolution des éléphants. *Comptes Rendus Palevol* 8:281–294.
- Göhlich, U. B. 1998. Elephantoidea (Proboscidea, Mammalia) aus dem Mittel- und Obermiozän der Oberen Süßwassermolasse Süddeutschlands: Odontologie und Osteologie. *Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie* 36:1–245.
- Göhlich, U. B. 1999. Order Proboscidea; pp. 157–168 in: G. E. Rössner and K. Heissig (eds.), *The Miocene ~~H~~and ~~M~~Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München.
- Gray, J. E. 1821. On the natural arrangements of vertebrate animals. *London Medical Repository* 15:296–310.

Gregory, J. T. 1945. An *Amebelodon* jaw from the Texas Panhandle. The University of Texas Publication 4401:477–484.

Guan, J. 1996. On the shovel-tusked elephantoids from China; pp. 124–135 in J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and Paleoeecology of Elephants and their Relatives*. Oxford University Press, Oxford.

Hautier, L., H. T. Mackaye, F. Lihoreau, P. Tassy, P. Vignaud, and M. Brunet. 2009. New material of *Anancus kenyensis* (proboscidea, mammalia) from Toros-Menalla (Late Miocene, Chad): Contribution to the systematics of African anancines. *Journal of African Earth Sciences* 53:171–176.

Hay, O. P. 1922. Further observations on some extinct elephants. *Proceedings of the Biological Society of Washington* 35:97–101.

Hopwood, A. T. 1935. Fossil Proboscidea from China. *Paleontologia Sinica* 9:1–108.

I.C.V.G.A.N. 2005. *Nomina Anatomica Veterinaria*. International Committee on Veterinary Gross Anatomical Nomenclature, Hannover, Columbia, Gent, Sapporo, 165 pp.

Illiger, C. 1811. *Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis Utriusque Classis*. C. Salfield, Berlin, 301 pp.

Kalb, J. E., D. J. Froehlich, and G. L. Bell. 1996. Palaeobiogeography of late Neogene African and Eurasian Elephantoidea; pp. 117–123 in J. Shoshani and P. Tassy (eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*. Oxford University Press, Oxford.

Kaup, J. J. 1832. Ueber zwei Fragmente eines Unterkiefers von *Mastodon angustidens* Cuv., nach welchen diese Art in die Gattung *Tetracaulodon* Godmann gehört. *Isis* 25:628–631.

- Khomenko, J. 1914. La faune méotique du village Taraklia du district de Bendery.
Trudy Bessarabskago Obshestva Estestvoispytatelei i liubitelei estestvoznania
5:1–55.
- Kittl, E. 1886. Fossile Säugetierfauna von Maragha. Annalen des Naturhistorischen
Museums in Wien. **Editor's note: Is this a paper or book? Need volume
number and/or page range**
- Klähn, H. 1931. Rheinhessisches Pliozän besonders Unterpliozän im Rahmen des
Mitteleuropäischen Pliozäns. Geologische und Paläontologische
Abhandlungen 18: 279–340.
- Konidaris, G. E. 2013. Palaeontological and biostratigraphical study of the Neogene
Proboscidea from Greece. Ph.D. dissertation, Aristotle University of
Thessaloniki, Thessaloniki, 326 pp.
- Konidaris, G. E., and G. D. Koufos. 2013. Late Miocene Proboscidea (Mammalia)
from Macedonia and Samos Island, Greece: preliminary results.
Paläontologische Zeitschrift 87:121–140.
- Korotkevich, E. L. 1988. History of the Formation of the *Hipparion*. **Editor's
comment: Is Hipparion meant to be the genus, or a common term?** Fauna of
Eastern Europe. Naukova Dumka, Kiev, 162 pp.
- Koufos, G. D. 2006. The Neogene mammal localities of Greece: Faunas, chronology
and biostratigraphy. Hellenic Journal of Geosciences 41:183–214.
- Koufos, G. D. 2009. The Neogene cercopithecids (Mammalia, Primates) of Greece.
Geodiversitas 31:817–850.
- Kovachev, D. 2004. Cranium of *Stegotetralodon* (Proboscidea, Mammalia) from
the Neogene in the East Maritsa basin. Review of the Bulgarian Geological
Society 65:167–173.

Formatted: Highlight

Formatted: Highlight

Formatted: Highlight

Formatted: Highlight

Lambert, W. D. 1990. Rediagnosis of the genus *Amebelodon* (Mammalia, Proboscidea, Gomphotheriidae), with a new subgenus and species, *Amebelodon* (*Konobelodon*) *britti*. *Journal of Paleontology* 64:1032–1040.

Lartet, E. 1859. Sur la dentition des proboscidiens fossiles (*Dinotherium*, Mastodontes et Éléphants) et sur la distribution géographique et stratigraphique de leurs débris en Europe. *Bulletin de la Société Géologique de France* 16:469–515.

Lehmann, U. 1950. Über Mastodonreste in der Bayerischen Staatssammlung in München. *Palaeontographica* 99:121–228.

Lungu, A., and A. Delinschi. 2006. Contribution in study meotien faunas of the Cioburciu site from Republic of Moldova. *Analele Științifice ale Universității “Al. I. Cuza”. Iași* 52:111–117.

Maglio, V. J. 1969. A shovel-tusked gomphothere from the Miocene of Kenya. *Breviora* 310:1–10.

Markov, G. N. 2008. The Turolian proboscideans (Mammalia) of Europe: preliminary observations. *Historia naturalis bulgarica* 19:153–178.

Markov, G. N., and S. Vergiev. 2012. *Tetralophodon* (Mammalia: Proboscidea) from the vicinities of Varna, Northeast Bulgaria. *Historia naturalis bulgarica* 20:151–156.

Mecquenem, R. de 1924. Contribution à l’étude des fossiles de Maragha. *Annales de Paléontologie* 14:1–36.

Osborn, H. F. 1936. Proboscidea. A Monograph of the Discovery, Evolution, Migration and Extinction of the Mastodonts and Elephants of the World, Volume I: Moeritherioidea, Deinotherioidea, Mastodontoidea. American Museum Press, New York, 802 pp.

- Osborn, H. F., and W. Granger. 1931. The shovel-tusked, Amebelodontinae, of Central Asia. American Museum Novitates 470:1–12.
- Pavlow, M. 1903. *Mastodon angustidens* Cuv. et *Mastodon* cf. *longirostris* Kaup de Kertch. Annuaire géologique et minéralogique de la Russie 6:130–139.
- Pavlow, M. 1914a. Mammifères tertiaires de la Nouvelle Russie. Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou 17:1–52.
- Pavlow, M. 1914b. Aperçu sur la nouvelle faune des mammifères tertiaires de la Russie méridionale. Annuaire géologique et minéralogique de la Russie 16:181–191.
- Pickford, M., L. Gabunia, P. Mein, J. Morales, and B. Azanza. 2000. The Middle Miocene mammalian site of Belometchetskaya, North Caucasus: An important biostratigraphic link between Europe and China. Geobios 33:257–267.
- Riabinin, A. N. 1929. Faune de mammifères de Taraklia. I. Carnivora vera, Rodentia, Subungulata. Travaux de Musée Géologique près l'Académie des Sciences de l'URSS 5:75–134.
- Roth, J., and A. Wagner. 1854. Die fossilen Knochen-Ueberreste von Pikermi in Griechenland. Abhandlungen der Bayerischen Akademie der Wissenschaften 7:371–464.
- Sanders, W. J. 2008. Review of Fossil Proboscidea from the Late Miocene–Early Pliocene Site of As Sahabi, Libya; pp. 241–256 in N. T. Boaz, A. El-Arnauti, P. Pavlakis and M. J. Salem (eds.), Circum-Mediterranean **g**Geology and **B**iotic **e**Evolution during the Neogene **p**Period: The **p**Perspective from Libya. University of Garyounis, Benghazi.
- Sanders, W. J., E. Gheerbrant, J. M. Harris, H. Saegusa, and C. Delmer. 2010. Proboscidea; pp. 161–251 in L. Werdelin and W. J. Sanders (eds.), Cenozoic

~~m~~Mammals of Africa. University of California Press, Berkeley, Los Angeles, London.

Schlesinger, G. 1917. Die Mastodonten des K. K. Naturhistorischen Hofmuseums. Denkschriften des K. K. Naturhistorischen Hofmuseums 1:1–230.

Schlesinger, G. 1922. Die Mastodonten der Budapester Sammlungen. Geologica Hungarica 2:1–284.

Shoshani, J. 1996. Para- or monophyly of the gomphotheres and their position within Proboscidea; pp. 149–177 in J. Shoshani and P. Tassy (eds.), The Proboscidea: Evolution and ~~p~~Palaeoecology of ~~e~~Elephants and their ~~r~~Relatives. Oxford University Press, Oxford.

Shoshani, J., and P. Tassy. 2005. Advances in proboscidean taxonomy & classification, anatomy ~~&~~and physiology, and ecology ~~&~~and behavior. Quaternary International 126–128:5–20.

Simionescu, I., and V. Barbu. 1939. Mamiferele ~~p~~Pliocene dela Cimişlia (România). III. Proboscidiieni. Academia Română Publicaţiunile Fondului V. Adamachi 9:1–20.

Solounias, N. 1981. The Turolian fauna from the island of Samos, Greece. Münchner Geowissenschaftliche Abhandlungen, Contributions Vertebrate Evolution, Basel, 232 pp.

Stefanescu, G. 1892. On the existence of the *Dinotherium* in Roumania. Bulletin of the Geological Society of America 3:81–83.

Steininger, F. 1965. Ein bemerkenswerter Fund von *Mastodon* (*Bunolophodon*) *longirostris* Kaup 1832 (Proboscidea, Mammalia) aus dem Unterpliozän (Pannon) des Hausruck-Kobernaußerwald- Gebietes in Oberösterreich. Jahrbuch der Geologischen Bundesanstalt 108:195–212.

- Tassy, P. 1983a. Les Elephantoidea Miocènes du Plateau du Potwar, Groupe de Siwalik, Pakistan. Ire Partie: Introduction, cadre chronologique et géographique, mammutidés, amébelodontidés. Annales de Paléontologie 69:99–136.
- Tassy, P. 1983b. Les Elephantoidea Miocènes du Plateau du Potwar, Groupe de Siwalik, Pakistan. Ile Partie: Choerolophodontes et gomphothères. Annales de Paléontologie 69:235–297.
- Tassy, P. 1985. La place des mastodontes Miocènes de l’Ancien Monde dans la phylogénie des Proboscidea (Mammalia): Hypothèses et conjectures. Ph.D. dissertation, Université Pierre et Marie Curie, Paris, 862 pp.
- Tassy, P. 1986. Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. CNRS, Paris, 135 pp.
- Tassy, P. 1987. A hypothesis on the homology of proboscidean tusks based on paleontological data. American Museum Novitates 2895:1–18.
- Tassy, P. 1996a. Dental homologies and nomenclature in the Proboscidea; pp. 21–25 in J. Shoshani and P. Tassy (eds.), The Proboscidea: Evolution and **pP**aleoecology of **eE**lephants and their **rR**elatives. Oxford University Press, Oxford.
- Tassy, P. 1996b. Growth and sexual dimorphism among Miocene elephantoids: the example of *Gomphotherium angustidens*; pp. 92–100 in J. Shoshani and P. Tassy (eds.), The Proboscidea: Evolution and **pP**aleoecology of **eE**lephants and their **rR**elatives. Oxford University Press, Oxford.
- Tassy, P. 1996c. Who is who among the Proboscidea?; pp. 39–48 in J. Shoshani and P. Tassy (eds.), The Proboscidea: Evolution and **pP**aleoecology of **eE**lephants and their **rR**elatives. Oxford University Press, Oxford.

Tassy, P. 1999. Miocene Elephantids (Mammalia) from the Emirate of Abu Dhabi, United Arab Emirates: Palaeobiogeographic implications; pp. 209–233 in P. J. Whybrow and A. Hill (eds.), Fossil Vertebrates of Arabia. Yale University Press, New Haven and London.

Tassy, P. 2003. Elephantoida from Lothagam; pp. 331–358 in M. G. Leaky and J. M. Harris (eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York.

Tassy, P. 2005. Proboscideans (Mammalia) from the late Miocene of Akkaşdağı, Turkey; pp. 707–714 in S. Sen (ed.), Geology, ~~m~~Mammals and ~~e~~Environments at Akkaşdağı, ~~H~~Late Miocene of Central Anatolia. Geodiversitas, Paris.

Theodorou, G., A. Athanassiou, and G. Iliopoulos. 2001. Proboscidea from the Late Miocene of Kerassiá (Euboea, Greece). The Palaeontology Newsletter 48(Supplement):50.

Theodorou, G., A. Athanassiou, S. Roussiakis, and G. Iliopoulos. 2003. Preliminary remarks on the Late Miocene herbivores of Kerassiá (Northern Euboea, Greece); pp. 519–530 in J. W. F. Reumer and W. Wessels (eds.), Distribution and ~~m~~Migration of Tertiary Mammals in Eurasia . A volume in honour of Hans de Bruijn. Deinsea, Rotterdam.

Theodorou, G. E., S. J. Roussiakis, A. Athanassiou, and A. Filippidi. 2010. Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece) pp. 109–119 in G. Christofides, N. Kantiranis, D. S. Kostopoulos and A. A. Chatzipetros (eds.), 19th CBGA Congress, Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Thessaloniki.

- 1
2
3
4
5
6 Tobien, H. 1973. On the evolution of mastodonts (Proboscidea, Mammalia). Part I:
7
8 The bunodont trilophodont group. Notizblatt des Hessischen Landesamtes für
9
10 Bodenforschung zu Wiesbaden 101:202–276.
11
12 Tobien, H. 1978. On the evolution of mastodonts (Proboscidea, Mammalia). Part 2:
13
14 The bunodont tetralophodont groups. Geologisches Jahrbuch Hessen 106:159–
15
16 208.
17
18 Tobien, H., G. Chen, and Y. Li. 1986. Mastodonts (Proboscidea, Mammalia) from the
19
20 Late Neogene and Early Pleistocene of the People's Republic of China. Part 1:
21
22 Historical account; the Genera *Gomphotherium*, *Choerolophodon*,
23
24 *Synconolophus*, *Amebelodon*, *Platybelodon*, *Sinomastodon*. Mainzer
25
26 geowissenschaftliche Mitteilungen 15:119–181.
27
28 Vacek, M. 1877. Über österreichische Mastodonten und ihre Beziehungen zu den
29
30 Mastodon-Arten Europas. Abhandlungen der Kaiserlich-Königlichen
31
32 geologischen Reichenstalt 7:1–45.
33
34 Wagner, A. 1839. Fossile Ueberreste von einem Affenschädel und andern Säugthieren
35
36 aus Griechenland. Gelehrte Anzeigen 8:306–311.
37
38 Wagner, A. 1857. Neue Beiträge zur Kenntnis der fossilen Säugerthier-Ueberreste
39
40 von Pikermi. Abhandlungen der bayerischen Akademie der Wissenschaften
41
42 8:109–158.
43
44 Woodward, A. S. 1901. On the bone-beds of Pikermi (Attica) and on similar deposits
45
46 in Northern Euboea. Geological Magazine 8:481–486.
47
48
49 Submitted July 05, 2013; revisions received November 14, 2013; accepted December
50
51 3, 2013.
52
53 Handling editor: Edward Davis.
54
55
56
57
58
59
60

FIGURE CAPTIONS

FIGURE 1. Geographic position of Greece and map of Greece indicating the location of Pikermi. The globe was taken from www.wikipedia.com and the map from www.shaded-relief.com. [planned for page width]

FIGURE 2. *Konobelodon atticus*, Pikermi, Greece. **A**, part of right maxilla with DP2–DP3 (MNHN PIK-1704a) in occlusal view; **B–D**, part of left maxilla with DP2–DP3 (BSPG AS II 182), holotype, in **B**, occlusal, **C**, labial, and **D**, lingual views; **E**, m3 sin (taken from Vacek, 1877) in occlusal view. [planned for [page-column](#) width]

FIGURE 3. *Konobelodon atticus*, Pikermi, Greece. **A–D**, skull with right and left DP3–DP4 (AMPG PA3933/91) in **A**, ventral, **B**, dorsal, **C**, lateral, and **D**, caudal views (“x” indicates restored areas); **E–F**, part of right mandible with dp3 (MNHN PIK-1704b) in **E**, labial, and **F**, occlusal views; **G–H**, part of mandible with right and left dp3–dp4 (AMPG PA3708/91) in **G**, labial, and **H**, occlusal views; **I**, part of mandible with right and left dp3 (AMPG PA3935/91) in occlusal view; **J–L**, part of right mandible with i1 and dp2–dp3 (AMPG PA3936/91) in **J**, occlusal, **K**, lingual, and **L**, labial views; **M–O**, part of left mandible with part of i1 and dp2–dp3 (AMPG PA3937/91) in **M**, occlusal, **N**, lingual, and **O**, labial view. [planned for page width]

FIGURE 4. *Konobelodon atticus*, Pikermi, Greece. **A–E**, right i1 (AMPG PA3936/91) in **A**, ventral, **B**, lateral, and **C**, dorsal views, **D**, cross-sectional basal view through

the mandibular symphysis, and **E**, cross-sectional apical view 30 mm from the tip; **F**, left i1 (AMPG PA3937/91) in cross-sectional basal view through the mandibular symphysis; **G–J**, right i1 (AMPG PA3929/91) in **G**, cross-sectional apical view, **H**, ventral, **I**, lateral, and **J**, dorsal views; **K**, left dp2 (AMPG PA3937/91) in occlusal view; **L**, right dp3 (MNHN PIK-1704b) in occlusal view; **M**, right dp3 (AMPG PA3935/91) in occlusal view; **N**, left dp3 (AMPG PA3937/91) in occlusal view (reversed); **O**, right dp3 (AMPG PA3708/91) in occlusal view; **P**, left DP3 (AMPG PA3933/91) in occlusal view; **Q**, right DP4 (AMPG PA3933/91) in occlusal view; **R–T**, left dp4 (AMPG PA3708/91) in **R**, occlusal, **S**, labial, and **T**, lingual views.

[planned for page width]

FIGURE 5. *Konobelodon atticus*, lower tusks. **A–D**, right i1 (AMPG PA1972/61), Pikermi (Greece), in **A**, dorsal, and **B**, ventral views (‘‘1’’ and ‘‘2’’ indicate cross-sectional levels), **C**, cross-sectional basal view at level 1 (about 320 mm from base), and **D**, cross-sectional basal view at level 2 (about 950 mm from base); **E**, left i1 (NHMW 1893/0012/0006), Maragheh (Iran), holotype of ‘*Mastodon grandincisivus*’, cross-sectional apical view. [planned for page width]

FIGURE 6. Cross-sections of lower tusks. **A**, *Tetralophodon longirostris*, Rudabánya, Hungary (HGI V.11909); **B**, *Tetralophodon longirostris*, Grossweissendorf, Austria (Steininger, 1965); **C**, *Platybelodon* cf. *danovi*, Arapli, Turkey (Gaziry, 1976; Tassy, 1986); **D**, *Konobelodon* sp., Sahabi, Libya (Gaziry, 1987); **E**, *Konobelodon* sp., Yulafli, Turkey (Geraads et al., 2005); **F**, *Konobelodon* sp., Kertch, Ukraine (Pavlow, 1903); **G**, *Konobelodon atticus*, holotype of ‘*Mastodon grandincisivus*’, Maragheh, Iran (NHMW 1893/0012/0006); **H**, *Konobelodon atticus*, Pestszentlörinc, Hungary (HNHM V.79.34); **I**, *Konobelodon atticus*, Pikermi, Greece, 320 mm from base (AMPG PA1972/61); **J**, *Konobelodon atticus*, Pikermi, Greece, 950 mm from base

(AMPG PA1972/61); **K**, *Konobelodon britti*, Texas, U.S.A. (Gregory, 1945; Lambert, 1990); **L**, *Konobelodon britti*, Florida, U.S.A. (Lambert, 1990); **M**, scatter diagram (width vs. height) of the lower tusk cross-sections of *Konobelodon* from various localities (based on Tassy, 1986:fig. 140). [planned for page width]

FIGURE 7. Scatter diagrams (length vs. width) of dp2/DP2, dp3/DP3, dp4/DP4 and m3 of tetralophodons from various localities. The symbol “?” indicates questionable measurements. Data from Pavlow (1913), Khomenko (1914), Schlesinger (1917, 1922), Riabinin (1929), Hopwood (1935), Burchak-Abramovich (1940), Lehmann (1950), Antunes and Mazo (1983), Tassy (1983b, 1986, 2005), Gaziry (1987, 1997), Lambert (1990), Göhlich (1998), Theodorou et al. (2003), Gasparik (2005) and own measurements from AMPG, BSPG, HGI, MNHN, NMNH and SU. [planned for page width]

FIGURE 8. Geographic distribution of *Konobelodon* in the Old World. **1**, Pikermi, Greece; **2**, Samos, Greece; **3**, Kerassia, Greece; **4**, Akkaşdağı, Turkey; **5**, various localities in Bulgaria; **6**, Dolni Disan, FYROM; **7**, various localities in Moldavia; **8**, various localities in Ukraine; **9**, Kertch, Ukraine; **10**, various localities in Hungary; **11**, Maragheh, Iran; **12**, Oryahovo, Bulgaria; **13**, Yulafli, Turkey; **14**, Sahabi, Libya; **15**, Middle Siwaliks (Dkoh Pathan Fm), Pakistan; **16**, Jebel Barakah, United Arab Emirates. The map was taken from www.bing.com/maps. [planned for page width]