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An early mammoth maxilla from north-western Greece

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ABSTRACT

A right elephantine maxilla bearing the two last molars is described and discussed here. The specimen comes from the fluvial deposits filling up the post-molassic morpho-tectonic valleys of the upper Haliakmon river-system in NW Greece. According to indirect evidence it would be chronologically framed between 3.5 and 3.0 Ma (late Pliocene). A detailed morphological and metrical comparison supported by computed tomography allows ascribing the maxilla to a primitive Eurasian mammoth species, more advanced than the "Hadar type" of mammoth from Ethiopia and less than *Mammuthus africanavus* from North Africa or Pleistocene southern mammoths (*Mammuthus meridionalis*) from Eurasia. The molars show strong affinities to several Eurasian specimens recently referred to *Mammuthus rumanus*, a species that needs, however, a systematic revision.

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1. Introduction

A set of newly discovered or re-examined specimens from southeastern Mediterranean, and China indicate that the mammoth lineage invaded Eurasia from Africa as early as 3.0 Ma (Lister et al., 2005; Wei et al., 2006; Markov, 2012), a time that roughly coincides with the first appearance of *Elephas* Linnaeus, 1758 in the Indo-Pakistani region (Nanda, 2002). Early steps of the Eurasian evolutionary history and distribution patterns of both lineages remain, however, little understood (Lister et al., 2005, 2013; Saegusa and Gilbert, 2008; Obada, 2010; Todd, 2010). There is also uncertainty about the taxonomic identity of the important but rare pre-Pleistocene Eurasian fossil mammoth finds, an issue complicated by the plesiomorphic similarities on dental remains among early representatives of *Mammuthus* Brooks, 1828, *Elephas* and *Loxodonta* Anonymous, 1827 (e.g., Sanders, 2007; Saegusa and Haile-Selassie, 2009; Obada, 2010; Todd, 2010), and their radiation in quick succession during latest Miocene-early Pliocene (Shoshani et al., 1998; Capelli et al., 2006; Brandt et al., 2012).

Elephants are common elements of the Quaternary mammal faunas of both continental and insular Greece, though findings, especially from the mainland, are usually isolated, fragmentary, and often lacking stratigraphic information (see Doukas and Athanassiou, 2003; Tsoukala et al., 2011 for recent overviews). Since the late 19th century but especially between 1960 and 1980, numerous mammoth remains, mostly isolated molars and tusk fragments, were reported from several late Pliocene and Pleistocene sites across Greece (Doukas and Athanassiou, 2003, and literature listed). A significant number of those sites are located in northwestern Greece, along the post-molassic morpho-tectonic valleys of the upper Haliakmon river-system (Fig. 1).

A right maxilla from this area, housed today in the Museum of Geology and Palaeontology of the Aristotle University of Thessaloniki (LGPUT), exhibits particularly primitive features that deserve a separate description and comparison. This specimen belongs to the old collections of the LGPUT, dated between 50s and 70s, and most probably represents a surface finding delivered by local residents to the Museum.

Abbreviations

Institutional: LGPUT, Museum of Geology and Palaeontology of the Aristotle University of Thessaloniki; NHML, Natural History Museum of London; MMK, MacGregor Memorial Museum, Kimberley; IGF, Museum of Geology and Paleontology, Florence University; FGGUB, Laboratory of Paleontology and Stratigraphy, University of Bucharest; **Metrical/nomenclatural**: L#, serial lamella number; NP, number of plates/lamellae; LF, lamellar frequency; ET, enamel thickness; HI, hypsodonty index; OA, occlusal angle of M3; acca, anterior central accessory conule; pcca, posterior central accessory conule

2. Regional and chronological setting

The partial maxilla LGPUT MP-04 lacks original stratigraphic information. A handwritten label states "Tsotylion" as the area of its provenance, suggesting it collected from the fluvial mid-late Pliocene to early Pleistocene (hereinafter referred to as Plio-

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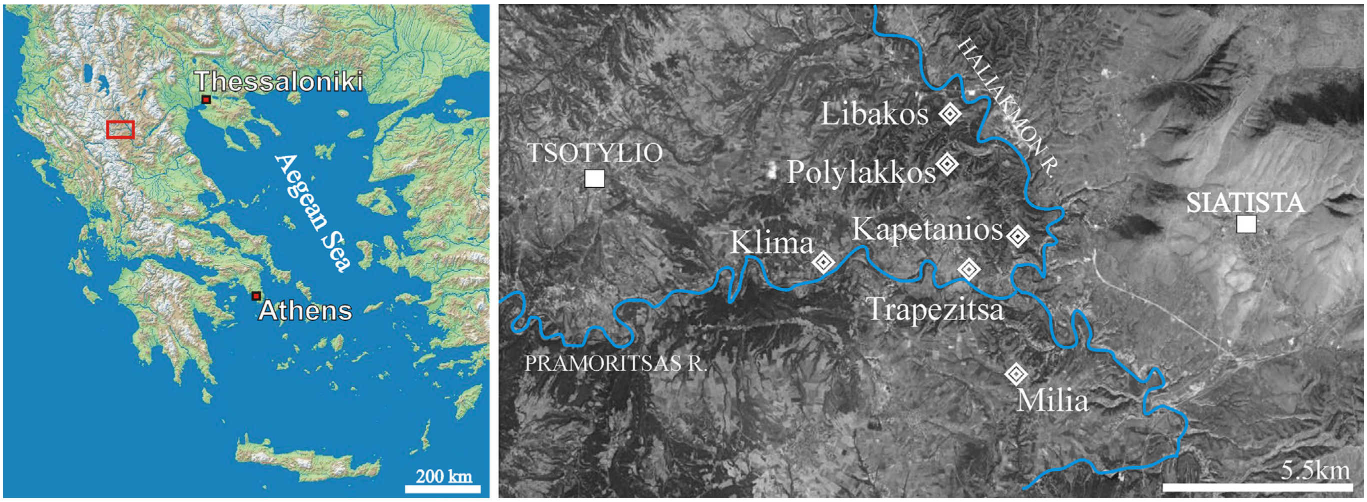

Fig. 1. Geographical context of Tsotylio region, provenance area of LGPUT MP-04, and location of main neighbouring late Pliocene-early Pleistocene mammal fossil sites (diamonds) referred into the text. Map adapted from Google Earth.

Pleistocene) sandy deposits exposed mainly E–SE of Tsotylion village and along Pramoritsas river in NW Greece (Fig. 1). Eltgen (1986) and Fountoulis et al. (2001) indicate that continental deposition in this area started no earlier than 3.4 Ma. In agreement with this age, the oldest well-documented fossil mammal assemblage from this region comes from Milia, a few kilometers south (Fig. 1). Milia fauna includes among others *Homotherium crenatidens*, *Ursus etruscus*, *Agriotherium* sp., *Mammut borsoni*, *Anancus arvernensis*, *Tapirus arvernensis*, *Stephanorhinus jeanvireti*, *Sus arvernensis*, *Alephis* sp., *Gazella borbonica*, *Croizetoceros ramosus*, and *Procapreolus cusanus*, altogether indicating an MN16a mammal fauna of about 3.0 Ma (Tsoukala, 2000; Guerin and Tsoukala, 2013; Cregut-Bonnoure and Tsoukala, 2014; Tsoukala et al., 2014). Hence, we suggest that oldest land mammal fossils from the strict studied area should be roughly dated between 3.5 and 3.0 Ma. Judging from the similar rusty-reddish coloration of LGPUT MP-04, and the Milia fossils we suspect that they may come from a similar lithology, i.e., strongly oxidized sand to muddy sand deposits. Personal observations on the wider area indicate that this particular lithostratigraphic unit is restricted between Milia, Klima, and Trapezitsa villages (Fig. 1). From the same region, Steensma (1988) described several mammal remains from different fossil spots (Klima, Libakos, Polylakkos, Kapetanios; Fig. 1) discovered during the 1980s in the thick bedded light-yellow to whitish coarse sands and gravels dominating around Polylakkos village, W–SW of Siatista city. Except for the Klima fossil spot, from where only two isolated *Anancus* Aymard molars are known, the rest of the sites include hippos, and small stenonoid horses indicating an age between 2.0 and 1.4 Ma (Steensma, 1988; pers. obs. 2014). Fossils from these sites show a different type of fossilization than LGPUT MP-04, whereas elephant remains represent more advanced mammoth morphs (Steensma, 1988; pers. obs. 2014). The Trampatzion fossil collection of the neighbouring Siatista city also includes several elephant specimens from the same area collected by locals; none of them resemble, however, LGPUT MP-04 in fossilization and primitiveness.

3. Methods

The third (last) and the penultimate upper molars are indicated as M3 and M2, respectively. Dental description follows Todd (2010). As in Sanders (2007: Figs. 4 and 5) the anterior (acca) and posterior (pcca) accessory central conules, originally representing unfused conules between lamellae in primitive proboscideans, are here used equally to mark midline expansions of the occlusal enamel figures. Root terminology follows Sher and Garrutt (1987). Measurements are according to Maglio (1973) and Lister (1996). The number of lamellae (NP) does not include anterior and posterior talons (-ids), and platelets that are indicated by a "x" or "p" respectively (see Lister and van Essen, 2003: 48); a "+" symbol before or after the number of lamellae, and/or the measured length indicates that the tooth is incomplete mesially or distally, respectively (e.g., Palombo and Ferretti, 2005 and later authors). All linear measures are in millimeters. We introduce a new measure for the M3, called the "occlusal angle" (OA). OA is the angle formed during the emergence process between the tangent lines on the worn and unworn occlusal surfaces of the tooth in (ortho-)lateral view (Fig. 2A). OA differs from the angle of eruption introduced by Aguire (1969 *fide* Lister, 1996) in that it takes into account only the functional surfaces of the crown and does not require early wear stages. The occlusal angle of mammoth M3's is independent from the wear stage of the tooth ($r^2 = 5\times10^{-4}$, p(uncorrelated) = 0.90; n = 29; Fig. 2B) but highly related to the well-known mesiodistal shortening of the mammoth skull through time (Maglio, 1973; Lister, 1996; Lister and Stuart, 2010) in combination with the relative lengthening and the increase of plate density of the last upper molar itself.

Principal components analyses were performed using PAST free software, version 2.03 (Hammer et al., 2001). A computed tomography of LGPUT MP-04 has been performed by a MX16 PHILIPS CT scanner at Platon SA, Thessaloniki. The specimen has been set with the occlusal surface of M2 in horizontal position and X-slices were taken at 1.5 mm intervals.

Primitive *Elephas* comparative molar morphology is based on *E. ekorensis* from Ekora and Kanapoi, Kenya and Omo, Ethiopia (ranging from 4.2 to 2.7 Ma), and *E. recki brumpti* from Woranso-Mille, Afar, Member B of Shungura, Omo, Ethiopia (3.8–3.6 and 3.5–2.9 Ma, respectively), and Koobi Fora, Kenya (3.5–3.3 Ma) (Maglio, 1970, 1973; Beden, 1979; Sanders et al., 2010; Sanders and Haile-Selassie, 2012). The earliest *E. nawataensis* from Nawata Fm, Lothagam, Kenya, dated between 6.7 and 5.2 Ma, is known only by a juvenile mandible and some molar fragments (Tassy, 2003) that cannot be directly compared with our specimen. We suspect that *E. planifrons* dental sample from Siwaliks described by Falconer and Cautley (1845–1849) and Osborn (1942) may be not homogeneous either chronologically or taxonomically (see also Markov,

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