

***Mammuthus meridionalis* from Apollonia-1 (Mygdonia Basin, Northern Greece) and its Importance within the Early Pleistocene Mammoth Evolution in Europe**

G.E. Konidaris¹, D.S. Kostopoulos², G.D. Koufos²

(1) Palaeoanthropology, Senckenberg Centre for Human Evolution and Palaeoenvironment, Eberhard Karls University of Tübingen, Rümelinstr. 23, 72070 Tübingen Germany, geo.konidaris@gmail.com

(2) Laboratory of Geology and Palaeontology, Department of Geology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece

Introduction-Fossiliferous locality

Mammoths originated in Africa at the end of the Miocene and during the late Pliocene migrated through the Levant to Eurasia, where they thrived until the Late Pleistocene. Eurasian mammoths show significant morphological adaptations through time, related to the general dietary trend from browse-dominated mixed feeding towards grazing, as a response to the changing environments of the Pleistocene (Lister & Sher, 2001). These adaptations are related to biomechanical advantages for grazing and increased resistance to abrasion, and are evident in skull and dental morphology: shortening and heightening of the cranium and mandible, enamel thinning, and increase in the height of the molar crown (hypsodonty) and the number of enamel plates in the molars (Lister, 1996). Mammoths (*Mammuthus*) are distinguished in Europe into four species: 1) a primitive morph, commonly, but tentatively, attributed to *M. rumanus* (early Villafranchian, late Pliocene); 2) the southern mammoth *M. meridionalis* (middle Villafranchian–Epivillafranchian, Early Pleistocene); 3) the steppe mammoth *M. trogontherii* (Middle Pleistocene); and 4) the woolly mammoth *M. primigenius* (late Middle–Late Pleistocene). Although most of the mammoth species are properly defined, the time and mode of the transitions/replacements are still open issues, and several intermediate/mosaic morphotypes or subspecies have been proposed by various researchers. Here, we conduct a preliminary study on the mammoth from Apollonia-1, and we discuss its evolutionary and biostratigraphic importance within the evolution of the Early Pleistocene European mammoths.

The fossiliferous locality Apollonia-1 (APL) is located in Mygdonia Basin (Northern Greece), about 45 km east of Thessaloniki. The locality was discovered in 1991 (Koufos *et al.*, 1992) and subsequently excavated in 1992–1996 and 2012–2014, and provided a wealth of mammal fossils. APL is situated within the Platanochori Formation (Pre-Mygdonian Group), which consists of sands, sandstones, conglomerates, silty sands, silts, clays, marls and marly limestones, indicating the local development of small lakes and swamps (Koufos *et al.*, 1995). The APL fauna is younger than Dmanisi (~1.8 Ma; Georgia) and older than Untermaßfeld (~1.0 Ma, Epivillafranchian; Germany), showing similarities with Pirro Nord (1.5–1.2 Ma; Italy); therefore, a correlation to the second half of the late Villafranchian is possible for the locality.

Description-Comparison

The APL sample includes a hemi-mandible with the third lower molar (m3) (Figure 1), an isolated m3, two isolated upper third molar (M3) fragments (Fig. 2) and a maxilla fragment with deciduous dentition (DP2–DP3), the latter briefly discussed in Athanassiou & Kostopoulos (2001). The m3 of the hemi-mandible (Fig. 1) is characterized by PN (plate number): >11, LF (lamellar frequency): 4.6 and ET (enamel thickness): 3.1; the M3 (Fig. 2) by PN: >13, LF: 5.5, ET: 2.8 and HI (hypsodonty index): 1.48; the DP2 and DP3 bear 4 and 8 plates, respectively. The APL molars are different from those of *M. rumanus*, the latter having lower PN, LF and HI, and higher ET values. On the other side, the APL molars are also clearly outside the range of the *M. trogontherii* sample from its type locality Süßenborn (Germany) and the sample of *M. primigenius* from Předmostí (Czech Republic), which have higher PN, LF and HI values, and thinner enamel. The values of all these parameters of the APL molars are comfortably within the range of *M. meridionalis*, showing the diagnostic features of this species (Lister, 1996), and unambiguously indicate an attribution to the southern mammoth, in accordance with the morphology of the mandible, e.g., caudal border of the ramus posteriorly inclined (Fig. 1).

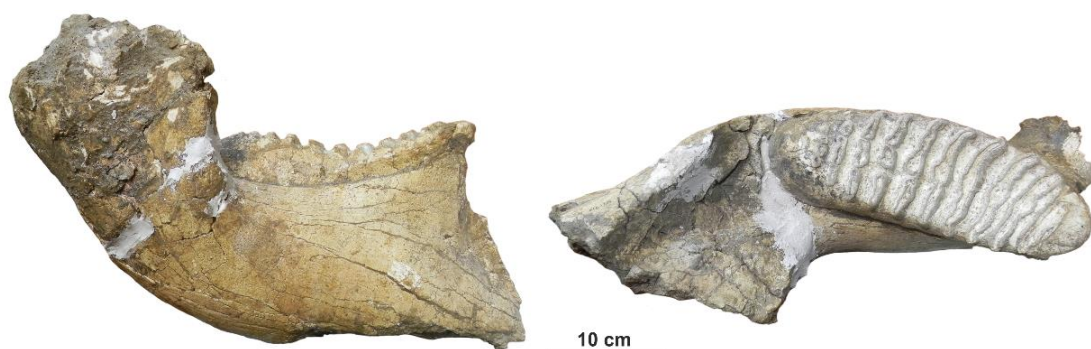


Figure 1. Right hemi-mandible with m3 of *Mammuthus meridionalis* from Apollonia-1 in lateral and dorsal view. Anterior to the right.

Within *M. meridionalis*, the APL molar sample is more derived than *M. m. gromovi* from Liventsovka (middle

Villafranchian, Russia). On the other side, it is more primitive from the post-Jaramillo–pre-Brunhes specimens from Imola (Italy) and Dorst (The Netherlands) [both “*M. meridionalis* advanced” according to Lister et al. (2005) and Palombo & Ferretti (2005)], which show a higher HI in their M3s, within the range of *M. trogontherii*, and they could alternatively belong to the steppe mammoth as in the case of the Voigtstedt and Edersleben specimens (Germany; Van Essen, 2011). The APL mammoth fits well within the late Villafranchian *M. m. meridionalis* (typical) sample from Upper Valdarno (Italy), however, occupying its upper range in terms of PN and LF, and slightly surpassing its HI values (data from Van Essen, 2003). On the other side, the APL molars are plotted at the lower values of *M. m. tamanensis* from Sinyaya Balka (Russia; Baygusheva & Titov, 2012). The best match of the APL molars is perhaps with the sample from the post-Upper Valdarno late Villafranchian localities from Italy, correlated to the Farneta Faunal Unit and attributed to *M. m. vestinus* by Azzaroli (1977) [although the validity of this subspecies is questioned (Palombo & Ferretti, 2005)], as well as with the Epivillafranchian (Jaramillo) *M. m. depereti* from St. Prest (France) sample. Finally, the eight plates of the APL DP3, combined with its large length, is unique so far within *M. meridionalis*.



Figure 2. Left M3 fragment of *Mammuthus meridionalis* from Apollonia-1 in occlusal and labial view. Anterior to the left.

Taxonomic and biostratigraphic conclusions

The dentognathic remains of the APL mammoth permit its attribution to *M. meridionalis*. The relatively deep mandibular corpus is a derived condition. The dental features also indicate an evolutionary stage somewhat more derived than the Upper Valdarno mammoth (beginning of late Villafranchian) in terms of the higher NP in the DP3 and the marginally higher HI in the M3. In this aspect, the APL mammoth fits better with corresponding specimens from localities correlated to the second half of the late Villafranchian and the Epivillafranchian. Whether this sample should be distinguished at subspecific level is open to discussion. These results are in agreement with the existing biochronological correlation of the APL fauna and further support the potential biostratigraphic significance of *M. meridionalis* within the Early Pleistocene, although conclusions based on limited/fragmentary sample should always be taken with caution.

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