Cause and timing of late Early – early Middle Pleistocene European mammoth turnover with special emphasis on Hungary

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During the period between 1.0-0.7 Ma, the climate became drier and colder, consequently the forested areas were rolled back and the steppe vegetation was expanded in Europe. The process begun in the Eastern margin of the continent (e.g. at Taman Peninsula or at the lower Don River area; Tesakov, 2008 and Shchelinsky et al., 2010), and coincided with the first immigration of the steppe mammoth (*Mammuthus trogontherii*), which progressively replaced the indigenous *Mammuthus meridionalis* (often associated with closed habitats). The transition between the two species in Europe was achieved by input from Eastern Asia, either in the form of migrating herds or by gene flow without the long distance movement of individual animals (Lister et al., 2005).

Micromammal assamblages from Russia (Sarkel and Sinyaya Balka) indicate mosaic environment combining closely spaced steppe-like (*Spermophilus, Spalax, Allocricetus, Cricetulus, Cricetus*), wooded (*Sorex, Apodemus, Clethrionomys*), meadow (*Desmana*), and desert (*Plioscirtopoda*) biotopes under conditions of relatively warm climate. At the Taman Peninsula, both *M. meridionalis* and *M. trogontherii* are documented (third molars with low tooth crown and 14-15 plates and third molars with 16-19 plates and higher crown). Van Essen (2011) mentioned some individuals, which show mosaic characteristics (low crown and high plate number) due to the hybridization of the overlapping *M. meridionalis* and *M. trogontherii* populations in such a mosaic environment. At

the same time, *M. trogontherii* was absent from the central and western part of Europe (e.g. Saint-Prest, France, where the large mammalian community indicates an open forest landscape under a temperate wet climate; Guerin et al., 2003).

The older layers of the rich 900 ka micromammal fauna from the Somssich Hill 2 locality (South Hungary) are characterized by the dominance of *Lagurus* and cricetids (mainly *Cricetus runtonensis*), which are indicators of probably the oldest known open steppe vegetation of Hungary. In contrast, mice (*Apodemus*), dormice (*Glis, Muscardinus, Dryomimus*) and the dominance of voles like *Pitymys, Myodes* and *Pliomys* in younger parts of the section are indicative of warmer, more humid climate and more closed (shrubby or forested) habitats (Pazonyi et al., 2013). *M. trogontherii* remains has not been found so far from this period in Hungary.

The 800 ka micromammal fauna of Villány 8 (South Hungary) indicates mosaic environment with the co-occurrence of both steppe (e.g. *Spermophilus, Spalax, Cricetus, Allocricetus, Prolagurus*) and forest elements (e.g. *Sorex, Apodemus, Myodes*) (Jánossy, 1986).

About 800-700 ka, the opening of the vegetation reached Western Europe. The first *M. trogontherii* remains in the central and western part of the continent can be dated to the beginning of this period, nevertheless, contemporaneously *M. meridionalis* populations were also

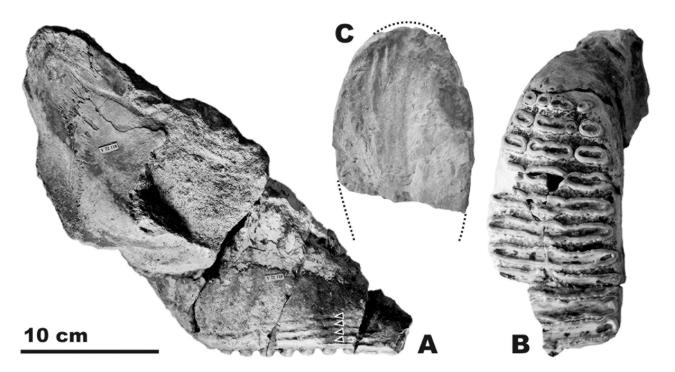


Fig. 1. *Mammuthus trogontherii* upper left third molar (Hungarian Natural History Museum, V.72.116) from Üröm Hill (North-Hungary) from lingual (A) and occlusal (B) view. C, posterior view of a plate in midcrown area. The arrows on A indicate well-developed cement furrows.

documented in the region (e.g. from Győrújfalu in Hungary or from the Ponte Galeria Formation in Italy, and from Dorn-Dürkheim 3 in Germany; Palombo & Ferretti, 2005 and van Essen, 2011). Despite the slight recovery of closed vegetation, M. meridionalis almost entirely disappeared from Europe by the end of this period. Only the remains of hybrid individuals support, that the last representatives of the species had to be present in some refugia at that time. Such mosaic specimen (an upper third molar with a reconstructed plate number of 17 or even 18 and relatively high crown but with plesiomorph enamel, thicker than 3.0 mm, see Fig. 1. and Virág, 2009 for details) was found at the 800-700 ka locality, called Üröm Hill (North Hungary). Similar specimens turned out from Campo del Conte in Italy (although Palombo et al., 2003 identified the molar as M. meridionalis) or from Voigtstedt and Edersleben in Germany (van Essen, 2011).

The fauna of Üröm Hill mainly contain hygrophilous taxa (like *Desmana thermalis*, *Mimomys savini* or *Hippopotamus antiquus*) and the micromammal fauna of the contemporaneous Kövesvárad locality (North Hungary) unequivocally indicate warm, humid climate and closed, forested vegetation with the dominance of dormice (*Glis, Muscardinus*) and forest voles (*Myodes*) (Jánossy, 1986). Similar warm-temperate conditions with mainly forest elements and scanty open landscape indicators (such as *Spermophilus*) are typical for Voigtstedt (Maul & Parfitt, 2010).

By 600 ka, only *M. trogontherii* occurred in Europe, as at Süssenborn (Germany), the type locality of the species (Lister et al., 2005). The extinction of the *M. meridionalis* populations was most plausibly triggered not solely by the immigration of the steppe-adapted, grazer *M. trogontherii* from Eastern Asia, but the arrival of the browser or mixed-feeder *Elephas antiquus* from Africa through the Levant, which happened broadly 900-800 ka (Albayrak & Lister, 2012). The earliest occurrence of the latter species in Hungary is most plausibly Győrújfalu. Following this period, *E. antiquus* has unfortunately very scanty record in Hungary.

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