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Palaeodietary reconstruction of fossil proboscideans from Hungary and Romania

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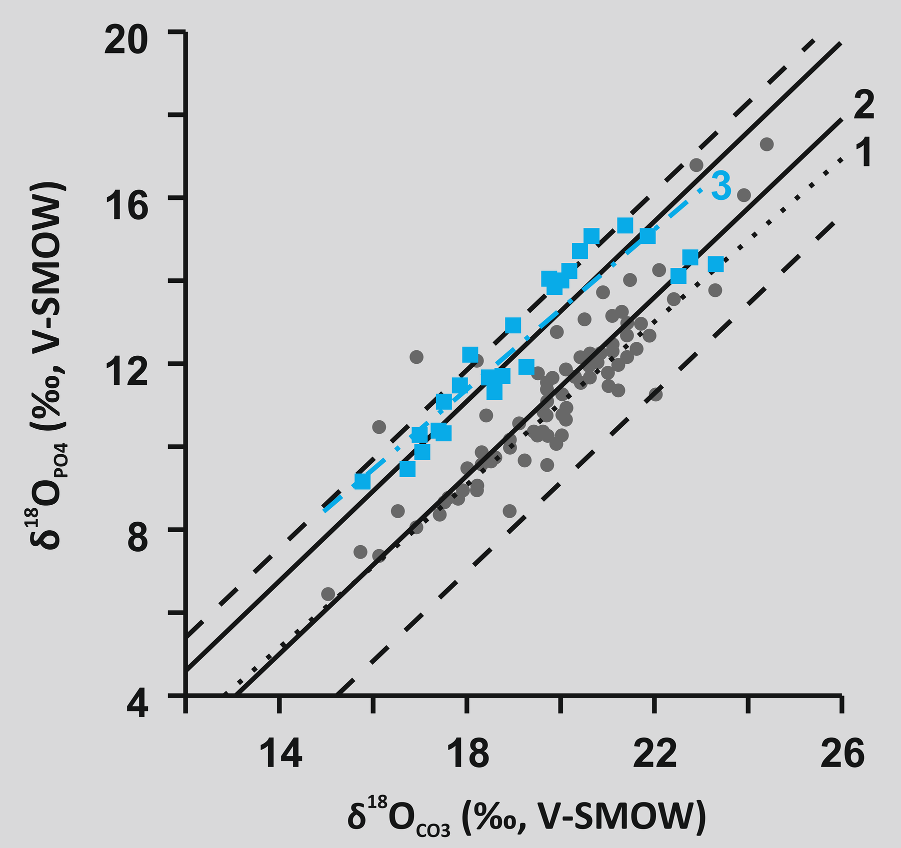
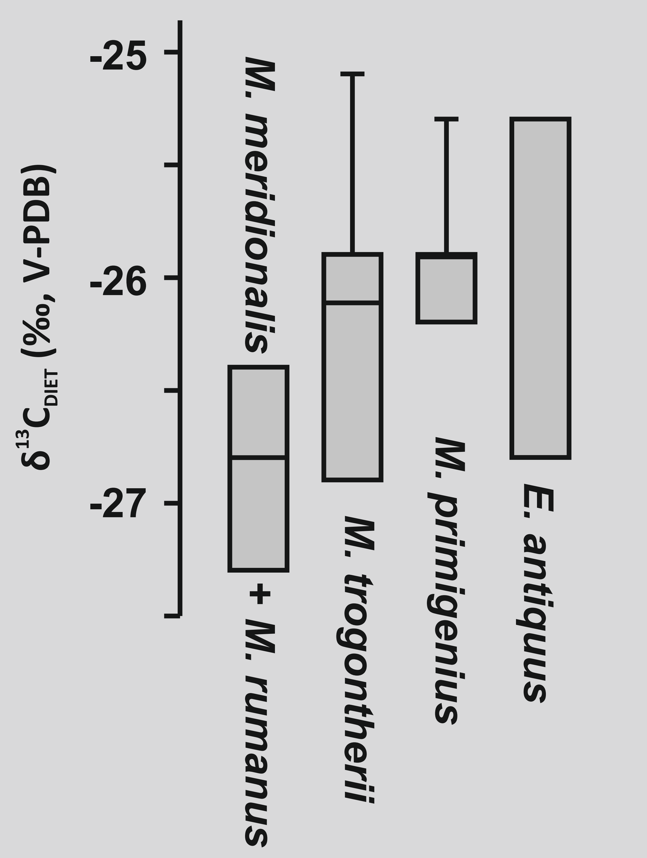
INTRODUCTION

According to Maglio (1973) the emergence of elephantids from Miocene gomphotheres reflects an adaptive shift in their method of chewing, which helped to process a newly available food source, grass. Since the latter is more abrasive than leaves, it provided a selective force on the evolution of tooth crown height. Although this assumption is widely accepted, it is not yet properly confirmed and only few studies dealt with the alimentary habits of the successive species so far (e.g. Palombo & Curiel 2003, Green et al. 2005 or Rivals et al. 2012). The present study is based on samples taken from molar teeth of *Mammuthus meridionalis*, *M. trogontherii*, *M. primigenius*, and *Elephas antiquus* from Hungary and *Mammuthus rumanus* (including the holotype and proposed neotype) from Romania.

ISOTOPIC COMPOSITION

The oxygen isotopic composition of phosphate in enamel of homoeothermic obligate drinkers is directly related to the $\delta^{18}O$ of body water, which is related to the $\delta^{18}O$ of ingested water. The latter can be linked to the isotopic composition of the local meteoric water, which shows significant correlation with mean annual temperature (MAT). The carbon isotopic composition of molars of herbivorous mammals reflects the photosynthetic pathway of the consumed plants (with a 14.1‰ offset according to Cerling et al. 1999), hence indirectly the paleoflora. As a consequence, the isotopic composition of molar enamel can be interpreted as an archive of dietary and climatic information. In addition, since the phosphate and carbonate are cogenetic oxygen-bearing phases in isotopic equilibrium with the same reservoir (body water) at the same temperature (37°C for mammals), a linear correlation exists between the $\delta^{18}O_{PO_4}$ and $\delta^{18}O_{CO_3}$ values. Due to this fact, coupled measurements can be used for obtaining information about post-mortem alteration effects (Iacumin et al. 1996).

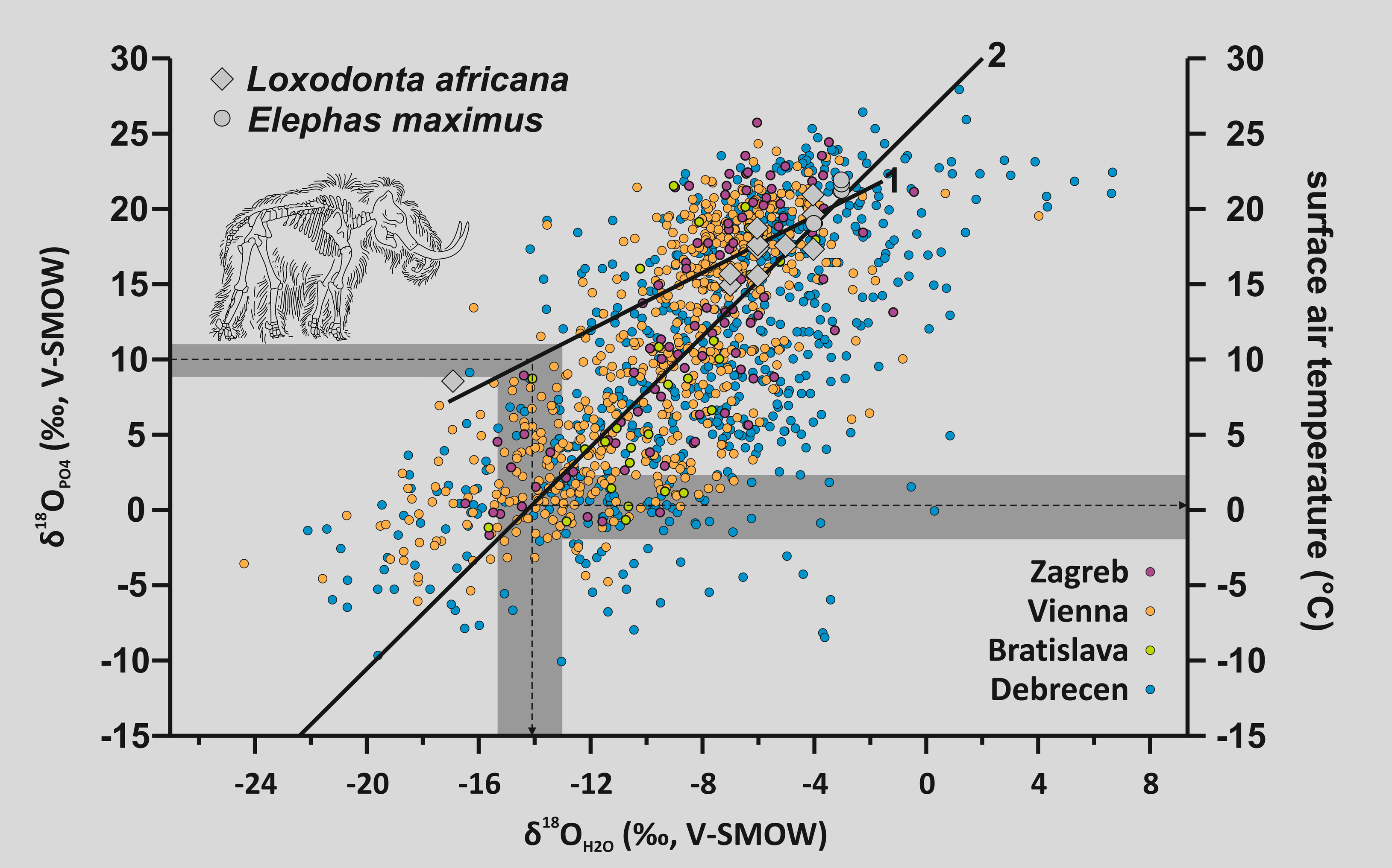




1: Equilibrium line of Iacumin et al. (1996) for modern mammals, 2: mammoth equation of Kovács et al. (2012) with its 95% confidence zone for grey dots, 3: reduced major axis regression line ($\delta^{18}O_{PO_4}=0.97\times\delta^{18}O_{CO_3}-6.1$) fitted to the data of the present study (blue squares).

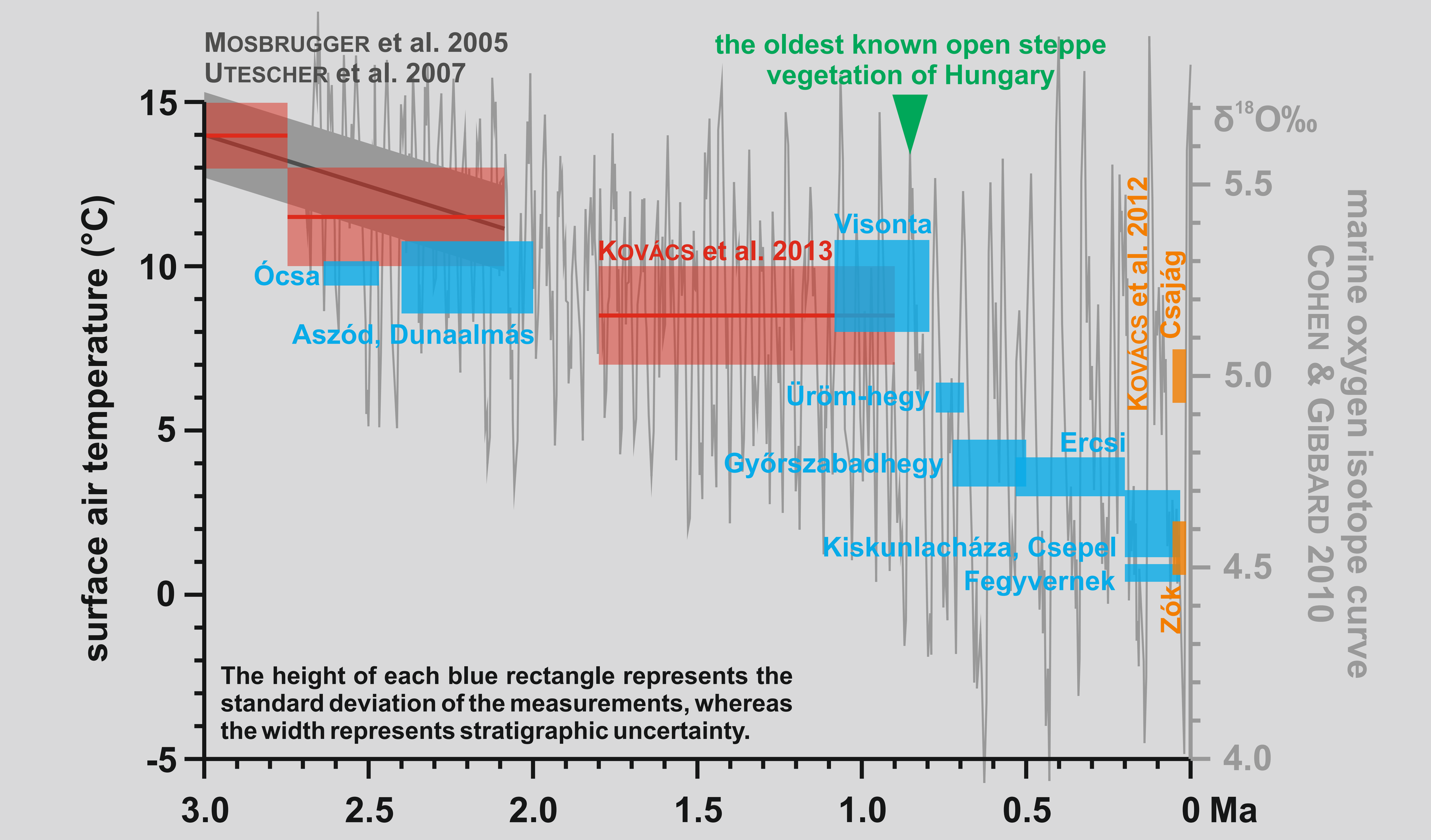
The $\delta^{13}C$ values range from -13.2‰ to -7.4‰ (V-PDB), which suggest a C3 diet. The average and minimum values of the successive species were increasing with 1‰ during the Pleistocene which is explicable by drier climate and more open vegetation.

Samples were pre-treated following the method of Koch et al. (1997) and the isotopic compositions were measured by the method of Vennemann et al. (2002) and Spötl & Vennemann (2003). The oxygen isotopic composition of the carbonate and phosphate from enamel show strong linear correlation (r^2=0.75) and plot close and parallel to the expected equilibrium line derived from modern mammals, however with an average of 2‰ higher intercept.



An equation made by Ayliffe et al. (1992) was used for converting the raw $\delta^{18}O_{PO_4}$ data into a value, which represents the isotopic composition of the meteoric waters in the time of the deposition of enamel (1) . A linear regression (2) was fitted with reduced major axis method to the present-day precipitation and surface air temperature data of four proximal GNIP meteorological stations (Zagreb, Vienna, Bratislava, Debrecen) and the resulting equation was used in order to calculate MAT estimates for the region: $T=1.84\times\delta^{18}O_{H_2O}+26.4$ (r^2=0.46, n=1300).

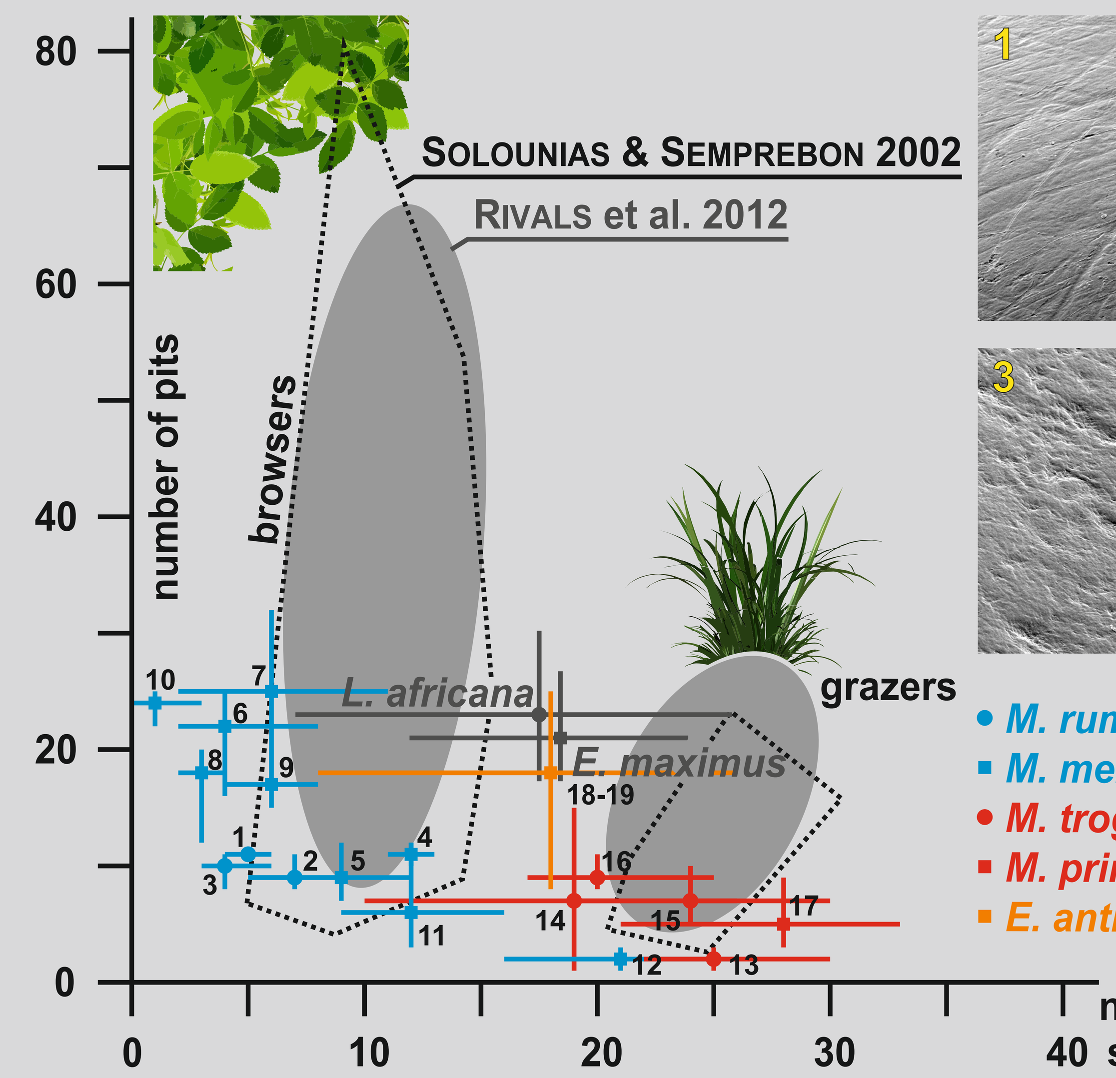
PALAEOTEMPERATURE ESTIMATES

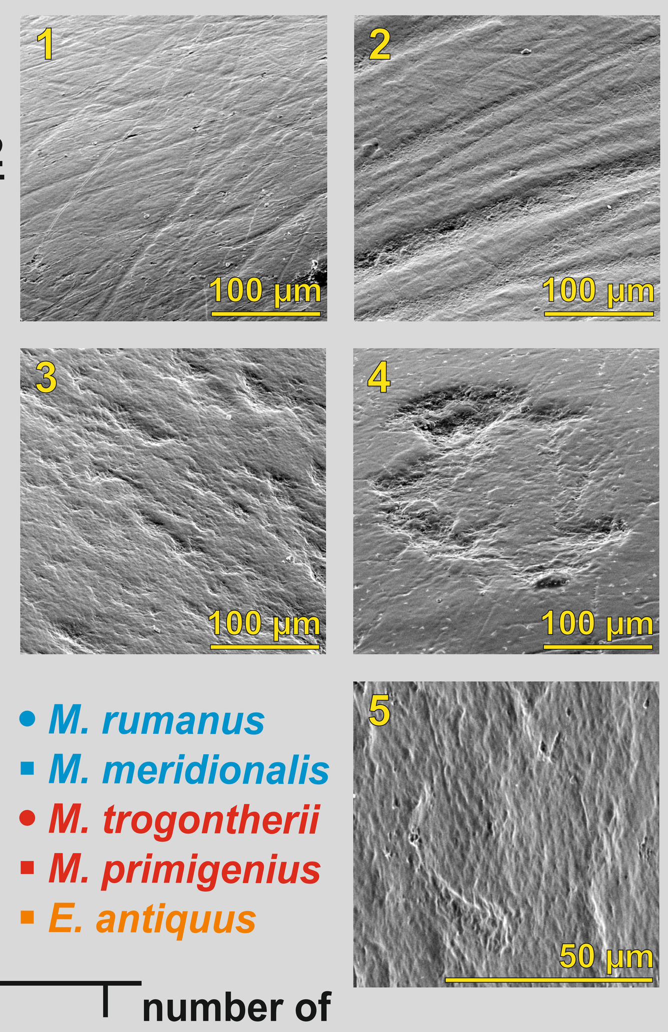


Each isotopic sample in the present study is a bulk of three or more subsamples over the whole height of a single plate, in order to represent the whole period of tooth formation. The overall $\delta^{18}O_{PO_4}$ range is 10.4‰-15.4‰ (V-SMOW). Early Pleistocene samples reflect a MAT range of 8-10°C, similar to present value in Hungary (11°C), whereas our results suggest that the MAT was approximately 5°C lower during the cold periods of the Middle Pleistocene and up to 9-10°C lower during the Late Pleistocene glaciations. The data are in good agreement with other climatic proxies from the same period (e.g. Kovács et al. 2013 or Szabó et al. 2014).

MICROWEAR SCAR ANALYSIS

As an independent dietary proxy, the microwear pattern of enamel was examined, which is attributed to the interaction during mastication between tooth and abrasives. The microwear tracks are represented in browsers by more circular wear features (pits) and fewer elongated ones (scratches), whereas the opposite is true for grazers. The analysis was carried out using Microware 4.0 software on SEM micrographs made from the surface of high-resolution epoxy casts. Although the magnification used here (300×) differs from the 35× magnification used in regular light-microscopic studies, the field of view (0.4×0.3 mm) and the total number of observed scars (usually 20-40 on each image) was approximately the same, therefore we used the light microscopic data of Solounias & Semprebon (2002) and Rivals et al. (2012) for comparison. Palombo et al. (2005) or Todd et al. (2007) reached similar conclusions regarding the comparability of these methods.





Microwear features of enamel samples from Hungarian and Romanian elephantids. Abbreviations: 1: Tuluceşti, 2: Cernăteşti, 3: Ócsa, 4: Aszód, HNHM V.82.6., 5: Aszód, HNHM V.69.1120., 6: Szomód, HNHM. V.75.35.1., 7: Süttő, HNHM V.72.113., 8: Nyergesújfalu, HNHM V.79.9., 9: Almásfüzitő, HNHM V.79.13., 10: Budapest, HNHM V72.7., 11: Visonta, HNHM V.90.14., 12: Visonta, HNHM V.82.61., 13: Visonta, HNHM V.82.60., 14: Visonta, 644/3., 15: Üröm-hegy, HNHM V.72.116., 16: Ercsi, HNHM V.75.138., 17: Kiskunlacháza, HNHM V.80.119., 18-19: Győrszabadhegy.

Abbreviations: HNHM = Hungarian Natural History Museum.

Typical microwear features of the studied specimens. 1: Fine scratches on a *M. trogontherii* molar (HNHM V.72.116.) from Üröm-hegy. 2. Coarse scratches on a *M. primigenius* molar (HNHM V.90.14.) from Visonta. 3: Pits on a *M. meridionalis* molar (HNHM V.72.7.) from Budapest. 4: Gouge on a *M. meridionalis* molar (HNHM V.59.1120.) from Aszód. 5: Enamel area of a *M. meridionalis* molar (HNHM V.79.9.) from Nyergesújfalu, on which prisms are visible due to attritional wear.

According to our microwear data, *M. rumanus* and *M. meridionalis* were browsers, whereas *M. trogontherii* and *M. primigenius* were mixed feeders or more likely grazers. Variation of wear features within a single molar is less than 30% (or usually less than 10% in the case of grazers).

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