MORPHOMETRICAL AND PALAEOECOLOGICAL STUDY OF HUNGARIAN PLIOCENE AND PLEISTOCENE ELEPHANTIDS

Theses of the PhD dissertation

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BUDAPEST

2013

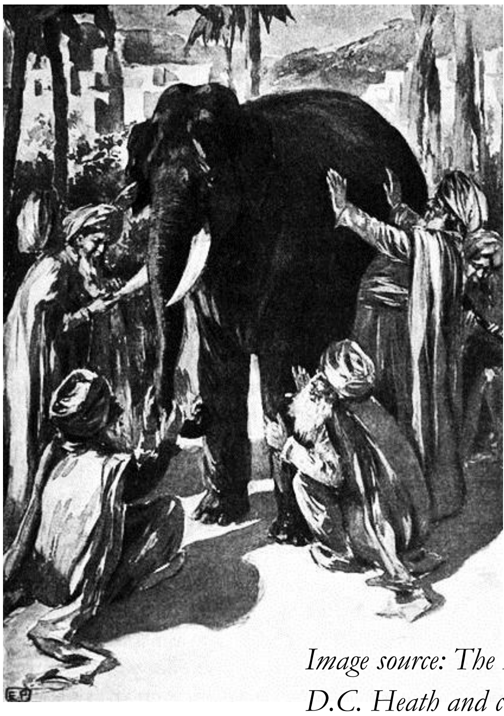

Image source: The Heath Readers by Grades, D.C. Heath and co. (Boston), 1907., p. 69.

The Blind Men and the Elephant
(John Godfrey Saxe)

It was six men of Indostan
To learning much inclined,
Who went to see the Elephant
(Though all of them were blind),
That each by observation
Might satisfy his mind.

The *First* approach'd the Elephant,
And happening to fall
Against his broad and sturdy side,
At once began to bawl:
"God bless me! but the Elephant
Is very like a wall!"

The *Second*, feeling of the tusk,
Cried, -"Ho! what have we here
So very round and smooth and sharp?
To me 'tis mighty clear
This wonder of an Elephant
Is very like a spear!"

The *Third* approached the animal,
And happening to take
The squirming trunk within his hands,
Thus boldly up and spake:
"I see," quoth he, "the Elephant
Is very like a snake!"

The *Fourth* reached out his eager hand,
And felt about the knee.
"What most this wondrous beast is like
Is mighty plain," quoth he,
"'Tis clear enough the Elephant
Is very like a tree!"

The *Fifth*, who chanced to touch the ear,
Said: "E'en the blindest man
Can tell what this resembles most;
Deny the fact who can,
This marvel of an Elephant
Is very like a fan!"

The *Sixth* no sooner had begun
About the beast to grope,
Then, seizing on the swinging tail
That fell within his scope,
"I see," quoth he, "the Elephant
Is very like a rope!"

And so these men of Indostan
Disputed loud and long,
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
And all were in the wrong!

Introduction

Proboscideans were widely distributed on almost all continents during the Pliocene and the Pleistocene. The presence of 5 different taxa is documented from the Hungarian sediments deposited in the aforementioned period. Those are the *Elephas antiquus* (straight-tusked elephant), the *Mammuthus rumanus* (Rumanian mammoth), the *M. meridionalis* (southern mammoth), the *M. trogontherii* (steppe mammoth) and the emblematic representative of the Late Pleistocene cold periods as well as one of the most frequent fossil herbivore large mammals of Hungary, the *M. primigenius* (woolly mammoth).

Despite the fact, that the proboscideans (especially the elephantids) are an extremely intensively studied group, there are several gaps in our current knowledge on these animals. It is widely accepted, for example, that the emergence of the family Elephantidae from the Miocene gomphotheres reflects a major adaptive shift in their method of chewing and the increase in molar hypsodonty as well as the further morphological changes of the elephantid cheek teeth appears to be a response to help process a newly available food source (i.e. grass) (see MAGLIO, 1973 or CERLING 1997, 1999). The latter assumption is however not yet confirmed by independent studies related to the dietary preferences of the successive species. It is not clear, that the apparently gradual steps of the molar evolution can be traced back to purely anagenetic change of European mammoth populations or rather explicable by cladogenetic events, which occurred outside the continent. The number of the species in the mammoth-lineage and the boundaries between the successive taxa are also controversial.

The aims of the dissertation were to make a comprehensive revision of the Hungarian elephantid molars and tusk remains and to clarify the chronology of the most important in-country localities. Consequently, it was possible to study a more than 2.5 million year-long, well-documented evolutionary process and the underlying environmental factors, furthermore, to discuss the above mentioned uncertainties.

Material and methods

Since my masters thesis focuses on all the available and informative Hungarian elephantid molars and mandibles (142 remains from 40 different localities) stored in the Invertebrate and Vertebrate Palaeontological Collection of the Hungarian Natural History Museum and in the Geological Museum of the Geological and Geophysical Institute of

Hungary (formerly Geological Institute of Hungary) and due to the page limitation of the present dissertation, only the most important fossils and localities are discussed in this work (those, which are morphologically and stratigraphically unique or interesting). In the case of the *M. rumanus*, which is statistically underrepresented in the aforementioned collections, the holotype material and some plesiomorph molars stored in the Palaeontological Laboratory of the University of Bucharest and in the Emil Racoviţă Institute of Speleology in Bucharest were also studied for comparative purposes.

The taxonomical revision of the elephantid remains were partly based on previously known and on newly developed identification methods. In order to study the microstructure of the molar enamel and the tusk dentine, more than 50 thin sections were made. The measurements were taken from photomicrographs with the ImageJ software (RASBAND 2011, ABRAMOFF et al. 2004). In addition, Michael LOCKE (University of Western Ontario, London, Canada) made available to me his own unpublished data related to recent elephants.

For the stratigraphical interpretation, data from the scientific literature related to the Hungarian and the contemporaneous Eurasian localities were collected. The evolutionary and palaeobiogeographic framework of the present study was achieved in the light of the most resent results and by the re-interpretation of the contradicting information.

Microwear scar analysis in the present study was carried out on photomicrographs made by a Hitachi S-2600-N scanning electron microscope in the Department of Botany of the Hungarian Natural History Museum from the surface of 84 high-resolution epoxi casts, although SOLOUNIAS & SEMPREBON 2002 or SEMPREBON et al. 2004 developed a method, which uses low-magnification stereomicroscopy. The number, dimensions and orientation of each wear feature were analyzed with the Microware 4.02 software, developed by Peter UNGAR (Department of Anthropology, University of Arkansas, Fayetteville, USA).

Tooth enamel and cementum powder were manually separated with the usage of tungsten-carbide impregnated rotary tools. Each sample was pre-treated according to the method of KOCH et al. (1997). The stable oxygen and carbon isotopic composition of the structural phosphate and carbonate were analysed with a ThermoFinnigan Gasbench II and a TC-EA linked to a Finnigan Delta Plus XP gas mass spectrometer in the Stable Isotope Laboratory of the University of Lausanne.

In order to make palaeotemperature estimates, the raw oxygen isotopic ratios of the structural phosphate were converted by the equation of AYLIFFE et al. (1992) to a value, which represents the isotopic composition of the meteoric waters in the time of the deposition of molar enamel. The mean annual paleotemperature was calculated with the equation of a linear regression, which was fitted to the stable oxygen isotopic and the surface air temperature data of four proximal GNIP stations (Zagreb, Vienna, Bratislava, Debrecen) with the reduced major axis method of the PAST software (HAMMER et al. 2001).

Theses

1. Thin sections of 13 molars (including the type material of *Mammuthus rumanus*) were made in order to expand the database of FERRETTI (2003) on enamel microstructure of the Eurasian mammoth taxa. It seems that the relative thickness of the enamel layers significantly differs in the case of each successive species.
2. It was showed, that the enamel layers are not only visible on polished and etched surfaces under reflected light microscopy, but are easily distinguishable in thin sections using trans-illumination as well.
3. It was proved, that the enamel microstructure of the molars from Montopoli (see FERRETTI 2003 for details) is essentially identical to the type material of *M. rumanus*.
4. The analysis of the enamel layers confirmed that the lower left third molar from Ócsa described by GASPARIK (2010) and VIRÁG & GASPARIK (2012) is indeed referable to *M. rumanus* despite of its anomalously thin enamel.
5. It was showed, that not only the molar morphology, but the enamel microstructure of the most ancient *M. meridionalis* teeth as well are intermediate between *M. rumanus* and the typical representatives of the taxon.
6. Based on more than 40 thin sections of 5 different proboscidean tusks, a comprehensive three-dimensional model was introduced, which (in contrary to the helicoidal dentinal tubule arrangement of LOCKE 2008) explains the observed morphology in all the three main sectional plane of ivory. The model is in good agreement with the extinction pattern in tangential sections and the propagation of natural cracks.
7. The analysis of small tusk fragments with reduced opacity detached along the incremental surfaces confirmed, that the dentinal tubules are not straight (see LOCKE 2008) but sinusoidally curved structures (see e.g. MILES & WHITE 1960, MILES & BOYDE 1961, MILES & POOLE 1967) and there are systematic shifts in the undulatory pathway of the adjacent tubules.

8. Based on the dimensions of the observed features, the phase shift of the adjacent dentinal tubules is caused by the undulation (with a radial extension of about 250 μm) of the cementum-dentine junction.
9. It was suggested, that the undulatory nature of the dentinal tubules cannot solely be explained by a model based on intercellular pressure only (as RAUBENHEIMER et al. 1998 or RAUBENHEIMER 1999 did), but rather can be traced back to a genetic regulation, which appeared once within the group Elephantoidea.
10. On the basis of the taxonspecific nature of the so-called Schreger pattern, which can be seen by unaided eye on transverse profiles of several proboscidean tusks, *E. antiquus* remains were identified from the Quaternary gravels of the open cast lignite mine near Bükkábrány.
11. New taxonomic identification methods were based on the complex underlying structure of the Schreger pattern. If rhomboid shaped areas are visible in the transverse section of a tusk fragment or longitudinal ridges and the so-called feather pattern are present on the tangential crack surfaces or the dentinal tubules have sinusoidally undulating pathway on radial profiles, it is sure that the specimen belongs to an elephantoid (any proboscidean more derived than *Phiomia* according to the phylogenetic system of GHEERBRANT & TASSY 2009). If the wavelength of the tubules is less than 1 mm or the radial height of the rhomboid-shaped areas is less than 500 μm, than the fragment belongs to an elephant, but not to a mammoth. The same is true if the rhomboid-shaped areas or the longitudinal ridges are wider than 900 μm.
12. Through the summary and interpretation of the most current research of several Eurasian mammoth-bearing localities, a palaeobiogeographical and evolutionary scenery was made for the region, on which an accurate chronology of the most important in-country localities was based. The stratigraphical system of GASPARIK (2001, 2004, 2010) was further expanded by 6 standard biozones related to the Late Pliocene and Early Pleistocene of Hungary. A taxon-free chronology with 5 zones was also introduced based on the evolution of molar morphology. For the broad applicability, the regional differences of the zonations were discussed briefly.
13. It was suggested, that the hybridization between the indigenous *M. meridionalis* and the immigrant *M. trogontherii* populations was responsible for the observed mosaic morphology of the holotype specimen (inventory number: HNHM V.72.116) of the „*Archidiskodon meridionalis ürömensis*" VÖRÖS, 1979 taxon. It was showed, that

similar teeth are not unprecedented in the contemporaneous (i.e. 800-700 ka) European mammoth material.

14. The microwear scar analysis of 17 Hungarian elephantid remains and the type material of *M. rumanus* confirmed that the increasing abrasiveness of the masticated food in the case of the successive species indeed provided a selective force on the evolution of molar morphology. On the basis of the observed wear features *M. rumanus* and *M. meridionalis* were both browsers, often with extensive bark consumption, while *M. trogontherii* and *M. primigenius* were rather mixed feeders or more likely grazers.
15. The carbon isotope composition of molar enamel suggests a C3 diet for all the Hungarian elephantids. The average and minimum values of the successive taxa were increasing with approximately 1‰ during the Pleistocene. The latter phenomenon is explicable by drier climate and more open vegetation.
16. The palaeotemperature estimates (made from the raw oxygen isotopic ratios of the phosphate in enamel) are in good agreement with the environmental history of the surrounding areas. The mean annual temperature was approximately 5°C lower than the recent value during the cold periods of the Middle Pleistocene and up to 9-10°C lower during the Late Pleistocene glaciations.

Summary and conclusions

Three different methods are described and refined in the first part of the dissertation, which can be used for taxonomic identification of elephantid cheek teeth and tusks on a generic or specific level. These methods allowed to make a comprehensive revision of the Hungarian elephantid remains.

The second part clarifies the exact chronology of the most important in-country localities and places them within the framework of the evolution and paleobiogeography of the mammoth-lineage in Eurasia. A standard taxon based chronology of the local material is given, but a taxon-free zonation was also established based on the evolution of molar morphology. For the broad applicability, the regional differences of the zonations are discussed briefly.

The third part reveals the dietary and habitat preferences of the elephantids with a multiproxy approach (stable carbon isotopic analysis of the structural carbonate in molar enamel and microwear scar analysis of the enamel surface). The study of alimentary habits not only provided information about the ecological interrelationships of the contemporaneous species, but gave valuable insights on palaeovegetation. The resulting environmental data was compared with the palaeotemperature estimates inferred from the stable oxygen isotope analysis of the structural phosphate in enamel.

It appears that the increasing abrasiveness of the food (achieved by more phytolith content and more exogenous grit and dust) indeed provided a selective force on the evolution of tooth crown height within the mammoth-lineage and sooner or later the increasing hypsodonty triggered the rest of the morphological changes of the molars.

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