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Taxonomic identification of mammoth molars based on enamel microstructure

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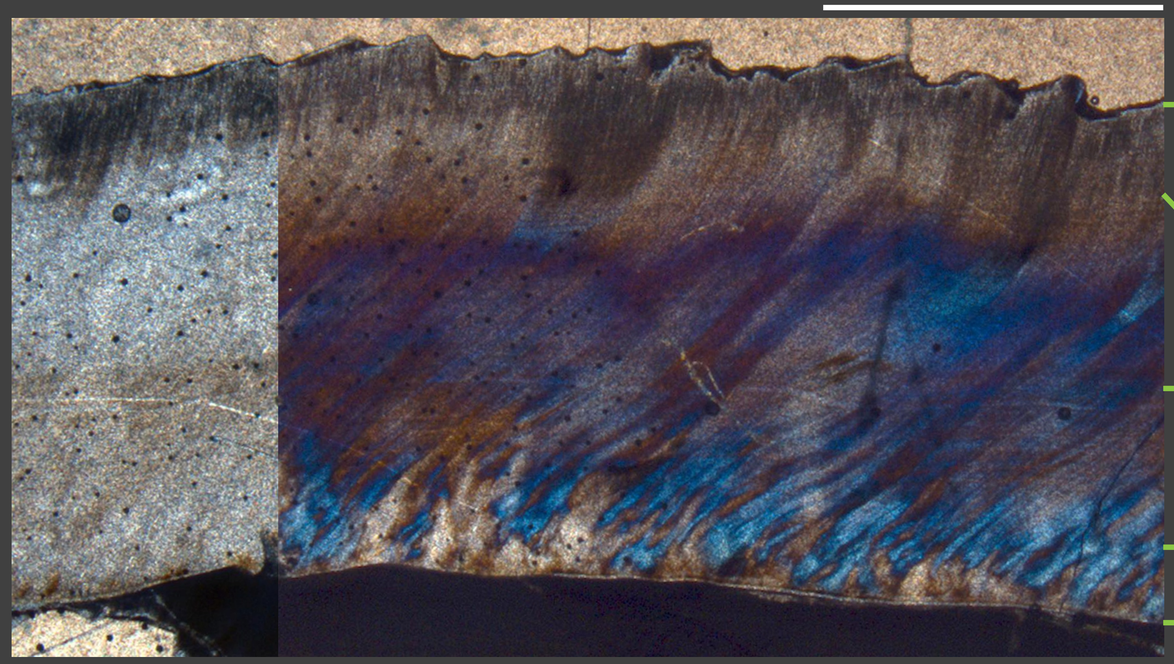
INTRODUCTION

Enamel matrix is secreted by a closely linked sheet of cells (ameloblasts) that differentiate from the internal enamel epithelium of the tooth (Dean 2006). Enamel maturation involves removing the protein and water content of the original matrix, and increasing the size of the crystallite nuclei deposited during matrix production. As a consequence of the latter processes, mature enamel becomes heavily mineralised, and so, normally the best preserved of hard tissues (Hillson 2005 and Ungar 2010). The enamel crystallites are usually organised into approximately 4-12 µm wide bundles, which are called prisms. These prisms almost never run straight through the enamel which is achieved by a coordinated movement of ameloblasts within the internal enamel epithelium. According to Hillson (2005), this complex arrangement makes the enamel stronger and gives the worn surface particular characteristics that enable it to function in grinding or cutting. Based on the shapes, orientations and packing patterns of the adjacent prismatic bundles, the enamel of the elephantids can be separated into four different layers (Ferretti 2003):

2 mm



Sagittal thin section of the enamel of a *M. rumanus* right upper third molar from Cernăteşti (Romania). The photograph on the left were made using transillumination without polarizing filters, whereas the image on the right were made with crossed polarizer and analyzer lenses (i.e. crossed Nicol prisms).

MATERIAL AND METHODS

Enamel samples detached from *Mammuthus rumanus, M. meridionalis, M. trogontherii, and M. primigenius* molars found in Hungary and Romania were analysed. In addition, samples were taken from the material found on the St. Paul Island (Pribilof Islands, Alaska, USA). Although Ferretti (2003) examined the same enamel features using reflected light microscopy on sections etched with hydrochloric acid, Vasile et al. (2012) showed that transillumination of sagittal thin sections is also applicable for the analysis due to the difference in the optical properties of each layer when viewed under crossed polarizing filters. Thickness measurements of the layers were taken on photomicrographs of the sections along a line perpendicular to the EDJ with the usage of ImageJ software. As the thickness may vary locally, a minimum of 10 measurements was taken at different sites on each section, and then a mean value was calculated for each specimen. The enamel cap at the apex of the tooth cones where (according to Ferretti 2008) 3D enamel is absent were avoided during sampling.

ENAMEL MICROSTRUCTURE

The enamel cementum junction (ECJ) is heavily wrinkled, and the enamel can often be seen to bulge along the boundary plane.

Adjacent to the ECJ there is a thin layer which lacks prismatic organization. Since this prismless part is often hardly distinguishable from the layer discussed below under relatively low magnification, it was treated here together with the outer layer.

In the outer layer, the prisms are parallel to the occlusal plane.

In the middle layer, the prisms are rising concordantly towards the outer surface of the enamel. The boundary between this middle and the above discussed outer layer is marked by a sudden decrease of the inclination of the prisms.

Adjacent to the EDJ, there is a part in which the orientation of the prisms makes an irregular impression. This part is often called inner or 3D enamel.

The enamel dentine junction (EDJ) is more or less smooth.

RESULTS

Our results showed that the enamel microstructure of the molars from Montopoli (see Ferretti 2003 for details) is essentially identical to the type material of *M. rumanus* from Tuluceşti and Cernăteşti (Romania) and a *M. rumanus* specimen from Ócsa (Hungary). The inner layer makes up 15-16%, the middle makes up 50-55% and the outer makes up 30-35% of the total enamel thickness. Based on molars from e.g. Aszód, Szomód, or Dunaalmás in Hungary, an approximately 4-5% relative thickening of the middle layer at the expense of the outer one is characteristic for mammoths from the beginning of the Early Pleistocene (former MN17 Biozone). Typical *M. meridionalis* remains (such as the type material from Upper Valdarno, see Ferretti 2003 for details) show additional 5% relative thickening of the middle layer which was compensated by the further thinning of the outer layer. The type material from Süssenborn (Ferretti 2003) and the specimens from several contemporaneous or younger Hungarian localities (e.g. Ercsi, Kiskunlacháza and Kecskemét) prove that the enamel evolution continued in the case of the *M. trogontherii*. According to our data, the middle layer of the latter species makes up 2-3% more of the full enamel thickness than in the case of the latest *M. meridionalis* populations, whereas the inner layer is proportionately thinner. The middle layer of *M. primigenius* samples (from e.g. Tiszalök and Fegyvernek in Hungary) makes up even 70-80% of the full enamel thickness which means additional 5-10% thickening related to the *M. trogontherii*. This was compensated by the approximately 5% thinning of both the inner and the outer layer separately. The inner layer makes up roughly 5%, whereas the outer makes up 10-20% of the total enamel thickness in the case of *M. primigenius* samples. The latest *M. primigenius* material (e.g. from the Pribilof Islands) show the most thinned inner and outer layers. In contrast to the mammoth lineage, the inner layer makes up usually more than 20% of the total enamel thickness in the case of our *E. antiquus* samples.

DISCUSSION

During the more than 2.5 million years of evolution of the Eurasian mammoth lineage, the molar morphology underwent several important changes, such as the multiplication of the plates forming the tooth, the heightening of the crown, and the thinning of the enamel. All of these processes are usually considered as a probable adaptation to a progressively predominant grass diet (see e.g. Maglio 1973). According to Ferretti (2008), decussating prisms (e.g. in the inner layer) enhances resistance to crack propagation in the enamel of teeth subjected to high occlusal stresses, whereas occlusally rising prisms (e.g. in the middle layer) are more resistant to abrasive wear. Therefore the above discussed evolution of the inner structure of the enamel (i.e. the proportional thickening of the middle layer, in which the prisms are angled to the occlusal surface, at the expense of the less resistant parts) can be interpreted as an adaptation which kept the rate of wear to a minimum as the whole enamel had become thinner and the diet had become more abrasive. As consequence of this process, the relative thicknesses of the enamel layers slightly but significantly differ in the case of each successive species, therefore the analysis of the inner enamel structure could be used as a diagnostic character for intrageneric systematic which allows the rapid and coarse identification of mammoths from even a small fragment of a molar.