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Functional aspects of the enamel evolution in *Mammuthus* (Proboscidea, Elephantidae)

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The functional significance of the change in enamel thickness and microstructure shown by the molar of the European mammoth lineage is discussed. It is suggested that the extreme reduction of the enamel thickness in *Mammuthus primigenius* may represent an adaptation to increase occlusal pressure during mastication. Consistently, the enamel microstructure underwent a differentiation that led to a relative thickening of the layer with occlusally oriented prisms, as a probable response to the more intense abrasion caused by the increased occlusal stress. The evolution of the enamel in *Mammmuthus* can be interpreted as an optimisation of the occlusal structures related to a progressive specialisation towards a predominantly grazing diet.

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INTRODUCTION

A major trend in the evolution of *Mammuthus* is the progressive thinning of the enamel of the molars. This trend was accompanied by an increase in plate number and crown height. While these last changes can intuitively be explained as a means to increase tooth durability and grinding ability (see Janis & Fortelius 1988), the functional meaning of the enamel thinning is less obvious. Maglio (1972, 1973) suggested that this trend, paralleled in several elephant lineages, is aimed at maintaining an optimal distance between adjacent enamel crests on the occlusal surface, as plates, increasing in number during evolution, become more crowded. Indeed, an inverse relationship links enamel thickness to lamellar frequency and thus to plate number (Fig. 1). In fact, as the structural limitation of the skull and jaws prevents any major increase in tooth length, the only way to add new plates is to increase their frequency. However this tendency would progressively reduce the spacing between successive crests, eventually bringing them into contact. Nevertheless, if at the same time enamel thickness is also reduced, an optimal interval between successive crests is maintained and so is the efficiency of the tooth.

A basically different function is however also possible. An important role performed by the occlusal structures of mammalian teeth, particularly in herbivores, is in fact the attainment of a rather high occlusal ‘pressure’, hereafter referred to as stress (Rensberger 1973). The critical stress, necessary for food breakage, is controlled by the load applied by the masticatory muscles and by the area of contact between opposite teeth. In particular, occlusal stress is inversely proportional to the contact area (Rensberger 1973; Fortelius 1985). In elephants, during occlusion, the enamel crests of the upper molars meet those of the lower ones, which move mesially in the power stroke, determining food comminution (Fig. 2). It can be thus hypothesised that the progressive reduction of the enamel thickness, as it occurred in the evolution of *Mammuthus*, counterbalanced the multiplication of the enamel crest, in order to maximise occlusal stress. To test this hypothesis molar samples representing three time-successive populations of European mammoths have been analysed.

MATERIAL AND METHODS

The relative occlusal area occupied by the enamel has been measured in upper M3s of *M. meridionalis* from Upper Valdarno (Early Pleistocene), *M. trogontherii* from Süssenborn (early Middle Pleistocene) and *M. primigenius* from Predmostì (Late Pleistocene; raw data from Musil 1968), by calculating an enamel surface index (ESI). Only moderately worn molars with fully developed occlusal surface were considered. These molars were either the only tooth in use in each jaw, or were functioning with the remains of the M2. A standard occlusal area was chosen in order to obtain comparable values for each specimen. This zone is located in the anteriormost portion of the occlusal surface and corresponds to a rectangle with an antero-posterior size of 100 mm (Fig. 3). Within the standard area the occlusal width of the tooth is more or less uniform. Each wear figure (the transverse section of the plates on the masticatory plane) forms a complete, subrectangular, enamel loop which can be represented, with good approximation, as two parallel transverse crests. The ESI has been calculated for each tooth as follows:

$$ESI = Ncrest \times FW' \times ET / (FW' \times 100)_{occl.surf}$$

where Ncrest is the number of crests in 100 mm of occlusal length, FW' is the maximal width of the occlusal surface (functional width) in the standard zone and usually coincides with the greatest occlusal width of the tooth (FW), ET is the average enamel thickness of the crests and occl.surf. is the total standard occlusal area. ET has been measured for each enamel crest perpendicularly to the

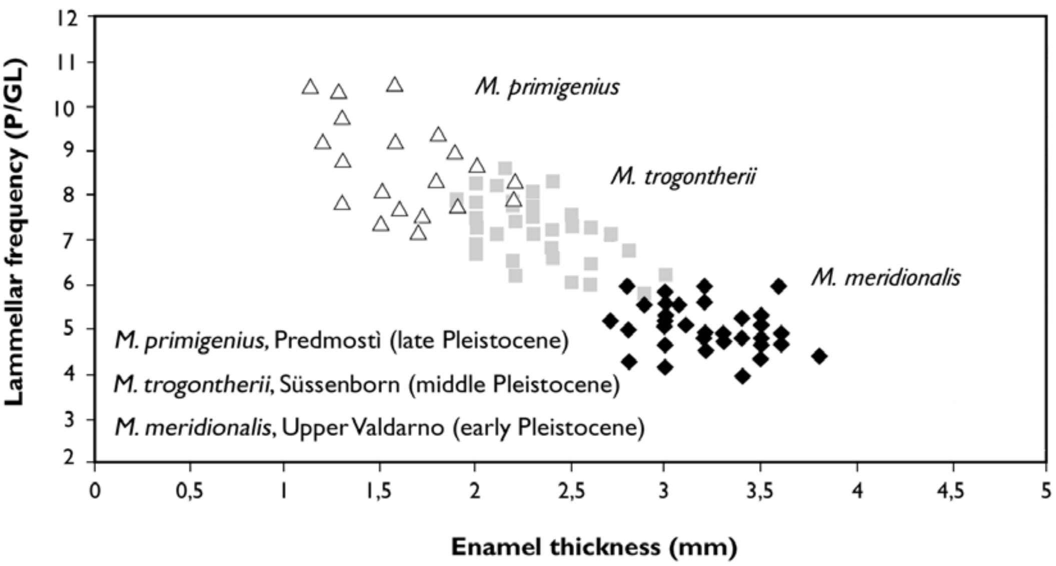

Figure 1 Relationship of enamel thickness to lamellar frequency in M3 of *Mammuthus*. P= number of plates; GL = greatest length.

Table 1 Enamel surface index (ESI) for *Mammuthus* upper M3. n = number of specimens; SD = standard deviation;
* = molar measures from Musil (1968).

taxon	sample	n	ESI	SD	t test significance
M. meridionalis	upper Valdarno	19	0.34	0.47	
M. trogontherii	Süssenborn	14	0.32	0.35	$p = 0.05$
M. primigenius	Predmosti *	15	0.26	0.56	$p < 0.05$

plate's vertical axis. The index gives a rough estimate of the relative area occupied by enamel on the molar occlusal surface, and is independent from the absolute size of the tooth. Even if care is taken in order to use teeth at a similar stage of wear, there is nonetheless a certain amount of variability within the samples as far as this parameter is concerned. However, differences in enamel thickness between molar subsamples representing successive stages of wear are not great and became significant only in highly worn specimens (Ferretti 1998).

RESULTS

In each of the considered species the relative enamel occlusal surface represents approximately one third of the total standard masticatory surface (Table1). There is, however, an evident decrease of the ESI from the oldest species (*M. meridionalis*) to the youngest one (*M. primigenius*) (Table 1). The difference between the *M. meridionalis* (0.34) and *M. trogontherii* (0.32) samples is indeed still very slight, closely approaching significance ($P = 0.05$), while *M. trogontherii* and *M. primigenius* are separated by a more marked change of the ESI, which reduces from 0.32 to 0.26. A pair-wise comparison, using Student's t-test, proved that the difference between the *M. trogontherii* and *M. primigenius* means is significant at the $P< 0.05$ level. The Predmosti sample is characterised by a relatively high variability if compared to that displayed by the other two samples (Table 1). This may be due either to the presence of different morphotypes in the *M. primigenius* population from Predmosti or, more generally, reflect a greater morphological variability of the molar of the woolly mammoth.

DISCUSSION

The present analysis shows the role of the enamel thickness in controlling the area of contact between opposing teeth in *Mammuthus*. In fact, despite an almost two-fold increase in lamellar frequency (from 5.4 to 9.5) the ESI sensibly reduced from *M. meridionalis* to *M. primigenius*, as a consequence of the enamel thinning. Considering that the woolly mammoth is sensibly smaller than its forerunners (2.5-3 m versus 3.5-4 m shoulder height), it cannot be excluded that the extremely thin enamel that characterises *M. primigenius* is the result of a positive allometric scaling related to the body size reduction. However, the even more dramatic size reduction that characterised the evolution of the endemic *Elephas (Palaeoloxodon) mnaidriensis* from Sicily, left the enamel thickness

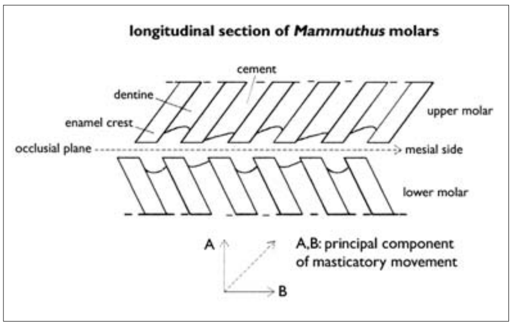

Figure 2 Diagrammatic longitudinal section of two molars (upper and lower) of *Mammuthus* near the occlusal plain.

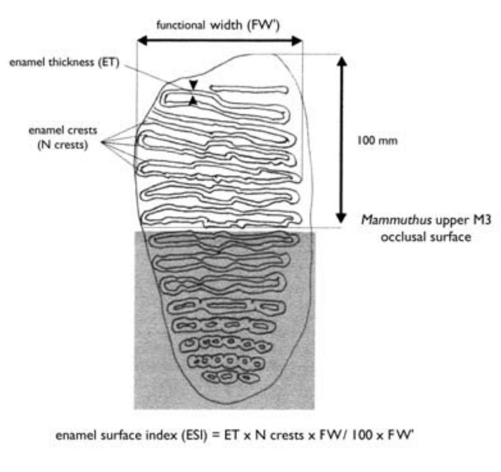

Figure 3 Tooth measurements used to calculate the ESI.

almost unchanged (Ferretti 1998). This suggests that enamel thickness is not directly related to size, but is controlled by the functional requirement of the masticatory apparatus. The enamel thinning in *M. trogontherii* compensated for the increase in the number of enamel crests, leaving practically unchanged the enamel surface/total occlusal surface ratio (ESI). This would have assured the maintenance of the critical occlusal stress during mastication.

A further enamel thinning caused, on the contrary, a sensible reduction of the ESI in *M. primigenius*, with the result of increasing occlusal stress, other parameters (as muscular loading) being unchanged. At present it is not possible to quantify the effect of such an increase on masticatory efficiency, pending a detailed knowledge of the dynamics of the mastication process in elephants, in particular at a small scale. Anyway, possible advantages deriving from relatively higher stresses applied between occluding structures could be those of cutting plant fibers more efficiently, and more firmly blocking food particles between opposing crests, as they tend to slide away during the power stroke. Furthermore, as the shearing ability is improved, the number of chews per bolus should diminish, allowing, in theory, a greater food intake per unit of time.

Enamel structure and occlusal stress

Elephants possess a rather complex enamel structure (Bertrand 1988; Pfretzschner 1994; Ferretti 1998). According to the orientation of prisms relative to the occlusal surface, three layer can be distinguished from the EDJ to the layers surface (Ferretti 1998; Fig. 4): an inner layer formed by prism bundles running in the three dimensions of space (3-D enamel of Pfretzschner 1994), an middle layer where prisms run at an angle toward the occlusal surface, and an outer layer where prisms are parallel to the occlusal surface. The enamel microstructure so far described underwent a differentiation during the evolution of the *Mammuthus* lineage that led to a relative thickening of the zone with occlusally oriented prisms (Ferretti 1998), as shown in Table 2. Rensberger & Koenigswald (1980) showed that resistance to abrasion depends also on the orientation of the prisms with respect to the occlusal plane. In particular the situation offering the highest resistance against wear is that with prisms running normally to the occlusal surface. Thus, the differentiation of

Table 2 Enamel differentiation in *Mammuthus* upper M3. ET = enamel thickness (from Feretti 1998).

		enamel layers thickness (%)			
taxon	sample	inner layer	intermediate layer	outer layer	ET(mm)
M. meridionalis	upper Valdarno	17	62	21	3.2
M. trogontherii	Süssenborn	13	66	21	2.3
M. primigenius	various sites	9	75	16	1.5

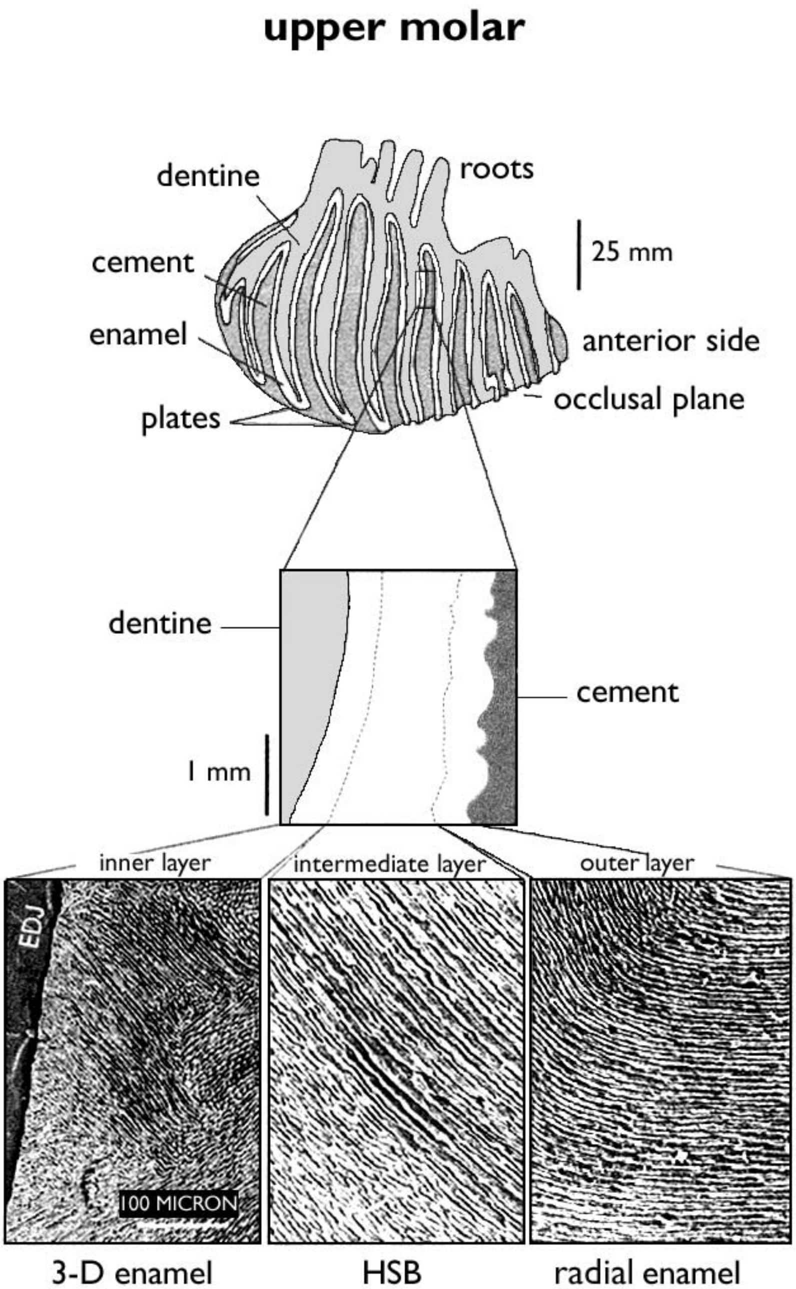

Figure 4 Morphology and enamel microstructure (SEM micrographs at the bottom) of an upper molar of *Mammuthus*. HSB: Hunter-Schreger bands; EDJ: enamel - dentine junction.

the enamel as occurred in *Mammuthus* seems to be consistent with the hypothesis of the increased occlusal stress, as this would cause a more intense abrasion of the tooth.

CONCLUSION

The present analysis suggests that, as in other groups of mammals, also in elephants changes in enamel thickness could be related to the control of critical occlusal stress ('pressure'). In particular the extreme reduction of the enamel thickness in *Mammuthus primigenius* may represent an adaptation to increase occlusal stress during mastication. The evolution of the enamel in *Mammmuthus* can be thus interpreted as an optimisation of the occlusal structures related to a progressive specialisation toward a predominantly grazing diet. In fact an increase in occlusal stress could have had the twofold function of blocking the grass fibers between opposite crests and of improving shearing ability. This could have resulted in an increased capacity to deal with rather flat and fibrous plants. Moreover, if grinding efficiency is augmented, fewer chews per bolus should be needed, allowing a major food intake per time unit, which is advantageous if only low quality food is largely available. Finally, the enamel microstructure underwent to a differentiation in order to compensate for the increased wear caused by the augmented occlusal stress: the middle layer, composed of occlusally oriented prism, shows a relative thickening.

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REFERENCES

Bertrand , P., 1988 - Evolution de la structure de l'émail chez les Proboscidea primitifs: Aspect phylogénétique et fonctionnel - In: Russel, D.E., Santoro, J.P. & Sigogneau-Russell, D. (eds.): Teeth revisited: Proceedings of the VIIth international symposium on dental morphology. Paris 1986 - Memoires Muséum National d'Histoire Naturelle (C) 53: 109-124

Maglio, V.J., 1972 - Evolution of mastication in the Elephantidae - Evolution 26: 638-658

Maglio, V.J., 1973 - Origin and evolution of the Elephantidae - Transactions of the American Philosophical Society, n.s. 63 (3):1-144

Ferretti, M.P.,1998 - Gli elefanti del Plio-Pleistocene dell'Italia - Doctoral thesis, Modena, Bologna, Firenze and Roma Associated Universities, 119 pp.

Fortelius, M., 1985 - Ungulate cheek teeth: function, structure and evolution - Acta Zoologica Fennica 180: 1-76

Janis, C.M. & Fortelius, M., 1988 - On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors - Biological Review 63: 197-230

Pfretzschner, H.U., 1994 - Biomechanik der Schmelzmicrostruktur in den Backenzähnen von Großsäugern - Palaeontographica A 234: 1-88, Stuttgart

Rensberger, J.M., 1973 - An occlusion model for mastication and dental wear in herbivorous mammals - Journal of Paleontology 47(3): 515-528

Rensberger, J.M., & Von Koenigswald, W., 1980 - Funcional and phylogenetic interpretation of enamel microstructure in rhinoceroses - Paleobiology 6 (4): 477-495

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