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Tooth microwear analysis of *Mammuthus (Archidiskodon) meridionalis gromovi* (Alexeeva & Garutt, 1965) from Montopoli (Lower Valdarno, Tuscany, Italy): a methodological approach⁽¹⁾

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ABSTRACT – The alimentary habits of large mammals can be deduced from the microwear tracks on tooth enamel examined under the Scanning Electronic Microscope. The data obtained from a preliminary analysis of the last upper molars of a *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) specimen from Montopoli (Lower Valdarno, Tuscany; Montopoli faunal unit, Middle Villafranchian Mammal Age) are consistent with the hypothesis of a predominantly browser type of diet. During the deposition of the fossiliferous level, the paleoenvironment at Montopoli was likely to have been quite open, as shown by paleovegetation data; browsing in elephants may be explained by the increase in browse eaten during the dry period, when grass tended to wither, as reported for most extant savanna elephants.

RIASSUNTO – [Microtracce di usura dello smalto dei molari di *Mammuthus (Archidiskodon) meridionalis gromovi* (Alexeeva & Garutt, 1965) di Montopoli: approccio metodologico] – Le abitudini alimentari dei vertebrati possono essere dedotte dall'analisi al microscopio a scansione elettronica delle microtracce di usura, che si producono sullo smalto per il contatto diretto tra dente e alimento, o tra dente e dente. Il modello di microtracce presentato dai molari di un esemplare di *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) proveniente da Montopoli (Valdarno Inferiore, Toscana, Villafranchiano medio, unità faunistica di Montopoli) indica un'alimentazione costituita in prevalenza da foglie e germogli, povera di vegetali ad alto contenuto in fitoliti. Tenuto conto dei dati paleoambientali noti per il Villafranchiano medio basale del Valdarno inferiore, le attitudini alimentari dell'elefante di Montopoli possono essere spiegate con la tendenza, mostrata dagli attuali elefanti di savana, a cibarsi prevalentemente di foglie durante periodi in cui prevalgono condizioni di aridità.

INTRODUCTION

The alimentary habits of large mammals can be deduced from microscopic scars (tooth microwear) on tooth enamel examined under the Scanning Electronic Microscope (SEM). The pioneering study by Walker (1976), involving only the use of the light microscope, as well as several works (see Palombo *et al.*, in press; Ungar, 2001 and references therein) based on high magnification scanning microscope analysis, focused on the relationships between dental microwear patterns and different kinds of feeding, emphasising the interference of dietary-behavioural and enamel dental scars.

Despite the large number of studies on elephants, less attention has been paid to the role played by diet in the ecology of extinct elephants; therefore, microwear analysis of elephant tooth enamel is still almost unknown (Farkas, 1996; Capozza, 2001; Palombo *et al.*, in press), even if studies on browsing and grazing in modern and fossil proboscideans, based on isotopes have become more common (see Cerling *et al.*, 1999). This also depends on the great difficulty in determining which part of the enamel loop might be representative of the whole occlusal surface. In fact, in elephants the teeth of an individual continue to form and come through for decades, the masticatory surface of molars progressively changes in shape, and the orientation of each plate with respect to mechanical masticatory forces might also change. Moreover, elephants eat many different kinds of food and might change it frequently. Accordingly, the results of analysis carried out on a congruous sample of molars coming from the same site might be representative of the major alimentary preferences of an elephant population during the average time of bone accumulation. Therefore, tooth microwear analysis can be essential in elucidating the dietary adaptation of extinct elephants.

Preliminary data resulting from a multidisciplinary study (microwear and isotope analyses) carried on two rich *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847 samples belonging to two late Middle Pleistocene faunas from Campagna Romana, are consistent with the paleoenvironmental reconstruction hypothesised for the two sites (Filippi *et al.*, 2001; Palombo *et al.*, in press).

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Accordingly, a study of Italian *Mammuthus meridionalis* (Nesti, 1825) would seem to be interesting, as determining the diet of this species during its 1.5 Ma of existence, a period affected by some important global climate changes. To this end, a preliminary analysis on the last upper molars of a *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) specimen from Montopoli (Lower Valdarno, Tuscany; Montopoli faunal unit, Middle Villafranchian Mammal Age) was performed in order to test the validity of the methodology recently proposed for *Elephas (Palaeoloxodon) antiquus* on a representative of the *Mammuthus* genus.

MATERIALS AND METHODS

Two last upper molars belonging to a largely incomplete skull stored in the Palaeontological Museum of Florence (IGF 1077) have been analysed. The specimen, found in a sandy marine deposit outcropping in the Lower Valdarno basin near Montopoli, first described by Weithoffer (1893), was regarded by Maglio (1973), together with the specimen from Laiatico (Ramaccioni, 1936), as a less advanced representative of *Mammuthus meridionalis* (*Mammuthus meridionalis* "Laiatico stage"), while many other authors ascribed it to *Mammuthus gromovi*, the species erected by Alexeeva and Garutt in 1965 for the heterogeneous material from Livenzovka (Russia). Actually, the "gromovi" elephant represents the most primitive evolutionary stage of *Mammuthus meridionalis*. Even if undoubtedly archaic, both the morphological and biometrical characteristics of the Montopoli molars fall within the variation range for the Valdarno specimens.

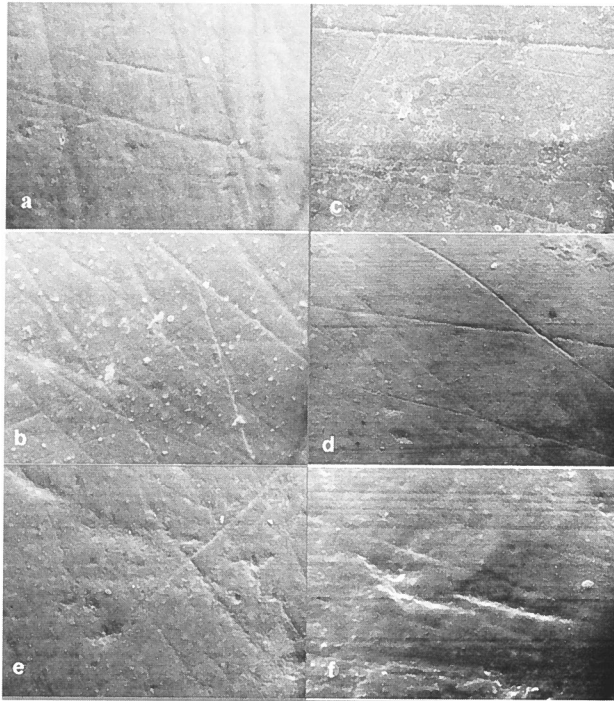
The first step in the study has been the analysis of microwear scars on all functional plates on the mesial (anterior and posterior sides), lateral and buccal sides of a very well preserved enamel loop belonging to the 5° plate, on which food-tooth and tooth-tooth attrition seem to be stronger. Then, the enamel loop of each functional plate has been analysed at about the same place on the right and left molars. All this was done in order to ascertain the variation range on the whole occlusal surface of a single tooth at different points, according to the varying attrition stress affecting the occlusal surface from the anterior to the posterior side, and to contrast the results obtained for each molar. The average percentages of pits, scratches and cross scratches were eventually calculated for each molar, as well as scar frequency (total number of scars on all photomicrographs of a given molar divided by the number of images).

Examination was carried out using a Cambridge Stereoscan 250, x200 and x500 photomicrographs have been used for analysis in order to contrast results at different magnification. Each image was qualitatively and quantitatively analysed. Quantitative analysis was effected using the Microwear 4.0 software programme, provided by Ungar (2001). Scars were respectively categorised as pits and scratches according to the length to width $> 0 < 1/4$ ratio, directly provided by the programme. Data for each photomicrograph (both x 200 and x500) have been summarised as percentages of pits and scratches.

RESULTS

Scanning electron microscope analysis of enamel loops performed at x200 magnification reveals the presence of quite similar morphological wear patterns on the whole occlusal surface of both molars. The microwear pattern is characterised by a relatively low number of tracks (frequency = 104.09 and 105.75 for the right and left molars respectively) and by a predominance of small pits with respect to scratches. The latter are usually large and relatively deep, with a U-shaped bottom (Text-fig. 1 a,b). Very long, narrow, deep, V-shaped scratches have occasionally been observed, although they are infrequent (Text-fig. 1 c,d). Rare large cavities are also present, especially on homogeneously worn surfaces showing an extremely low number of scratches; the presence of a very small fragment of enamel prism at the bottom of the cavities would suggest the eating of hard food such as seeds (Text-fig. 1 e,f). Analysis at x500 magnification confirms these results, and moreover shows that some wider scratches are characterised by minute cracks along their lateral edges, yielding information about the direction of movements producing the scratches. In some case, two chewing phases can be inferred by the crossing scars, which lie in a more accentuated preferential antero-lingual/postero-labial direction, or vice versa. Among the various enamel loops, the anterior ones, in a very advanced stage of wear, have a rather smooth surface and exhibit a microwear pattern quite different from the norm, possibly due to preservation factors. Consequently, they were not taken into account in the quantitative analysis. As expected, the plates of the central part of the tooth, which sustain the greatest attrition stress, show the most evident scars. The data obtained from quantitative analysis is consistent with qualitative observations, since the percentage of pits is always higher than the percentage of scratches.

The microwear scars observed on the medial (anterior and posterior), lateral and buccal sides of plates displaying average wear show a low variation range in both the left and right molars; the percentage of pits observed at 200x magnification on the 5° plate of the left molar ranges from 52.69% to 57.14%; the average value, 55.10% ($\delta = 2.11$), is very close to the average value calculated at 500x magnification (55.78%). The percentages resulting from analysis done at x200 and x500 magnification do not differ significantly, even if the number of scars is



Text-fig. 1 - Representative photomicrographs of microwear on the enamel worn surface of last molars of *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) (IGF 1077) from Montopoli: a) 5° right plate (x200); b) 5° left plate (x200) showing few scratches, with shaped-U bottom, some cross scratches and several very small pits, resulting from eating leaves (more), sprouts, not very hard seeds and twigs of relatively low fiber content; c) 7° right plate (x200); d) 7° left plate (x200) showing few thin scratches resulting from eating fibrous vegetation; e) 10° right plate (x200); f) 7° left plate (x500) showing very large pits, probably resulting from consuming hard food, seeds or bark fragments.

obviously higher at the lower magnification. The average percentage of pits and scratches obtained for each plate, from the 5° to the 10°, range from 54.22%-45.78% to 71.51%-28.49% (Mean = 61.75%-38.25%; δ = 5.72) in the left molar and from 54.10%-45.90% to 61.50%-38.50% (Mean = 58.16%-41.84%; δ = 2.11) in the right molar.

The comparison between pit and scratch percentages on the left and right molars shows greater variation for the left one, usually characterised by higher percentages of pits, mostly depending on the low number of scratches counted on the 6° plate (Text-fig. 2).

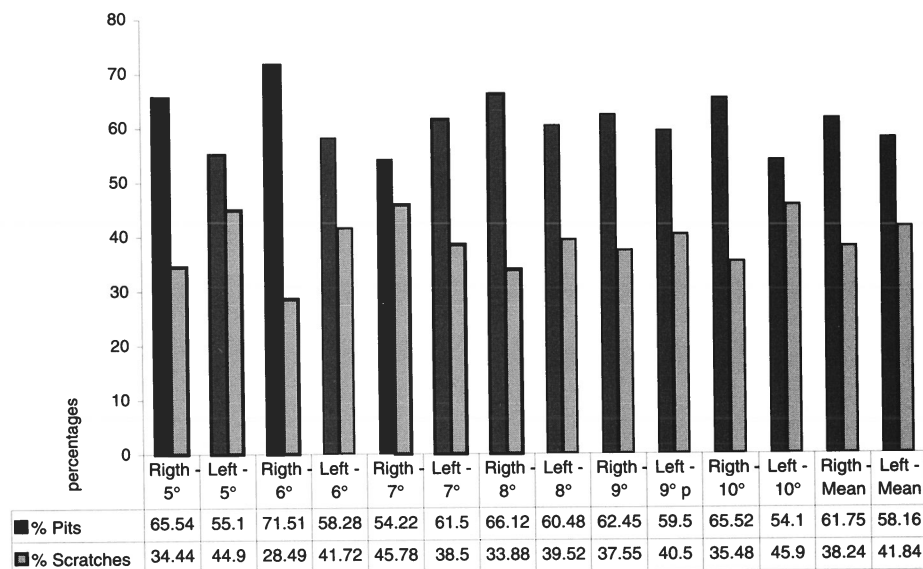
A comparison of the mean percentages of pits versus scratches between the two *M. m. gromovi* molars from Montopoli, some specimens of Middle Pleistocene *Elephas antiquus* (Palombo *et al.*, in press; Palombo, unpublished data) and extant species (browsers, grazers and mixed-feeders, after Solounias and Moelleken, 1992, modified) highlight their slight differences, even if a browser pattern is clearly confirmed (Text-fig. 3). With respect to the Italian *Elephas antiquus* specimens, the Montopoli teeth display microwear more similar to *E. antiquus* from La Polledrara di Cecanibbio (late Middle Pleistocene, OIS 9), which is not a browser to the extent that *M. m. gromovi* seems to be, while other *E. antiquus* samples mostly fall within the mixed-feeder area (see Palombo *et al.*, in press, for a discussion).

DISCUSSION

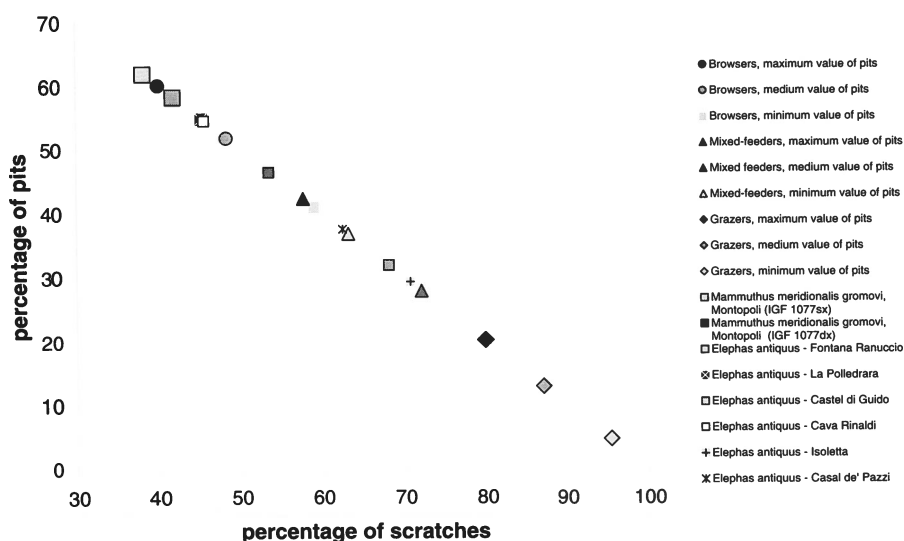
Qualitative and quantitative analyses of microwear in *Mammuthus meridionalis gromovi* from Montopoli are consistent with a predominantly browser dietary adaptation. In fact, leaf-eating browsers show scratches having rounded bottom, and the number of these tracks on occlusal surfaces is always low; moreover higher percentages of pits and the presence of cross scratches have generally been observed in browser herbivores.

Nevertheless, the Eurasian *Mammuthus* representatives, starting from the first appearance of the most archaic species, *Mammuthus rumanus* Stefanescu, 1929, about 3.1-3.2 Ma (Tulucesti and Cernatesti, Romania, middle Gauss submagnetochronozone, Radulesco & Samson, 2001), have generally been regarded as elephants, possibly grazers, inhabiting mainly open environments. In effect, starting from about 3.0 Ma, in the northwestern Mediterranean area, important climate variations led to the reduction of subtropical vegetation and warm-humid forest cover. Notably, around 2.6 Ma, the onset of a permanent North Hemisphere glacial cap determined the rapid spread of an open steppe environment in Central Europe, whereas the beginning of Glacial-Interglacial cycles led to rapid *Artemisia* steppe – deciduous forest alterations in the western Mediterranean as well as in central Italy (Suc *et al.*, 1995). The first appearance, in faunas belonging to Montopoli F.U., of some taxa inhabiting an open environment, such as *Equus stenonis livenzovens* and *M. m. gromovi* (the so-called Elephant-*Equus* event, Lindsay *et al.*, 1980), is consistent with this environmental change. At the time of Montopoli F.U., several taxa of a wooded habitat disappear and the percentage of taxa indicative of open landscapes clearly increases. Consequently, the browser attitude of the Montopoli elephant might be explained as a response to arid conditions that induced more leaf than grass-eating in this “steppe” species, as confirmed by the behaviour of living elephants.

Extant elephants are known as megaherbivores: both *Loxodonta* and *Elephas* feed on a large quantity of forage, about 100 and 300 kilograms per day. Descriptions of their diet indicate a mixture that includes both browse and grass; elephants may feed on more than 80 different plant species (Eltringham, 1992). During feeding bouts, elephants can eat low grass as well as tree branches or fruit (the latter is eaten especially by the forest species *Loxodonta cyclotes*). Consequently, microwear patterns can change considerably over a short time span. African elephants usually consume herbs, grass, leaves, fruit and bark, as well as aquatic vegetation, while Indian elephants



Textfig. 2 - Comparison between pit and scratches percentages, counted at 200x magnification, on the enamel worn surface of the right and the left last molars of *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) (IGF 1077) from Montopoli.



Textfig. 3 - Plot of microwear values of the right and left last molars of *Mammuthus meridionalis gromovi* (Alexeeva & Garutt, 1965) (IGF 1077) from Montopoli, compared with value of some samples of Middle Pleistocene *Elephas antiquus* Falconer & Cautley, 1847, and with the variability ranges of grazer, browser and mixed feeder extant taxa (data after Solounias & Moelleken, 1992, modified).

generally consume more grass than African ones. A considerable part of an African elephant's food can be in the form of browse (woody vegetation as opposed to grass); the percentage of browse varies widely, depending on the availability of different kinds of plants and on climatic conditions. The amount of browse eaten by African elephants increases during the dry season, when grass tends to wither, while during the wet season, grass consumption notably increases. During the dry season, Indian elephants also eat more browse, while in the wet season, browse and grass consumption are almost equal (Eltringham, 1992). Assuming that extinct elephant diet-behaviour did not differ significantly from that of extant species, browsing in *M. m. gromovi* is not so surprising. Moreover, the increase in crown height and plate number and a decrease in molar-enamel thickness in Elephantinae lineages have long been interpreted as progressive modifications, which also permit a grazing, diet. Accordingly, the low crowned molars with thick enamel of *M. m. gromovi* suggest a less graminiferous diet with respect to that of more advanced *Mammuthus* representatives.

FINAL REMARKS

The data obtained highlight the difficulty of establishing the dietary adaptation of fossil elephants on the basis of vegetation or paleoenvironmental data. Tooth microwear analysis seems to be a helpful tool, especially in support of isotopic and pollen data. Moreover, microwear analysis seems to enable us to infer the prevailing dietary adaptation of extinct elephants only by collecting a very large number of samples; however, samples belonging to the mesial side of average worn enamel loops seem to produce sufficiently-valid data.

On the other hand, most of our results are consistent with the hypothesis that *M. meridionalis gromovi* was a browser eating more leaves, sprouts and not very hard seeds than gramineae or plants containing a large amount of phytoliths. This kind of diet, in a species that is believed to have prevalently inhabited quite open, arid environments, suggests food-behaviour similar to that of extant savanna elephants.

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