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Coupling tooth microwear and stable isotope analyses for palaeodiet reconstruction: the case study of Late Middle Pleistocene *Elephas* (*Palaeoloxodon*) *antiquus* teeth from Central Italy (Rome area)

M.R. Palombo[a,b,*], M.L. Filippi[b,c], P. Iacumin[d], A. Longinelli[d], M. Barbieri[a,b], A. Maras[a]

[a] *Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza", Piazzale Aldo Moro 5, 00185 Roma, Italy*
[b] *CNR, Istituto di Geologia Ambientale e Geoingegneria—Sezione La Sapienza, Piazzale Aldo Moro 5, 00185 Roma, Italy*
[c] *Museo Tridentino di Scienze Naturali, Via Calepina 14, 38100 Trento, Italy*
[d] *Dipartimento di Scienze della Terra, Università degli Studi di Parma, Parco Area delle Scienze 157/A, 43100 Parma, Italy*

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Abstract

The identification of mammal palaeodiet is a useful tool for the reconstruction of palaeoenvironmental conditions. From the second half of the last century, two methodological approaches based on microwear enamel defects, produced on tooth enamel by the attrition with food particles, and on stable isotope analyses have been of increasing interest. The analysis performed on the two sets of *Elephas* (*Palaeoloxodon*) *antiquus* Falconer and Cautley, 1847 last molars, belonging to late Middle Pleistocene faunas from La Polledrara di Cecanibbio and Casal de' Pazzi (Central Italy, Rome area), highlights the possibility of establishing the dietary adaptation of elephants, on the basis of a large data set and of a multidisciplinary approach. Elephants from La Polledrara di Cecanibbio and Casal de' Pazzi are characterised by prevalently an intermediate type of dietary adaptation (grasses, leaves, bark and coarse stem), although the average microwear topographies of the samples are different in the two sets. In La Polledrara di Cecanibbio molars, coarse, often crossed scratches prevail, and pits, either large or small, occur in about the same percentage as striations. The Casal de' Pazzi sample is characterised by a larger number of mixed (coarse and fine) scratches and a lower percentage of pits. For these elephants, the amount in their diet of gramineae or vegetables relatively rich in phytoliths was important.

During the deposition of fossiliferous levels, similar features characterised the palaeoenvironment: wooded grassland in moderately humid and temperate climate conditions. The results of isotope analyses suggest differences in terms of temperature or humidity: warmer or more arid conditions for La Polledrara than for Casal de' Pazzi.

Taking into account that grazing among elephants may be related to increasing availability of grass during more humid periods, whereas browsing is augmented when the grass tend to be withered, as reported for extant savannah, the different patterns in microwear seem to be consistent with oxygen isotope data. Carbon isotope measurements on structural carbonate of biogenic apatite (enamel) suggest a more closed canopy forest at Casal de' Pazzi and more arid climate at La Polledrara di Cecanibbio. Strontium isotope composition ($^{87}Sr/^{86}Sr$) helps to define the geographical area where the two populations were living, which is confirmed to be limited to the volcanic province of Latium.

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1. Introduction

Palaeodiet reconstruction is of increasing interest to track environmental changes and to investigate a wide range of ecological issues. The dietary adaptations of large mammals can be deduced by microscopic scars

(dental microwear) produced on tooth enamel by both the tooth/food (abrasion) and tooth/tooth (attrition) interactions during chewing. A multidisciplinary approach, in which microwear is coupled with XRD and isotope analysis, may help to cast light on the diet of species having a complex feeding, as elephants are.

The purpose of this study is to reconstruct the dietary adaptation of two late Middle Pleistocene sets of *Elephas* (*Palaeoloxodon*) *antiquus* last molars according to results of different techniques such as: (1) analysis of the enamel scars observed by means of SEM and light

*Corresponding author. Universita degli Studi di Roma "La Sapienza", Dipartimento di Scienze della Terra, Istituto di Geologia Ambientale e Geoingegneria, P.le Aldo Moro, 5, Roma 00185, Italy.
E-mail address: mariarita.palombo@uniroma1.it (M.R. Palombo).

microscope, using quantitative and qualitative approaches; (2) monitoring the purity and crystallinity of fossil enamels by means of X-ray powder diffraction analysis; (3) measuring the oxygen and carbon stable isotope composition of structural carbonate in bioapatite and the oxygen isotope ratios in phosphate; and (4) measuring the strontium isotope ratio of skeletal tissues and comparing it with the strontium isotope composition of different substrata in the Roma area. The results from different methods are then compared and discussed also in order to test their reliability and usefulness to infer dominant palaeoenvironmental conditions during the deposition of the fossiliferous levels.

2. Microwear tracks and stable isotopes palaeodiet reconstruction: the state of the art

Pioneering studies by Walker (1976) and several subsequent works (e.g. Resenberg, 1978; Walker et al., 1978; Walker, 1980, 1981; Gordon, 1982; Teaford, 1988, 1991, 1994; Teaford and Oyen, 1989a, b; Walker and Teaford, 1989), focused on the relationships between dental microwear patterns and different kinds of feeding in primates, rodents and ungulates. These results emphasised the strict relationship between dietary-behaviour and enamel dental scars, but highlighted also the very short time turnover (formation/obliteration) of wear patterns, especially in taxa having a hard diet. Nevertheless, the rapid change of microwear patterns can constitute an advantage in studying extinct species. Indeed, depending on the long "average time" of bone accumulation, the bias of short time occasional feeding can be avoided, allowing evaluation of the average dietary preference during the span of time corresponding to the formation of a fossiliferous deposit. It follows that an important aspect of microwear analysis is the possibility of its use to infer the dietary adaptation of extinct mammals. Basically, the differences among enamel microscopic scars depend on the abrasive power of various kinds of food as well as on the direction of stress forces necessary for food breakage, that are applied by masticator muscles, as testified by studies on extant and extinct taxa from palaeontological and archaeological contexts (see e.g. Teaford and Walker, 1984; Taylor and Hannam, 1987; Teaford, 1988; van Valkenburgh et al., 1990; Maas, 1991; Strait, 1993; Janis, 1995; Ungar 1996, 1998; Ungar and Teaford, 1996; Mainland, 1997; King et al., 1999).

As pointed out by several authors (e.g. Rensenberg, 1978; Gordon, 1988; Solounias et al., 1988; Hayek et al., 1991; Solounias and Moelleken, 1992a, b; Solounias and Hayek, 1993; Solounias and Moelleken, 1993a, b; Caprini, 1998; Hayek et al., 1999; MacFadden et al., 1999; Solounias et al., 2000; Rivals and Deniaux, 2003),

differences among herbivores, grazers and browsers, are reflected by microwear tracks. Two principal types of scars have been recognised at high magnification (usually $500 \times$): (i) striation (or scratch), a linear depression whose length is always greater than its breadth (length versus wide ratio > 4, Solounias et al., 1988); and (ii) pit, a depression whose length and breadth are approximately equal (length versus wide ratio < 4, Solounias et al., 1988). Among browsers, the microwear tracks are represented by a higher percentage of pits and by a lower percentage of scratches than in grazers (Solounias et al., 1988, Solounias and Moelleken 1992a, Solounias and Hayek, 1993). Mixed feeders alternate seasonally, regionally or occasionally (meal-by-meal) between browsers and grazers (see Hofmann, 1989; Solounias and Moelleken, 1992a). Consequently, according to rapid changes in microwear, a specific mixed feeder pattern among ruminants seems absent (see discussion in Solounias and Moelleken, 1992a).

In microwear analysis, authors generally preferred a quantitative analytical approach (density and percentage of each type of scars) which was considered more objective. Nonetheless, as pointed out by Mainland (1997 and references therein), a qualitative approach can also represent a very useful tool to better discriminate the dietary adaptation. In fact, the combination of both quantitative and qualitative methods seems to be the more appropriate way to elucidate the dietary adaptation (Mainland, 2003 and references therein), especially in the case of a complex occlusal surface such as that of elephant molars (Palombo and Curiel, 2003; Palombo et al., in press).

Recently, Solounias and Semprebon (2002) proposed a simplified methodology for the assessment of dietary adaptation of ungulates, based on qualitative and semiquantitative analysis at low magnification ($35 \times$), performed using a standard stereomicroscope. The authors separated ungulates having an atypical grazer or browser pattern in the following additional categories: (i) seasonal or regional mixed feeders, (ii) meal-by-meal mixed feeders, (iii) rooters and tapir browser, and (iv) bark, coarse stem and leaf feeder (including elephants).

Despite the number of studies on elephants, little attention has been paid to the role played by diet in the ecology of extinct elephants. Reconstructing dietary adaptation of elephants, it must be considered that: (i) among different taxa eating similar food, the microwear patterns characterising equivalent enamel surfaces are similar; and (ii) among individuals belonging to the same taxa having different diets, the microwear patterns are different as well as they are on functionally different surfaces belonging to a single individual (Maas, 1991; Palombo unpublished data). Consequently, studying elephant microwears, the major difficulty is to determine which point of enamel loop might be representative of

the whole occlusal surface. The elephants exhibit a quite unusual manner of food comminution, depending on the wideness of masticator surface and on the high number of enamel bands. In elephants, the teeth of an individual continue to form and erupt for decades and the masticator surface of molar progressively changes in shape, and the orientation of each plate with respect to mechanical masticator forces might change (Maglio, 1972, 1973; Roth, 1989). Accordingly, only results of analysis carried out from a congruous sample of molars belonging to the same site might be representative of the major alimentary preferences of an elephant population during the average time of bone accumulation (see Curiel, 2001; Palombo and Curiel, 2003; Palombo et al., in press). Moreover, elephants eat different kinds of food and might change it frequently (Haynes, 1991; Eltringham, 1992).

Palaeodiet reconstruction can be based also on stable isotope analysis on biogenic materials, which record a combination of environmental parameters and biological processes. The correlation between the stable-isotope composition of collagene in vertebrate bones and that of their diet, proposed about 25 years ago for the carbon stable-isotope ratio (DeNiro and Epstein, 1978), is now well accepted and extended to other stable-isotope ratios of oxygen, nitrogen, hydrogen, and strontium (Kohn, 1999). For a comprehensive review of this topic, refer to Kohn and Cerling (2002) and references therein. One of the interesting applications of the stable isotopes–diet relationship is the reconstruction of dietary-preferences in herbivores. Plants are divided in two broad groups characterised by different photosynthetic pathways (C_3 and C_4) having different $\delta^{13}C$ values ($\delta^{13}C$ mean values, $-27‰$ and $-12‰$, respectively, versus PDB-1 isotopic standard): most trees and shrubs use a C_3 photosynthetic pathway, whereas most tropical grasses use the C_4 pathway. Moreover, there can be a variation during the year on the types of plants growing in the area and then of the $\delta^{13}C$ values of the potential elephant food. For instance, evergreen trees are about $+3‰$ relative to deciduous trees (Brooks et al., 1997). Woody plants have higher $\delta^{13}C$ values than herbaceous plants (Delawiche et al., 1979). It is therefore possible to distinguish between grazing mammals, which like grass, and browsing mammals, which prefer leaves, measuring the carbon isotope composition of their skeletal tissues. At the same time, the oxygen isotope composition of bioapatite is directly related to temperature and isotopic composition of the fluid from which it precipitates. In an organism with constant body temperature, such as a mammal, there is a direct relationship between the $\delta^{18}O$ of body water and the $\delta^{18}O$ of PO_4 and CO_3 components of bioapatite (Longinelli, 1984). The isotopic composition of body water depends on the isotopic composition of drunk water and consequently, in the case of wild animals, of environmental water. For

this reason, the oxygen isotope composition of palaeoenvironmental water ($\delta^{18}Ow$) can be calculated from the oxygen isotope composition of phosphate ($\delta^{18}Op$) of fossil mammal teeth after quantitative calibration of the existing relationship in modern specimens coming from different areas. It is then possible to obtain information about climatic changes in the past.

Strontium isotope geochemistry may yield environmental information on the substratum the studied animals where leaving on. Land animals assume their Sr isotope ratios from the underlying soil and bedrock: the comparison of the Sr isotope ratio measured in the mammal's skeletal remains with the same ratio in the soil and bedrock where the fossils were found can be used to distinguish between resident and non-resident animals.

The success of stable isotope analysis in fossil tooth enamel for palaeodietary and palaeoenvironmental reconstruction requires that the integrity of stable isotope ratios in biological apatite is maintained throughout the process of fossilisation. Fresh enamel is essentially fully crystalline, and so no change in crystallinity is evident among enamel belonging to extant mammalian taxa (Ayliffe et al., 1994, Fig. 1). Michel et al. (1995) observed carbonate alteration in fossil tooth enamel of *Cervus elaphus* as a function of time of fossilisation, while Rink and Schwarcz (1995) did not note any difference between modern and fossil
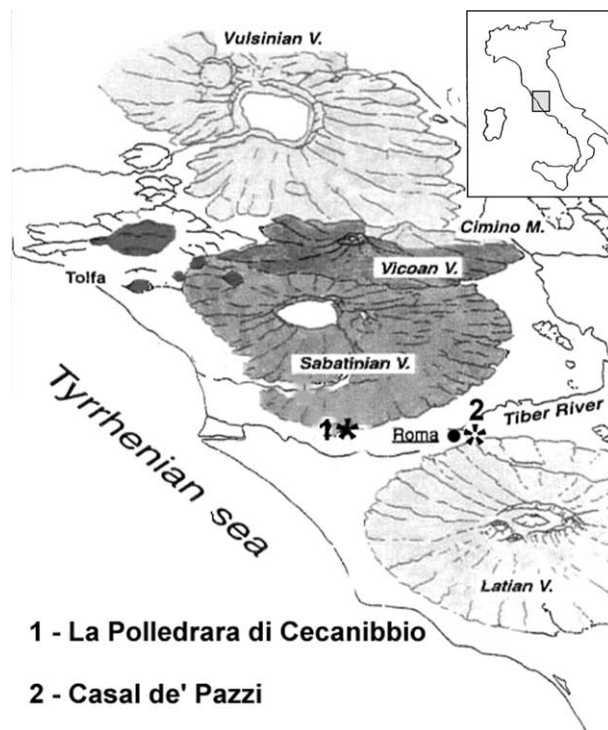

1 - La Polledrara di Cecanibbio

2 - Casal de' Pazzi

Fig. 1. Location map of La Polledrata di Cecanibbio and Casal de' Pazzi sites (after Parotto, modified).

enamel. Spondheimer and Lee-Thorp (1999), on the other hand, found a small but significant change in the properties of carbonate groups occupying hydroxyl and phosphate sites. Pasteris et al. (2001) detected variable low to moderate [OH] content in tooth enamel apatite. Moreover, as [OH] decrease and [CO$_3$] increases, the degree of crystallinity of the apatite decreases. Nevertheless they found a poor correlation between [OH] and [CO$_3$], suggesting that there is not much mutual substitution, in agreement with IR studies by Michel et al. (1995) indicating that the increase in [CO$_3$] during fossilisation was mainly associated with an increased replacement of [PO$_4$] by [CO$_3$].

3. Materials and methods

The studied *E. antiquus* molars belong to the rich samples coming from the late Middle Pleistocene (early Aurelian Mammal Age, Torre in Pietra Faunal Unit *sensu* Palombo et al., 2003) deposits of La Polledrara di Cecanibbio, correlated with oxygen isotope stage (OIS) 9, and Casal de' Pazzi, which has been correlated with OIS 7 (Anzidei et al., 1999; Anzidei and Cerilli, 2001) (Fig. 1). Nevertheless, the age of this latter deposit has yet to be confirmed.

3.1. Microwear

For microwear analysis, since variability linked to ontogenetic age has been demonstrated by many studies (e.g. King et al., 1999; Mainland, 2000), only the last molars were retained. Ten last molars from La Polledrara and 10 others from Casal de' Pazzi were examined. The analysis was made on cast of enamel bands. Methods were adapted from those described by Solounias and Moelleken (1992a) and Solounias and Semprebon (2002).

To obtain casts for analysis, the occlusal enamel surface was carefully and repeatedly washed with acetone and deionised water, and cleaned and dried using compressed air. Periodic examination was undertaken to ensure complete removal of microresidual impurities. After drying, the occlusal surface of the plate was covered with vinyl polysiloxane impression material, and the first mold was peeled off and discarded in order to remove impurities. Polyurethane casts were made from a second set of molds and used in microwear analysis.

According to the methodology proposed by Palombo et al. (in press), the first step of the study was the analysis of microwear of all functional laminae (with the exclusion of the posterior ones, if in very incipient wearing stage) of two last lower molars used as test: es. no. 330 from la Polledrara and es. no. 680 from Casal de' Pazzi. Ten points were examined for each enamel loop: three on the anterior medial side, three on the posterior medial, two on the lateral, and two on buccal sides. These analyses verified the range of variability on the occlusal surface of a single tooth at different points according to the different attrition/abrasion stress that affects the occlusal surface from the anterior to the posterior side. In agreement with the results of the analysis performed on the whole surface, which demonstrated that the microwears of enamel loops of these laminae are very similar to the average pattern of the tooth, on the other molars the analysis was made on the central four enamel loops of the occlusal surface.

Casts of each enamel loop were examined at 35× magnification using an Olympus stereomicroscope: lighting conditions and methodology are those illustrated by Solounias and Semprebon (2002). Scars were identified and counted within a standard 0.4 mm × 0.4 mm square area, approximately corresponding to the area investigated at 200× magnification using SEM. Scars have been organised into three major morphological groups: (i) scratches, more or less straight striations that can be thin, shallow with V shaped section (fine scratches) or large, larger and deeper with a U shaped section (coarse scratches); (ii) pits, oval or round depressions with regular perimeter that can be small or large according to their diameter; and (iii) gouges, irregular depressions 2–3 times larger than large pits, with ragged, quite irregular edges.

The casts were subsequently spatter-coated with 200 Å of gold and examined by means of a Cambridge Stereoscan 250. Microphotographs were taken at ×20, ×35, ×200 and ×500 magnification. The ×20 photomicrographs were taken in order to better check the region and orientation of the less magnified photomicrographs. The ×35 photomicrographs have been used for a comparison with the images obtained with the light stereomicroscope. Both ×200 and ×500 photomicrographs have been used for analysis in order to contrast results at different magnification. At ×200 and ×500 magnification, the observed area is about 0.16 and 0.04 mm^2. Taking into account the quality of microphotographs, sometimes a smaller surface was observed. The observed surface never was less than 0.033 mm^2 (a surface of about 0.22 mm × 0.15 mm).

The images were treated with Microware 4.0, a semi-automated image analysis software package developed by Ungar (2001). Images at magnifications ×500 are analysed with a resolution fixed at 148 dpi. Scars were respectively classified as pits and scratches according to the length to width ratio $> 0 < 1/4$ (cf. Solounias et al., 1988; Teaford, 1988), directly provided by the programme. Microwear density was calculated from the number of features counted divided by the analysed surface. The width/length ratio has been further used to separate fine from coarse scratches and small from large pits.

For each enamel loop, the average number of scars was calculated, excluding the points showing possible anomalous microwear patterns. For each molar, the average percentages of pits (large and small), scratches (fine and coarse) and cross scratches were calculated as well as the scar density (total numbers of scars, pits, scratches).

3.2. X-ray diffraction

The purity and crystallinity of fossil enamels were monitored through X-ray powder diffraction analysis. Samples were manually ground under alcohol to a fine powder in an agate mortar. Diffraction patterns were collected on a Seifert MkIV diffractometer using graphite-monochromatised CuKα radiation. Samples were scanned from $5°$ to $60°$ with a step size of $0.02°2\vartheta$ and a counting time of $2\,s$. Cell parameters were refined with GSAS (Larson and von Dreele, 1985).

3.3. Isotopes

Enamel samples for isotope analyses were manually separated from the central part of molar M_3 teeth, mechanically cleaned from dentine using tungsten-carbide or diamond-impregnated rotary tools, and then finely ground within an agate mortar. A total of 23 samples (12 from la Polledrara and 11 from Casal de' Pazzi) were studied. Enamel powders for carbon and oxygen isotope analyses of structural carbonate of biogenic apatite were first reacted with 2% NaOCl for 24 h, then reacted with 0.1 M acetic acid for 3 days (Koch et al., 1997), and finally washed with distilled water and dried at $40°C$. The resulting enamel powder was further checked under binocular microscope for possible contamination. 150–250 mg of powder was reacted in vacuum with phosphoric acid at $25°C$ for three days. The cryogenically separated CO_2 was analysed in a Finnigan MAT 252 mass spectrometer. Duplicate measurements of structural carbonate showed a mean standard deviation of $\pm 0.1‰$ (1σ) for carbon isotopes, and $\pm 0.2‰$ for oxygen isotopes. The protocol outlined by Crowson and Showers (1991) and Lécuyer et al. (1993) was used for the chemical treatment of samples for oxygen isotope measurements of enamel phosphate. The final products of the chemical treatment (Ag_3PO_4 crystals) were reacted with BrF_5 at ca. $600°C$ for 15 h. The oxygen obtained from the reaction was then converted to CO_2 by cycling over hot graphite in the presence of a Pt catalyst. The isotopic measurements were carried out by means of a Finnigan DeltaS mass spectrometer. The standard deviation of phosphate measurements ranges from about ± 0.1 to $\pm 0.2‰$ (1σ). Isotopic ratios are reported relative to the isotopic standard PDB-1 for C and V-SMOW for O using the conventional δ notation $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$.

To avoid diagenetic Sr, which can modify the $^{87}Sr/^{86}Sr$ ratios, samples were pre-treated with 1.0 N acetic acid and then washed with double-distilled water. 100 mg of sample were dissolved in 2.5 N HCl, and Sr chemical separations were performed using standard ion-exchange chromatographic methods. The measured ratios were fractionation-corrected to an $^{86}Sr/^{88}Sr$ value of 0.1194. Repeated analyses of NBS 987 Sr standard gave average $^{87}Sr/^{86}Sr$ of 0.71024 ± 2. Standard deviations are expressed as 2σ on the means.

4. Results

4.1. Microwear

The microwear patterns of medial, lateral and buccal side of each functional laminae of the molar 330 from La Polledrara and 680 from Casal de' Pazzi, show that in each enamel loop the scar patterns on lateral and buccal sides are the most variable, especially as density is concerned. Moreover, among the various laminae the posterior ones, in the initial stage of wear, seem to be the most different from the average in percentage of pits and stretches, while the most similar values correspond to the laminae of the central part of the tooth that sustains the greatest attrition/abrasion stresses. As expected, the plates of the central part of the tooth show the most evident scars, confirming Solounias and Semprebon (2002) selection of the area in the centre of the molar, at the centre of one of the loops, as representative of microwear patterns of an elephant tooth.

Analyses of enamel loops performed on the other molars belonging to La Polledrara, using both stereo-microscope and scanning electron microscope, reveal the presence of rather similar morphological wear patterns on the entire central occlusal surface of molars. The range of microwear variability of La Polledrara molars is small (Fig. 2). The microwear pattern is characterised by a predominance of pits, prevalently large, with respect to scratches. Coarse scratches, large and relatively deep, with a U-shaped bottom are usually more frequent than the fine. Very long, narrow, deep, V-shaped scratches have occasionally been observed. Cross-coarse scratches are always present, whereas fine parallel scratches are less frequent. Some large and deep cavities (gouges) are also observed; the presence of very small fragments of enamel prisms at the bottom of the cavities would suggest the eating of hard food such as wood or bark. Analysis at $\times 500$ magnification confirms these results, and shows that some wider scratches are characterised by minute cracks along their lateral edges, yielding information about the direction of chewing movements (Figs. 3 and 4).
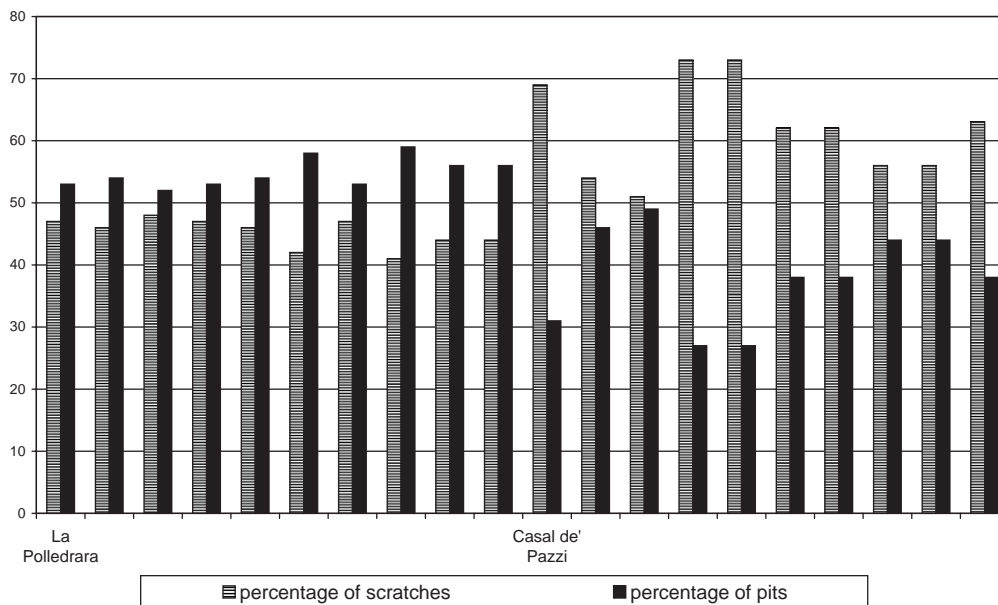
Fig. 2. Scatter diagram of the average percentage of scratches and pits of La Polledrara di Cecanibbio and Casal de' Pazzi samples (scars counted at 500× magnification).
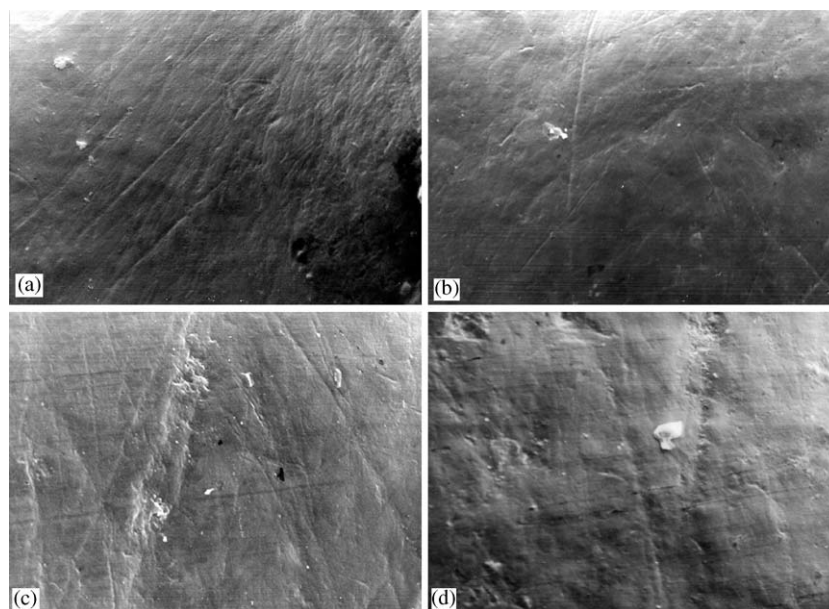

Fig. 3. SEM photomicrographs of the enamel worn surface of *E. antiquus* Falconer and Cautley, 1847 the last lower molar specimen no. Pl330 from La Polledrara di Cecanibbio. The surfaces prevalently show scratches with U-shaped bottom, some cross scratches, puncture-like pits and gouges resulting from eating leaves (more), seeds, grasses of relatively low fibre content as well as hard food such as bark fragments. (a) 4th plate, 200×; (b) 5th plate, 200×; (c) 6th plate, 500×; (d) 8th plate, 500×.

Data obtained from quantitative analysis is consistent with qualitative observations, since the percentage of pits in La Polledrara samples is always higher then the percentage of scratches (Fig. 5).

The stereomicroscope and scanning electron microscope analyses of all enamel loops of molar 680 from Casal de' Pazzi reveal the presence of quite similar morphological wear patterns on the whole occlusal surface. Though, the range of variability within the Casal de' Pazzi sample is significantly larger than that from La Polledrara (Fig. 2).

The microwear pattern is characterised by a number of scars quite similar to that found in La Polledrara sample, but Casal de Pazzi molars, despite their wider
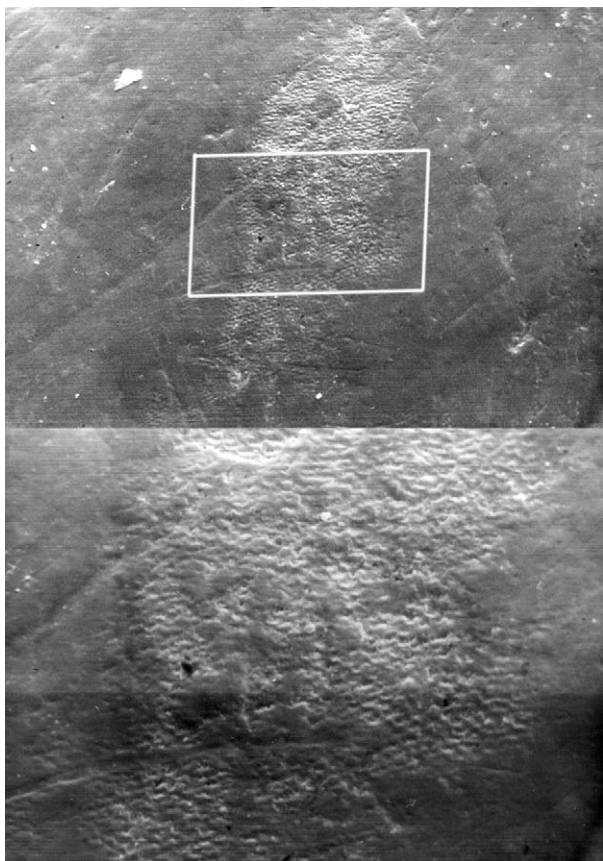
Fig. 4. SEM photomicrographs (at $200\times$, above and $500\times$, below) of the enamel worn surface of *E. antiquus* Falconer and Cautley, 1847 last lower molar (specimen no. PL330, 7th plate) from La Polledrara di Cecanibbio. The surface shows some coarse scratches, large and small pits, and an abraded area where prisms are visible.

variability, are always characterised by a predominance of scratches, both coarse and fine, with respect to pits (Fig. 6). The coarse scratches, large and relatively deep, with a U-shaped bottom are usually less frequent than in La Polledrara sample, whereas fine, parallel scratches are definitely more numerous. Very long fine and shallow scratches are frequent, while very long, narrow, deep, V-shaped striations have occasionally been observed. Cross-coarse scratches are present, but they are less frequent than in the La Polledrara sample. Rare large cavities (gouges) are also present, sometimes more frequent on buccal and lingual sides. Analysis at $\times 500$ magnification confirms these results, and shows some fine very shallow striations and some small pits not identifiable at lower magnification (Figs. 6c, d). The data obtained from quantitative analysis are consistent with qualitative observations, since Casal de' Pazzi molars always show a higher percentage of scratches than pits (Fig. 5).

The microphotographs show a fairly different density of microwear in the La Polledrara and Casal de' Pazzi samples. Casal de Pazzi specimens have a higher density

of striations than pits (Figs. 7a, b). The variation range of defect density showed by La Polledrara molars is lower than that generally observed in extant herbivore populations (Solounias et al., 2000). Conversely, the range of Casal de' Pazzi samples is quite large.

The comparison of scratch and pits dimensions (Table 1) does not show significant differences for scratch length and breadth between the La Polledrara and Casal de' Pazzi samples, even if the striations in the latter are relatively longer (Figs. 8a, b). For pits, the range of variability of Casal de' Pazzi samples is not larger than that of La Polledrara except for the specimen CdP 426037, characterised by unusually large pits. Scratches are longer and wider than those measured by Solounias and Hayek (1993) for extant ruminants.

Compared with Casal de' Pazzi, the La Polledrara sample is characterised by a significantly higher ratio between pits and scratches (Figs. 2,5), a narrower range of variability, a higher density of pits (Figs. 7a, b), slightly wider and shorter scratches (Figs. 8a, b), and more numerous gouges. The differences among the La Polledrara and Casal de' Pazzi samples are also summarised by the principal component analysis (Fig. 9).

4.2. X-ray diffraction

XRD patterns obtained from tooth enamel examined (Fig. 10) reveal a high degree of crystallinity, as peaks are sharp and well-defined, characteristic of apatite, without extra peaks belonging to significant impurities. Cell parameters varied from $a = 9.440(2)$ and $c = 6.894(1)\text{\AA}$ in the Casal de' Pazzi sample CdP1 to $a = 9.440(2)$, $c = 6.897\text{\AA}$ in sample Poll6 from La Polledrara di Cecanibbio. Values differ from hydroxylapatite, but are close to those of the tooth enamel of mammals (Elliott, 2002; Wilson et al., 1999; Michel et al., 1995). In fossil enamel of *Cervus elaphus* a negative correlation between the a parameter and the CO_3 content was found by Michel et al. (1995). Supposing the result is applicable to *E. antiquus*, sample Poll6 has a higher CO_3 content than sample CdP1. Only an IR spectrum can identify unambiguously CO_3, H_2O and OH groups, and this work is in progress.

4.3. Isotopes

Strontium isotope compositions for both the La Polledrara and Casal de' Pazzi samples range between 0.70983 and 0.71008 (Table 2). These values fall within the compositional range of pyroclastic volcanic rocks in the Rome area (0.70980 and 0.71050, Federico et al., 1994). Fig. 11a shows a box plot of carbon isotope composition of the analysed structural carbonates. $\delta^{13}C$ isotope values (Table 3) for La Polledrara range between $-10.9‰$ and $-9.0‰$ (versus PDB-1) with a mean
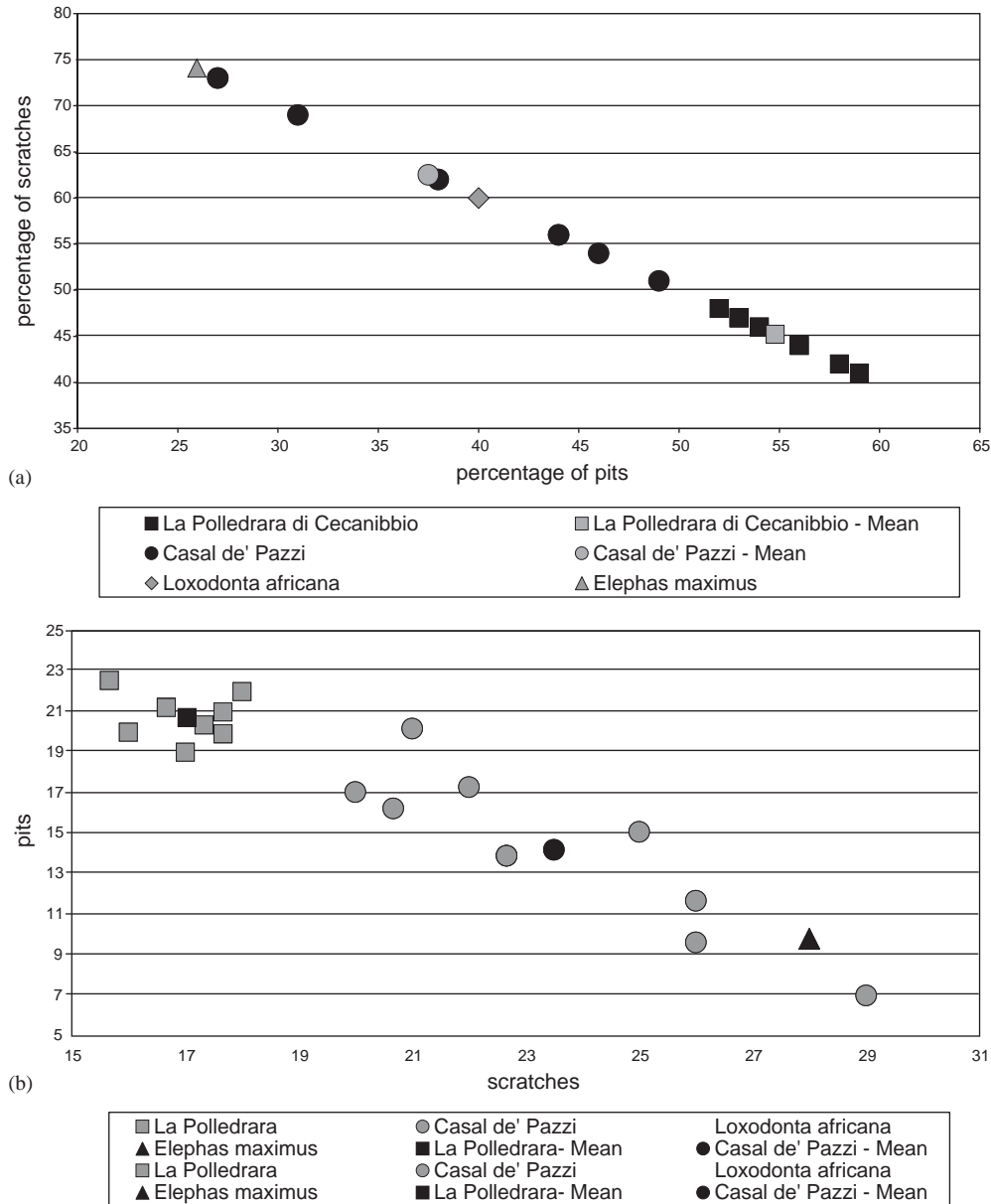
Fig. 5. Average percentage of pits plotted against average percentage of scratches as obtained for each analysed molar for each molar of *E. antiquus* Falconer and Cautley, 1847 from La Polledrara di Cecanibbio and Casal de' Pazzi analysed using SEM at 500 × magnification (a) and light microscope at 35 × magnification.

carbon isotope value of −10.6‰, whereas Casal de' Pazzi samples have a mean $\delta^{13}C$ value of –11.9‰ (range between −13.7 and −9.8‰). A reconstruction of *E. antiquus* palaeodiet is suggested in Fig. 11b and Table 3, using the carbon isotope fractionation between diet and bioapatite as proposed by Cerling and Harris (1999). All analysed samples fall in the "C_3 dominated diet" field, although La Polledrara shows more ^{13}C enriched values than Casal de' Pazzi. The mean oxygen isotope values obtained from teeth phosphate ($\delta^{18}Op$) are reported in Table 3 and Fig. 12a. These values were translated in terms of isotope composition of the environmental water ($\delta^{18}Ow$) by applying the equation established for

modern elephants (Ayliffe et al., 1992). To assess the reliability of the reported values, the oxygen isotope composition of tooth carbonate ($\delta^{18}Oc$) along with $\delta^{18}Op$ were measured on some of the studied samples (Fig. 12b). By comparing the relevant data, and according to the conclusions reported by Iacumin et al. (1996), it seems that no significant diagenetic changes took place apart perhaps for three samples (CdP1, CdP11 and Poll10) which were not further considered. The $\delta^{18}Ow$ values calculated for the Casal de' Pazzi and La Polledrara samples vary between −6.7 and −8.3 (mean 7.6 ± 0.65) and between −6.2 and −8.5 (mean 7.1 ± 0.65), respectively. The mean values are
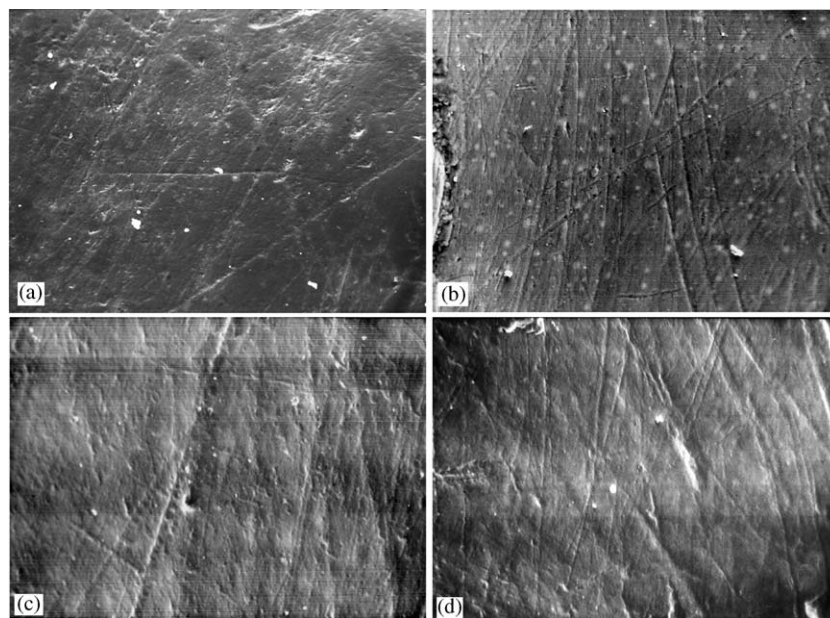
Fig. 6. SEM photomicrographs of the enamel worn surface of *E. antiquus* Falconer and Cautley, 1847 last molars from Casal de' Pazzi. The surfaces prevalently show thin and parallel scratches, some coarse scratches with U-shaped bottom, rare cross scratches, gouges and small pits, resulting from eating grasses with relatively high fibre content, leaves as well as hard food, seems or bark fragments. (a) specimen no. CdP 424898, 4th plate, 200 × ; (b) specimen no. CdP 424898 7th plate, 200 × ; (c) specimen no. CdP 680 4th plate, 500 × ; (d) specimen no. CdP 680 7th plate, 500 × .

statistically different ($P < 0.02$) and are more negative of about 1.3 and 0.8 per mil, respectively, than the mean $\delta^{18}Ow$ values of modern precipitation in the Rome area (around −6.3 per mil).

5. Discussion

The reported results assess the difficulty to establish the dietary adaptation of fossil elephants on the basis of one method only. In fact, elephants are among the extant species showing the highest range of variability in feeding.

Extant elephants are known as megaherbivores: both *Loxodonta* and *Elephas* feed on a large quantity of forage, about 100–300 kg 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). They prefer zones which provide a rich variety of food. The Indian species generally inhabits grassland or forests, including open grassy glades and transition areas rich in several kinds of plants. In some African regions, grazing can be very important. However, an important browsing component has been noted in savannah elephants (Dublin, 1995). During feeding bouts, elephants can eat low grass as well as tree branches or fruit (the latter is eaten especially by the forest subspecies *Loxodonta cyclotis*). As a result, microwear patterns can change consider-

ably, depending on geographic area, season and also during short time spans.

Accordingly, extant elephants, both African and Indian, can be regarded as a particular kind of mixed-feeder with a complex feeding. Despite this wide variability, the dietary adaptation of extant African and Indian species show some differences that have to be taken into consideration analysing microwear patterns in extinct species. African elephants usually consume herbs, grass, leaves, fruit and bark, as well as aquatic vegetation, while Indian elephants generally consume more grass than African ones. Consequently, 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 (Eltringham, 1992; De Boer et al., 2000). During the dry season, Indian elephants also eat more browse, while in the wet season, browse and grass consumption are almost equal (Eltringham, 1992). Microwear patterns of extant elephants, even if based on very limited data, seem to be consistent with these different average dietary preferences: "*Loxodonta africana* differs from *Elephas maximus* by having more pits, more gouges, and more cross scratches than does the latter" (Solounias and Semprebon, 2002, p. 29).

Table 1
Length and width of scratches, pits and gouges in La Polledrara di Cecanibbio (P) and Casal de' Pazzi (CdP) samples

|	Scratches length				Scratches width				Pits length				Pits width				Gouges length				Gouges width			
	min	max	M	S.D.	min	max	M	S.D.	min	max	M	S.D.	min	max	M	S.D.	min	max	M	S.D.	min	max	M	S.D.
P-330	53.80	130.43	79.98	17.60	2.52	4.04	3.17	0.40	4.43	6.98	5.54	0.61	3.41	5.15	4.11	0.45	37.21	64.57	56.54	10.15	13.26	24.60	19.32	2.13
P-606(6)	63.20	142.51	87.50	23.41	2.13	5.13	3.30	0.72	4.13	6.36	5.06	0.58	3.49	4.95	4.22	0.73	46.03	70.63	58.33	12.30	18.12	22.12	20.12	2.00
P-3160	64.17	148.87	106.52	42.35	2.76	5.24	4.00	1.24	4.45	6.11	5.28	0.83	3.39	5.11	4.25	0.86	43.17	61.93	52.55	9.38	14.35	18.31	16.33	1.98
P-3139	47.52	141.76	94.64	47.12	3.63	5.53	4.58	0.95	4.79	7.33	6.06	1.27	4.11	6.05	5.08	0.97	42.37	58.39	49.83	7.46	13.55	17.99	15.77	2.22
P-4010 dx	83.99	192.77	138.38	54.39	2.55	4.73	3.64	1.09	4.54	6.40	5.47	0.93	3.61	5.39	4.50	0.89	39.31	84.93	62.12	22.81	23.74	27.48	25.61	1.87
P-4010 sx	88.42	164.82	126.62	38.20	2.42	4.50	3.46	1.04	4.42	6.88	5.65	1.23	3.50	5.18	4.34	0.84	31.54	87.78	59.66	28.12	19.20	22.10	20.65	1.45
P-3879	75.47	149.73	112.60	37.13	2.33	4.63	3.48	1.15	4.61	6.39	5.50	0.89	3.50	5.22	4.36	0.86	42.33	56.87	49.60	7.27	13.43	15.55	14.49	1.06
P-C23	63.92	154.96	109.44	45.52	2.45	4.73	3.59	1.14	4.16	6.28	5.22	1.06	3.20	4.82	4.01	0.81	44.58	76.52	60.55	15.97	22.04	25.58	23.81	1.77
P-SUP. C5	80.45	159.93	120.19	39.74	2.97	5.81	4.39	1.42	4.91	6.39	5.65	0.74	3.52	5.08	4.30	0.78	42.90	63.02	52.96	10.06	15.44	18.52	16.98	1.54
P-Mand.sx	77.55	152.83	115.19	37.64	2.59	4.67	3.63	1.04	4.55	6.79	5.67	1.12	3.46	5.24	4.35	0.89	44.44	97.62	71.03	26.59	28.33	32.77	30.55	2.22
La Polledrara-Mean			100.81				3.72				5.51				4.35				59.32				20.36	
S.D.			17.84				0.46				0.28				0.29				7.50				5.03	
CdP-680	49.42	121.20	85.31	35.89	2.46	4.38	3.42	0.96	5.12	6.20	5.66	0.54	4.09	4.71	4.40	0.31	35.54	55.10	45.32	9.78	21.06	23.02	22.04	0.98
CdP-424898	91.65	149.95	120.80	29.15	3.13	4.91	4.02	0.89	4.98	6.49	5.64	0.51	3.79	4.87	4.33	0.54	33.64	55.70	44.67	11.03	28.66	33.34	31.00	2.34
CdP-GP.87	29.85	98.79	64.32	34.47	2.77	4.97	3.87	1.10	4.54	6.44	5.49	0.95	3.53	5.29	4.41	0.88	43.30	58.86	51.08	7.78	17.57	38.57	28.07	10.50
CdP-424896	50.00	181.38	115.69	65.69	2.32	4.50	3.41	1.09	4.01	6.83	5.42	1.41	3.16	5.08	4.12	0.96	50.16	61.38	55.77	5.61	3.30	22.40	12.85	9.55
CdP-424897	57.71	139.75	98.73	41.02	2.44	4.48	3.46	1.02	4.20	5.92	5.06	0.86	3.15	4.69	3.92	0.77	34.01	52.15	43.08	9.07	25.64	40.30	32.97	7.33
Cdp-426038	110.44	187.88	149.16	38.72	2.91	4.99	3.95	1.04	4.91	6.65	5.78	0.87	3.83	5.73	4.78	0.95	34.09	55.29	44.69	10.60	24.65	29.43	27.04	2.39
CdP-CP.82	26.23	141.63	83.93	57.70	2.53	4.17	3.35	0.82	4.39	6.09	5.24	0.85	3.29	4.87	4.08	0.79	43.91	57.61	50.76	6.85	16.99	20.51	18.75	1.76
CdP-906	107.98	202.02	155.00	47.02	2.74	5.54	4.14	1.40	4.47	6.57	5.52	1.05	3.21	5.17	4.19	0.98	41.78	50.88	46.33	4.55	26.19	36.85	31.52	5.33
CdP-426037	68.74	188.20	128.47	59.73	2.78	5.84	4.31	1.53	5.32	9.24	7.28	1.96	4.05	6.73	5.39	1.34	50.95	68.79	59.87	8.92	20.89	32.93	26.91	6.02
CdP-8487	53.33	164.47	108.90	55.57	2.57	5.59	4.08	1.51	4.87	7.57	6.22	1.35	3.25	6.37	4.81	1.56	28.40	51.36	39.88	11.48	33.40	41.02	37.21	3.81
Casal de' Pazzi-Mean			111.03				3.80				5.74				4.44				48.16				26.84	
S.D.			38.75				0.36				0.63				0.44				6.15				7.23	
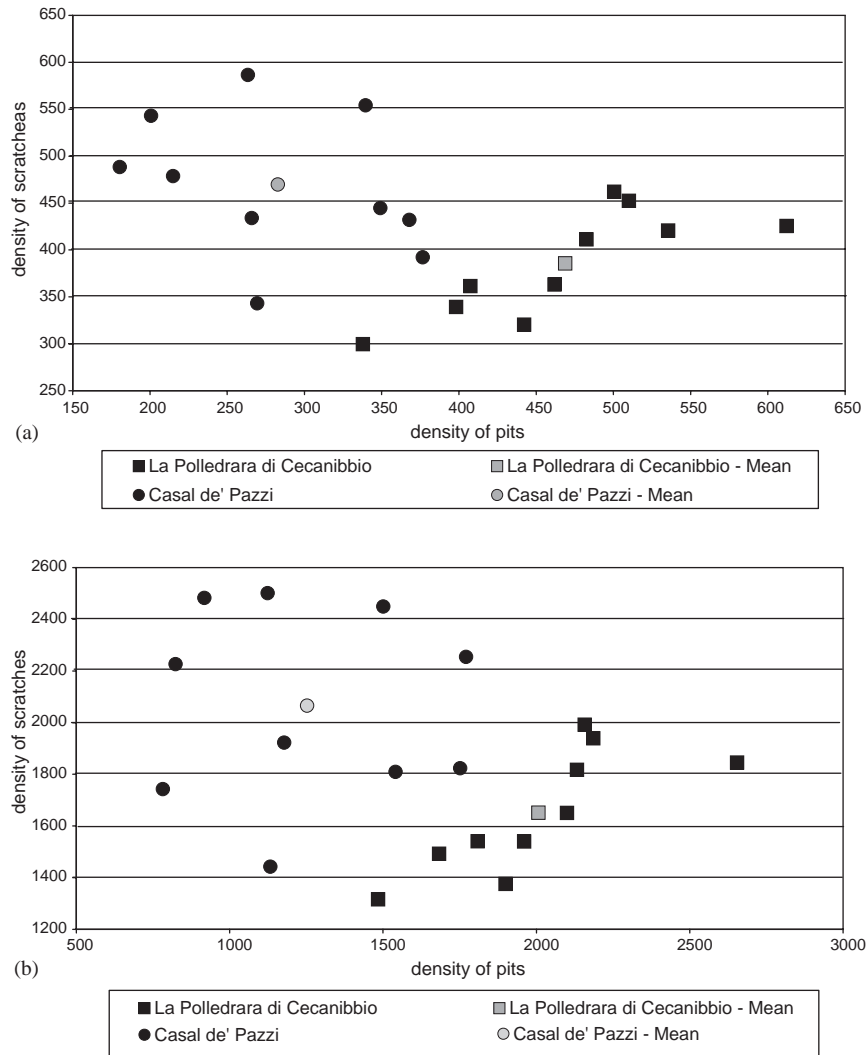
Fig. 7. Average density of pits plotted against average density of scratches as obtained for each analysed molar of *E. antiquus* Falconer and Cautley, 1847 from La Polledrara di Cecanibbio and Casal de' Pazzi. (a) magnification 200 × ; (b) magnification 500 × .

Qualitative and quantitative analyses of microwear in *E. antiquus* from both La Polledrara and Casal de' Pazzi samples are consistent with a mixed-feeder (prevalently meal-by-meal) versus browser dietary adaptation, being the browser attitude more accentuated in La Polledrara elephants. In fact, the percentage of pits is higher than in extant elephants, coarse, hypercoarse scratches and gouges are numerous, and some large pits suggest fruit, seed or roots feeding. Moreover, coarse scratches seem to be particularly frequent in extant C4 grazers, bark eaters and fruit browsers, while fine scratches characterise C3 grazers, mixed-feeders or leaf-eating browsers (see Solounias and Semprebon, 2002). It is worth noticing that La Polledrara molars show a higher occurrence of fine scratches than *L. africana*; besides fine scratches are more numerous in Casal de' Pazzi sample. Mainland (2003) suggests that a high percentage of fine scratches would depend not only on abrasiveness of food, notably on opal phytoliths, but also on soil particles ingested by grazers together with grasses. The hypothesis that the relative high percentage of fine and mixed-scratches should be attributed to the amount of abrasive soil/grit particle ingested cannot be ruled out. However, the differences between La Polledrara and Casal de' Pazzi indicate a different preferential diet. The molars belonging to La Polledrara sample differ from the Casal de Pazzi one by showing somewhere polished micro-areas where striations are separate each other by almost non-etched surface, such as resulting from teeth attrition. Attrition is more frequent in browsers, depending on planar wear from tooth-to-tooth contact after that soft food has been completely consumed. Conversely, in the Casal de' Pazzi sample abrasion is more important, as in grass-dominated mixed-feeders or in grazers.

Nevertheless, the Casal de' Pazzi specimens have an average scratch percentage similar to that of *L. africana*,
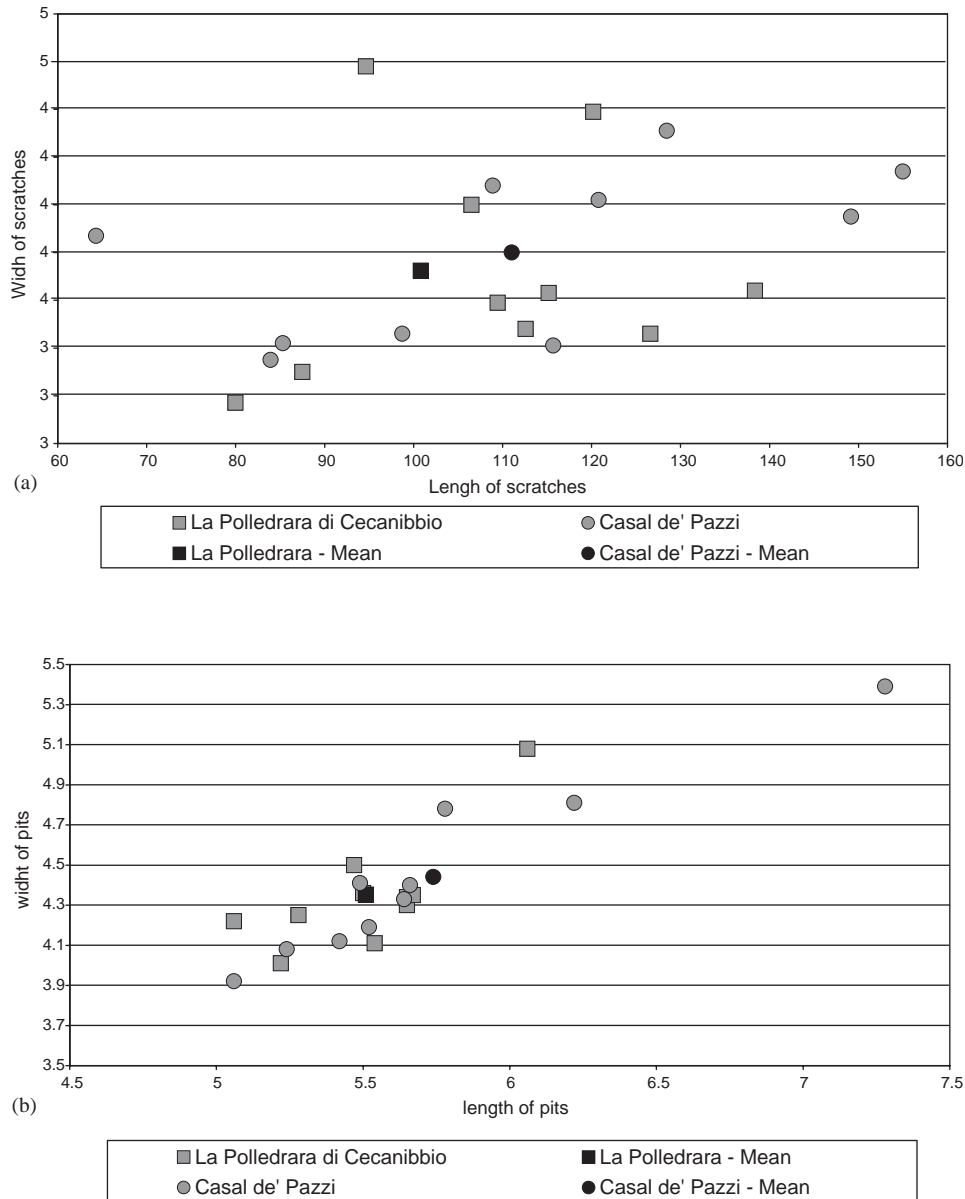
Fig. 8. Average length of scratches plotted against the average width of scratches as obtained for each analysed molar of *E. antiquus* Falconer and Cautley, 1847 from La Polledrara di Cecanibbio and Casal de' Pazzi. (a) magnification $200 \times$; (b) magnification $500 \times$.

but lower than that of *E. maximus*, a species having apparently a more accentuated attitude to grazing (Fig. 13). Diversities between La Polledrara and Casal de' Pazzi molars cannot be attributed to regional differences, as the strontium isotope composition (^{87}Sr/^{86}Sr), is indirect evidence of the similarity of the two areas of the volcanic province of Latium.

Carbon isotope measurements on the structural carbonate of biogenic apatite (enamel) suggest a prevailing C3 diet for the two families, La Polledrara being characterised by slightly higher δ^{13}C values than Casal de' Pazzi. This difference may indicate a more closed canopy forest, which is normally characterised by lower δ^{13}C (Medina et al., 1986), during OIS 7 and/or

more arid climate during OIS 9, as C3 plants tend to have higher carbon isotope composition in xeric climates (Cerling and Harris, 1999). Assuming for extinct elephants a diet-behaviour not significantly different from that of extant species (Cerling et al., 1999), the adaptation of *E. antiquus* from la Polledrara elephants to more browsing conditions than the Casal de Pazzi ones can be explained as a response to arid conditions that induced more leaf, seed or bark than grass-eating, as suggested by the behaviour of living elephants.

The wide ranges of δ^{18}Ow calculated from the measured δ^{18}Op values suggest that elephants watered both on ponds with local rain water (likely submitted to
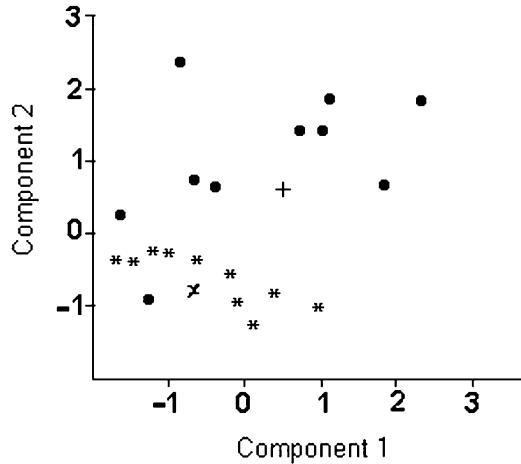
Fig. 9. Principal component diagram based on number, percentage, density of scars and their length and width counted on enamel surfaces of *E. antiquus* Falconer and Cautley, 1847 molars from La Polledrara di Cecanibbio (stars, χ = mean) and Casal de' Pazzi (points, + = mean).
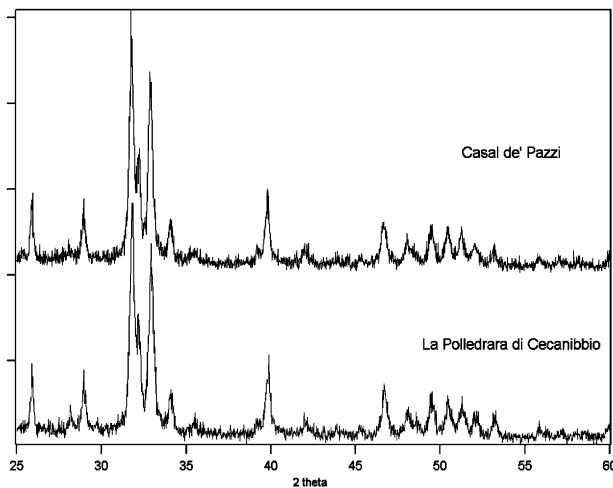

Fig. 10. XRD patterns of dental enamel of *E. antiquus* samples: traces are similar to those of Ayliffe et al. (1994), Fig. (1) obtained for extant *E. maximus* and fossil specimens belonging to *E. recki ileritensis* (ER 927) of about 1.5 Ma, and *E. recki brumpti* of about 3,5 Ma.

evaporation and consequently enriched in isotopically heavy molecules) and on river water. The latter normally is not affected by significant evaporation and/or can be more negative than local rain. Indeed, the river carries water from the catchment basin, far away and, perhaps, at higher elevation. This also suggests that mean environmental conditions during isotope stages 7 and 9 were not far from modern conditions. The isotopic differences between the mean values of $\delta^{18}O_w$ calculated from the fossil and modern local precipitations are small but not negligible. Differences of 0.8–1.3 per mil may refer to mean temperature differences from 1 °C to 2 °C.

The difference of 0.5 per mil between the mean $\delta^{18}O_w$ values could be related to a real difference in terms of

Table 2
$^{87}Sr/^{86}Sr$ ratio in enamel and dentine of La Polledrara di Cecanibbio (LP) and Casal de' Pazzi (CP) samples

Sample	Analysed material	Locality	87Sr/86Sr
LP 20	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70995
LP 21	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70986
LP 22	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70991
LP 23	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70994
LP 24	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70983
LP 25	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70994
LP 26	Tooth M3 cement	La Polledrara di Cecanibbio	0.70993
LP 27	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70987
LP 28	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70985
LP 29	Tooth M3 enamel	La Polledrara di Cecanibbio	0.71000
LP 30	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70983
LP 31	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70983
LP 32	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70980
LP 33	Tooth M3 dentine	La Polledrara di Cecanibbio	0.71000
LP 34	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70995
LP 35	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70998
LP 36	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70998
LP 37	Tooth M3 dentine	La Polledrara di Cecanibbio	0.70997
LP 38	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70985
LP 39	Tooth M3 enamel	La Polledrara di Cecanibbio	0.70995
CP 1	Tooth M3 dentine	Casal de' Pazzi	0.70989
CP 2	Tooth M3 enamel	Casal de' Pazzi	0.70989
CP 3	Tooth M3 enamel	Casal de' Pazzi	0.70987
CP 4	Tooth M3 enamel	Casal de' Pazzi	0.70998
CP 5	Tooth M3 enamel	Casal de' Pazzi	0.70996
CP 6	Tooth M3 enamel	Casal de' Pazzi	0.70995
CP 7	Tooth M3 enamel	Casal de' Pazzi	0.70987
CP 8	Tooth M3 enamel	Casal de' Pazzi	0.70985
CP 9	Tooth M3 enamel	Casal de' Pazzi	0.70985
CP 10	Tooth M3 enamel	Casal de' Pazzi	0.71004
CP 11	Tooth M3 enamel	Casal de' Pazzi	0.71003
CP 12	Tooth M3 enamel	Casal de' Pazzi	0.71015
CP 13	Tooth M3 enamel	Casal de' Pazzi	0.71010
CP 14	Tooth M3 enamel	Casal de' Pazzi	0.71026
CP 15	Tooth M3 enamel	Casal de' Pazzi	0.71005
CP 16	Tooth M3 enamel	Casal de' Pazzi	0.71016
CP 17	Tooth M3 enamel	Casal de' Pazzi	0.71021
CP 18	Tooth M3 enamel	Casal de' Pazzi	0.70995
CP 19	Tooth M3 enamel	Casal de' Pazzi	0.71008

temperature between the two periods (with stage 9 slightly warmer than stage 7) or to a difference in terms of relative humidity: more humid during stage 7 than during stage 9. The latter hypothesis is also supported by the $\delta^{13}C$ values, La Polledrara samples being ^{13}C enriched compared to the Casal de' Pazzi samples.

6. Final remarks

The analysis performed on the two sets of upper last molars belonging to late Middle Pleistocene faunas from La Polledrara and Casal de' Pazzi highlights the importance of a multidisciplinary approach in order to cross check the results, to obtain a greater reliability in both palaeodiet and palaeoenvironmental reconstructions. As far as microwear analysis is concerned, this
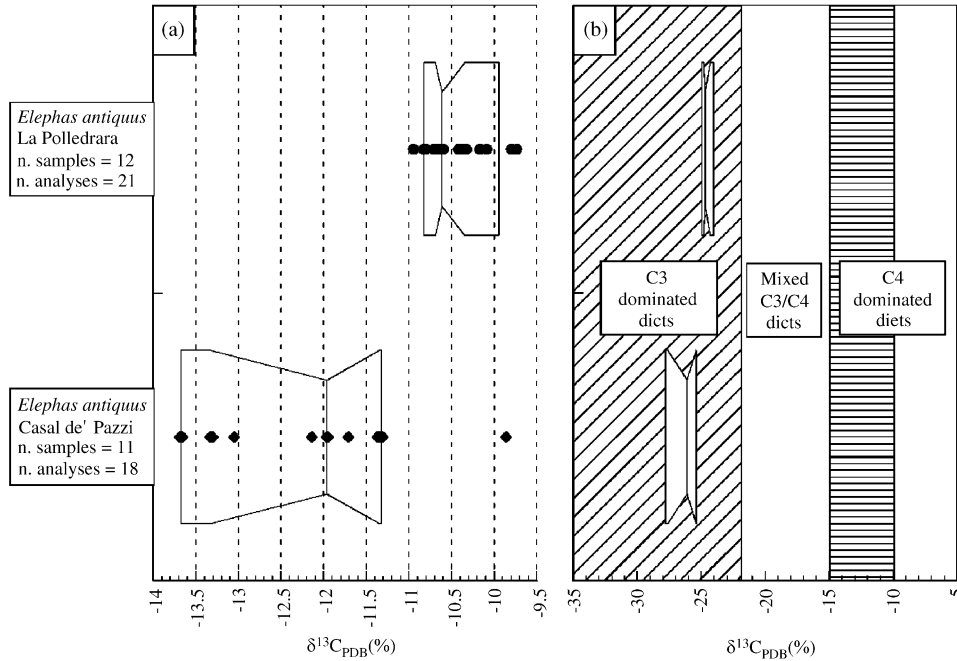
Fig. 11. (a) Plots of carbon isotope composition of analysed samples: samples values are reported as dots and diamonds; the vertical segment represents the median value. (b) Calculation of paleodiet for the two analysed families, following Cerling and Harris (1999).
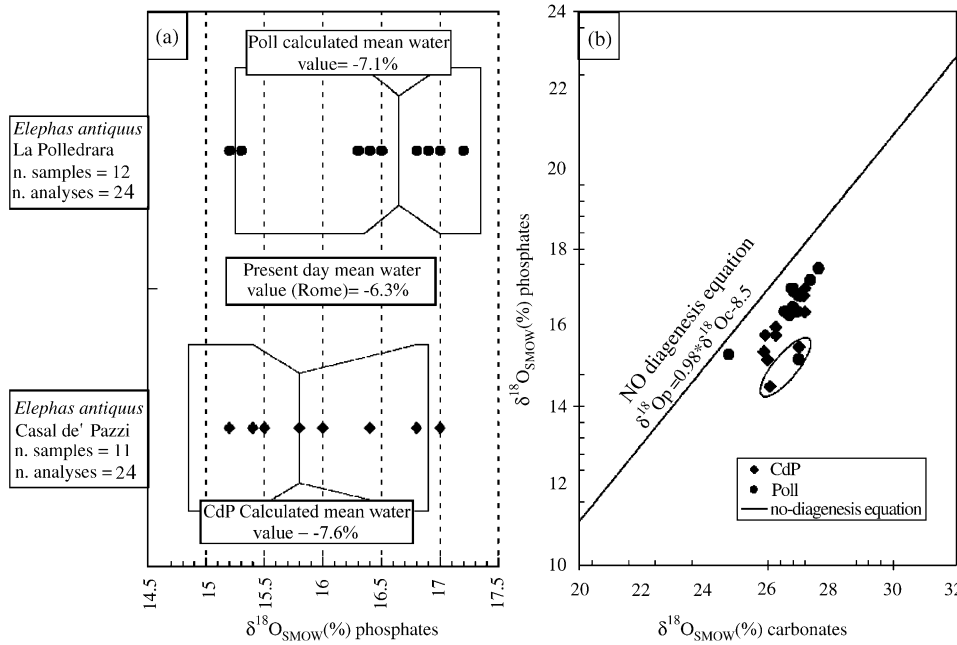

Fig. 12. (a) Plots of oxygen isotope composition of analysed phosphates: sample values are reported as dots and diamonds; the vertical segment represents the median value. Calculated mean oxygen isotope water values are added for the two families. Modern mean oxygen isotope value for atmospheric precipitation in the Roman area is added for comparison. (b) Cross plot of oxygen isotope values from carbonate and phosphate groups in bio-apatite. The three circled samples that are too far from the line of non-diagenetic effect (Iacumin et al., 1996) were not considered for mean water value calculation.

study points out the need of a large set of data from several points of the tooth occlusal surface to establish the dietary adaptation of elephants. In fact, La Polledrara and Casal de' Pazzi elephants are charac-terised, as well as the extant species, by a large amount of coarse scratches and by the occurrences of some gouges, especially on enamel lophs of central laminae, whereas cross scratches and large pits are sometimes

Table 3
Stable isotope values (carbon and oxygen in carbonate bioapatite and oxygen in phosphates) of the measured samples, with calculated $\delta^{13}C$ diet and $\delta^{18}Ow$ values. CdP = Casal de' Pazzi; Poll = La Polledrara di Cecanibbio

| Samples	$\delta^{13}Cc$ (PDB)	$\delta^{13}Cdiet$ (PDB)	$\delta^{18}Oc$ (SMOW)	$\delta^{18}Op$ (SMOW)	$\delta^{18}Ow$ (SMOW)
CdP1	−11.9	−26.0	26.1	14.5	−9.4
CdP2	−9.9	−24.0	27.2	17.0	−6.7
CdP3	−11.3	−25.4	27.0	16.8	−6.9
CdP4	−12.1	−26.2	25.9	15.4	−8.4
CdP5	−11.4	−25.5	25.9	15.8	−8.0
CdP6	−11.3	−25.4	26.3	16.0	−7.8
CdP7	−11.3	−25.4	26.0	15.2	−8.6
CdP8	−13.0	−27.2	26.3	15.8	−8.0
CdP9	−13.7	−27.8	27.2	16.4	−7.3
CdP10	−13.3	−27.4	27.1	16.8	−6.9
CdP11	−13.7	−27.8	*27.0*	*15.5*	*−8.3*
Poll1	−9.0	−23.1	24.8	15.3	−8.5
Poll2	−10.2	−24.3	27.4	17.2	−6.5
Poll3	−10.9	−25.0	26.8	17.0	−6.7
Poll4	−10.8	−24.9	26.5	16.4	−7.3
Poll5	−10.3	−24.4	26.8	17.0	−6.7
Poll6	−10.6	−24.7	27.0	16.4	−7.3
Poll7	−10.7	−24.8	27.6	17.5	−6.2
Poll8	−10.4	−24.5	27.0	16.8	−6.9
Poll9	−10.1	−24.2	26.8	16.5	−7.2
Poll10	−9.8	−23.9	*27.0*	*15.2*	*−8.6*
Poll11	−10.6	−24.7	26.8	16.9	−6.8
Poll12	−10.6	−24.7	26.7	16.3	−7.4
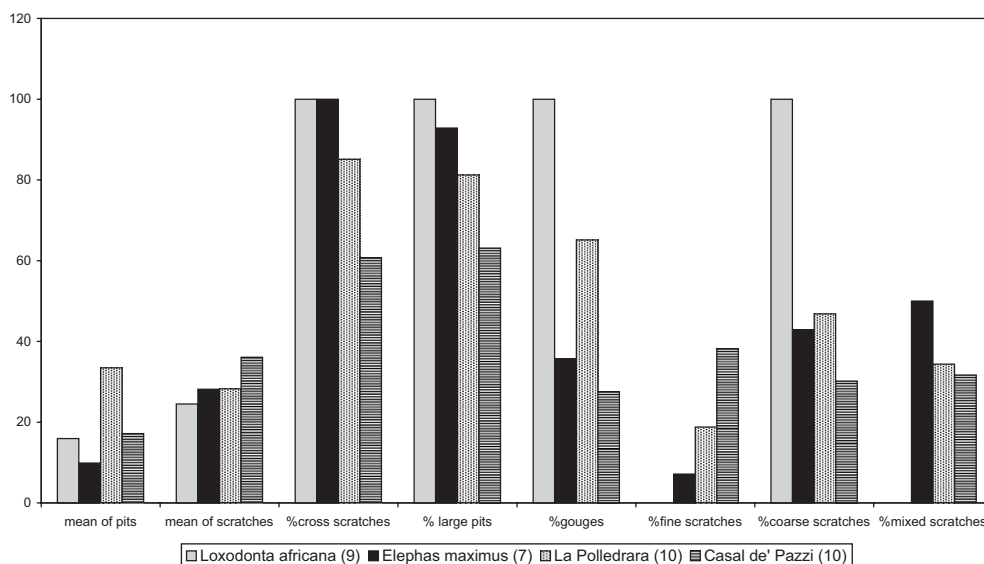
Fig. 13. Scatter diagram of percentages of microwear scars of the *E. antiquus* Falconer and Cautley, 1847 samples from La Polledrara di Cecanibbio and Casal de' Pazzi, compared with values of extant *Loxodonta africana* (Blumenbach, 1797), *E. maximus* Linnaeus, 1758 (data after Solounias and Semprebon, 2002). Scars were identified and counted using light microscope within a standard $0.4\,mm \times 0.4\,mm$ square area.

more frequent respectively on anterior (more worn) and posterior (less worn) ones. Our results are consistent with the hypothesis of a prevalently intermediate type of dietary adaptation (grasses, leaves, bark and coarse stem) for Polledrara and Casal de' Pazzi *E. antiquus,* although the average microwear topographies of the samples are different. In La Polledrara samples, coarse, often crossed scratches prevail and pits, either large and small, occur about in the same percentage as the striations, whereas the Casal de' Pazzi sample is characterised by a larger number of mixed (coarse and fine) scratches and a lower percentage of pits. For these

elephants the amount of graminaee or vegetables relatively rich in phytoliths in their diet was more important.

During the deposition of fossiliferous levels, rather similar features characterised the palaeoenvironment: wooded grassland under moderately humid and temperate climate conditions. The results of oxygen isotope analysis suggest a difference in terms of temperature and/or humidity: warmer and/or more arid conditions for La Polledrara and colder and/or wetter conditions for Casal de' Pazzi. Carbon isotope measurements on structural carbonate of biogenic apatite (enamel) also suggest a more closed canopy forest for Casal de' Pazzi and/or more arid climate for La Polledrara di Cecanibbio. Taking into account that grazing in elephants may be explained by the increase in grasses eaten during more humid periods, whereas browsing increases when the grass tend to be withered, as reported for the most savannah extant, the different patterns in microwears seems to be consistent with isotope data.

Strontium isotope composition ($^{87}Sr/^{86}Sr$) helps to define the geographical area where the two populations were living, which is confirmed to be limited to the volcanic province of Latium. Moreover the wider ranges of variability characterising the Casal de' Pazzi samples with respect to the La Polledrara ones suggests a different time average of bone accumulation at the two sites (see Milli and Palombo, this volume, for a discussion).

In synthesis, our results suggest, for Middle Pleistocene *E. antiquus* of Campagna Romana, a prevalently browser/intermediate type of dietary adaptation, rather rich also in graminaee or vegetables containing a rather large amount of phytoliths, as well as the occurrence of this species in quite arid environments also during middle climatic phases.

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