

Dental microwear analysis of bovids from the Vallesian (late Miocene) of Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea)

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ABSTRACT

The environment of the hominoid *Ouranopithecus macedoniensis* along the Axios Valley in Northern Greece during the late Vallesian is described using the feeding preferences of fossil bovids. To reach this aim, a quantitative dental microwear analysis is applied to nine extinct bovids (87 specimens) from three localities (Ravin de la Pluie, Pentalophos, Xirochori). Throughout a principal

KEY WORDS

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components analysis, the fossil data are compared to the microwear pattern of herbivorous mammals, whose feeding habits are known. These 490 wild-shot adult specimens of 22 extant species of ungulates compose the “Ungulates” database. This analysis points out that the microwear pattern of the Vallesian bovids shows similarities with that of extant grazers and mixed feeders. The dietary reconstructions of these bovids then suggest environments with a rich herbaceous layer dominated by graminoids, but a low tree cover. The dental microwear results complete the faunal, ecomorphological and sedimentological data to characterize the environment of *Ouranopithecus macedoniensis*.

RÉSUMÉ

Analyse de la micro-usure dentaire des bovidés du Vallésien (Miocène supérieur) de la vallée de l'Axios en Grèce: reconstitution de l'habitat d'Ouranopithecus macedoniensis (Primates, Hominoidea).

L'environnement de l'hominoïde *Ouranopithecus macedoniensis* du Vallésien supérieur le long de la vallée de l'Axios au nord de la Grèce est caractérisé par la reconstitution des préférences alimentaires des bovidés fossiles. Pour ce faire, une analyse quantitative de la micro-usure dentaire est effectuée sur les molaires de neuf bovidés fossiles (87 spécimens) provenant de trois localités (Ravin de la Pluie, Pentalophos et Xirochori). Les données de ces spécimens sont comparées au travers d'une analyse en composantes principales à la micro-usure dentaire de mammifères herbivores dont les habitudes alimentaires sont connues. Ces 490 spécimens, tous adultes et provenant tous du milieu sauvage, correspondant à 22 espèces actuelles d'ongulés composent la base de données « Ongulés ». Cette analyse révèle que le type de micro-usure dentaire des bovidés vallésiens présente des similarités avec celui des paiseurs et des mangeurs mixtes. Quelle que soit la localité, les reconstitutions alimentaires des bovidés fossiles suggèrent donc des environnements avec une strate herbacée abondante dominée par des graminoides et un faible couvert arboré. Les résultats de l'analyse de la micro-usure dentaire complètent les données fauniques, écomorphologiques et sédimentologiques pour caractériser l'environnement de l'hominoïde *Ouranopithecus macedoniensis*.

MOTS CLÉS

Primates,
Hominoidea,
Ouranopithecus,
micro-usure,
ongulés,
paléo-alimentation,
paléo-environnement,
Miocène,
Grèce.

INTRODUCTION

Numerous fossiliferous outcrops have been recovered along the Axios Valley in Northern Greece since 1972. The field excavations yielded a large sample of fossil remains from the Vallesian Nea Messimbrina Formation (Bonis *et al.* 1988, 1990, 1998; Bonis & Koufos 1999; Koufos & Bonis 2004). This regional sedimentary unit, whose thickness varies from 400 to 1,000 m, is composed of a succession of hard conglomerates, red clays and sands with gravels

(Sen *et al.* 2000). The Nea Messimbrina Formation is overlain by the Vathylakkos and the Dytiko ones, which are respectively correlated to the early/middle Turolian and to the late Turolian (Bonis *et al.* 1988; Sen *et al.* 2000). The Northern Greek Vallesian faunas mainly differ from the Turolian ones by the presence of the hominoid *Ouranopithecus macedoniensis* and the absence of cercopithecoids (Bonis & Koufos 1999). This hominoid was found in three localities in Northern Greece. The type locality is Ravin de la Pluie, where numerous re-

mains of mandibles, maxillaries and isolated teeth of adults as well as juvenile specimens were found (Bonis *et al.* 1973, 1998; Bonis & Melentis 1977; Koufos & Bonis 2004, 2006). Except for an almost complete face of a male specimen, the Xirochori locality has not yielded other primate remains (Bonis *et al.* 1990). The third locality, where remains of *O. macedoniensis* were unearthed, is Nikiti 1. This one is in Chalkidiki, outside the Axios Valley (Koufos 1993, 1995).

This study reconstructs the context of the late Vallesian environments along the Axios Valley. The analysis is focused on fossil bovids contemporaneous to *O. macedoniensis*. These ruminants, which are the more abundant ungulates among the late Miocene Greek localities (Bonis *et al.* 1992), were the first primary consumers of the food chain. Their diet is used to infer the vegetation and the environmental context because their feeding habits are tied to their habitats. To characterize their feeding preferences, the molar microwear pattern of these bovids is quantified from digitized photographs obtained with a light stereomicroscope (Merceron *et al.* 2004a, b). Then, the microwear pattern of these extinct ruminants is compared with that of extant ungulates whose feeding habits are well known. These approaches are used to better characterize the paleoecology of the extinct faunal assemblages (Solounias & Moelleken 1992; Caprini 1998; Solounias *et al.* 2000; Solounias & Semprebon 2002; Merceron *et al.* 2004a, 2005a, b; Merceron & Ungar 2005).

On the basis of their feeding behaviours and physiological adaptations (Hoffman 1989), extant ungulates can be divided into three main diet categories: browsers *sensu lato* (including exclusive-leaf and fruit/leaf browsers), grazers *sensu lato* (C_3 and C_4 grazers), and mixed feeders (seasonal and “meal by meal” mixed feeders). Browsers feed on leaves and fruits from various dicotyledons whereas grazing species feed mainly on herbaceous monocotyledons, i.e. graminoids (including grasses, sedges, and rushes). Mixed feeders graze or browse according to the environmental conditions.

Dental microwear results from the abrasion of teeth with items consumed during the last few

meals (Solounias *et al.* 1988; Teaford & Oyen 1989; Fortelius & Solounias 2000). Depending on the physical properties of last food and related items, the microwear signature varies. For instance, browsers (eating mainly dicotyledons) have more pits on shearing molar facets than grazers. The dental microwear pattern of grazing ungulates is characterized by a relative abundance of scratches over pits (Fig. 1A, B) (Solounias & Semprebon 2002; Merceron *et al.* 2004a). This is due to the higher concentration of silica phytoliths in the cell walls of graminoids than in those of dicotyledons (McNaughton *et al.* 1985). The fruit/leaf browsers have more scratches on enamel shearing facets than on that of the exclusive-leaf browsers, because of the consumption of fruits, seeds or stones (Fig. 1B, D) (Solounias & Semprebon 2002; Merceron *et al.* 2004a). The molar microwear pattern of mixed feeding species varies according to the seasonal fluctuations of the food availabilities. However, some species, such as the red deer (*Cervus elaphus*), are defined as “meal by meal” (or generalist) mixed feeders. Their diet mainly varies from grasses to various foliages on a daily basis. These subcategories within mixed feeders are also revealed by the dental microwear signature. The microwear pattern of seasonal mixed feeders is similar either to that of grazers or to that of browsers following a bimodal distribution. Unlike, the “meal by meal” mixed feeders do not have this bimodal pattern. They are often characterized by an abundance of both pits and scratches (Fig. 1C) (Solounias & Semprebon 2002; Merceron *et al.* 2004a).

ABBREVIATIONS

SEM	Scanning Electronic Microscopy;
Fm	Formation;
PCA	Principal Components Analysis;
PNT	Pentalophos;
RPL	Ravin de la Pluie;
XIR	Xirochori;
N fs	number of fine scratches;
N lp	number of large pits;
N p	number of pits;
N s	number of scratches;
N sp	number of small pits;
N ws	number of wide scratches;
% p	percentage of pits.

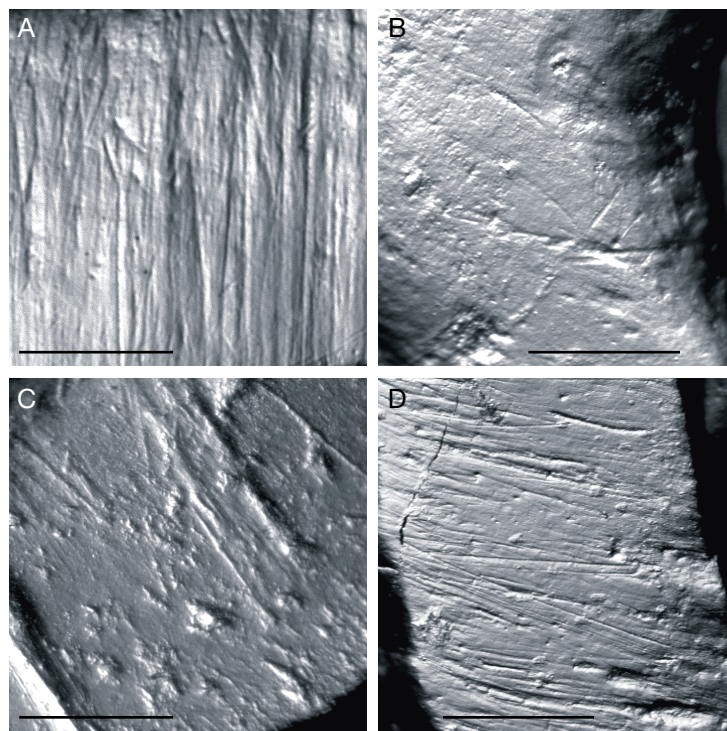


FIG. 1. — Photographs of molar shearing facets of extant ungulates: **A**, *Equus burchelli* (grazers); **B**, *Litocranius walleri* (leaf browsers); **C**, *Rangifer tarandus* (mixed feeders); **D**, *Capreolus capreolus* (fruit/leaf browsers). Scale bars: 300 μ m.

MATERIALS AND METHODS

MATERIALS

The bovids of three localities belonging to the Vallesian Nea Messimbria Fm along the lower Axios Valley are considered: Ravin de la Pluie, Xirochori and Pentalophos. Considering only the local past-environments along this valley, the Nikiti 1 hominoid locality, which is situated in Chalkidiki, is excluded from the analysis. No primate remains have been found at PNT. However, its closeness and similar age with RPL and XIR imply to integrate it in the study. These three localities are correlated with the late Vallesian mammal age MN 10 (Bonis & Koufos 1999). Both stratigraphy and faunal data indicate that PNT is the earliest locality and that RPL is the latest one (Sen *et al.* 2000).

All of the 87 studied fossil specimens are housed in the Department of Geology and Physical Geography at the Aristotle University (Thessaloniki, Greece).

Four bovid species were described at RPL (Bouvrain 1975, 1982; Bouvrain & Bonis 1985; Bonis & Koufos 1999): *Mesembriacerus melentisi*, *Samotragus praecursor*, *Prostrepsiceros vallesiensis* and *?Palaeoryx* sp. This latter taxa is not integrated to the analysis (see Appendix), because the rare material referred to this species is not sufficiently well preserved.

Four bovid species have been recognized at XIR (Bouvrain & Bonis 1985, 1986; Bonis & Koufos 1999): *Ouzocerus gracilis*, *?Palaeoryx* sp., *Protoryx* sp., and *Samotragus praecursor*. For the same reasons explained above regarding to *?Palaeoryx* sp. from RPL, *Samotragus praecursor* from this locality is not included in the analysis (Appendix).

Five bovid taxa have been described from PNT (Bouvrain 1997): *Helladorcas geraadsi*, *Ouzocerus pentalophosi*, *Protoryx* sp., *Gazella* sp. and a boselaphini indet. The gazelle is the lesser abundant species in this faunal assemblage whereas the boselaphini is represented by rare remains. These two latter

TABLE 1. — Results of principal components analysis of dental microwear pattern of 490 specimens from 22 extant ungulate species: **A**, eigenvalues; **B**, communities (r) and square communities (r^2) between variables and axis. Abbreviations: **N fs**, number of fine scratches; **N lp**, number of large pits; **N sp**, number of small pits; **N ws**, number of wide scratches; Σ , sum.

A				
Fact.	Eigenvalues	% eigenvalues	Σ eigenvalues	Σ % eigenvalues
1	1.557	38.93 %	1.557	38.93 %
2	1.022	25.55 %	2.579	64.48 %
3	0.882	22.05 %	3.461	86.53 %
4	0.538	13.47 %	4.000	100.00 %

B						
	Fact. 1		Fact. 2		Fact. 3	
	r	r^2	r	r^2	r	r^2
N ws	-0.566	0.320	0.383	0.147	-0.684	0.468
N fs	-0.141	0.020	-0.901	0.814	-0.404	0.163
N lp	0.724	0.524	0.231	0.054	-0.488	0.239
N sp	0.831	0.691	-0.094	0.009	-0.109	0.011

taxa are both excluded because the material is not sufficiently well preserved to apply a microwear quantification (Appendix).

The dental microwear pattern of 490 wild-shot adult specimens of 22 extant ungulate species, which compose the “Ungulates” database, is compared with that of fossil bovids (Appendix). These recent herbivorous mammals are ranged according to their feeding preferences (Appendix): grazers *sensu lato* (C_3 and C_4 grazers), browsers *sensu lato* (exclusive-leaf and leaf/fruit browsers) and mixed feeders *sensu lato* (seasonal and “meal by meal” mixed feeders) (e.g., Bell 1971; Hoffman 1989; Estes 1991; Tixier & Duncan 1996; Kingdon 1997; Gagnon & Chew 2000; for further specific references regarding feeding behaviours, see Merceron *et al.* 2005a).

METHODS

Preliminary researches of the dental microwear pattern of mammals were based on light microscopy (e.g., Walker *et al.* 1976). Later, most of the dental microwear studies on fossil ungulates were based on SEM (e.g., Solounias *et al.* 1988; Hayek *et al.* 1992). However, Solounias & Semprebon (2002) proposed the re-employment of light microscopy. This method reveals significant results, but suffers from the lack of digital images of the analyzed dental surfaces. Merceron *et al.* (2004a, b) then improved the approach of these authors (Solounias & Semprebon 2002) by using high-quality digital images

of dental surfaces before quantifying the dental microwear pattern with a semi-automatic method. In this study, the protocol shown in Merceron *et al.* (2004a, b) is applied for molding teeth and preparing casts, and for the digitization of microwear surfaces using the optical stereomicroscopy (Leica MZ 125, Leica Microsystems®) and then for the extraction of data.

The anterior lingual blade of the paracone and the posterior buccal blade of the protoconid on the second upper and lower permanent molars are considered. These facets occlude during the shearing masticatory phase I (Kay & Hiiemae 1974; Janis 1990). Because the dental microwear signature is not significantly different between upper and lower second molars, these teeth were grouped in a single sample (Teaford & Walker 1984; Semprebon *et al.* 2004). Shearing facets of the permanent M2 were digitized at 256 gray levels at 300-dpi resolution (1.0 $\mu\text{m}/\text{px}$) using a Spot CCD camera (Leica DC 300; 3.2 Mpixel, Leica Microsystems®) connected to a light stereomicroscope (Leica MZ 125) at low magnification ($\times 30$). Then, dental microwear was quantified in a 0.09 mm^2 square using Optimas version 6.5.2 software (Media Cybernetics®) by one of us (GM). Data was extracted and exported to statistical software (Statistica version 6, Statsoft®).

A PCA is generated with four variables: N fs (breadth lower than 15 μm), N sp (major axis lower than 15 μm), N lp (major axis higher than 15 μm),

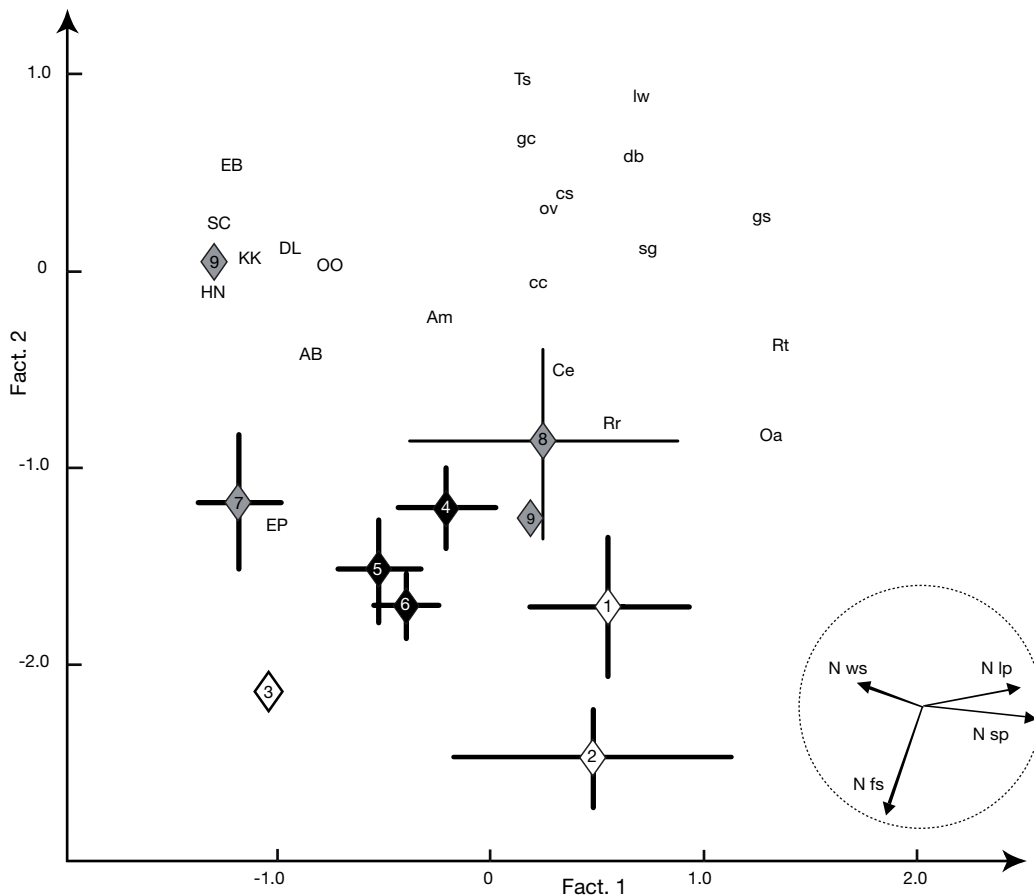


FIG. 2. — Principal components analysis (axes 1 and 2). The extant species compose the framework of the PCA, and the fossil bovids are secondly included as supplementary data. The four variables are shown within the circle of correlation. Except for *Helladorcas geraadsi* from PNT and *?Palaeoryx* from XIR, the specific samples are represented using their mean and their standard error of the mean for each axis. Abbreviations: **AB**, *Alcelaphus buselaphus*; **DL**, *Damaliscus lunatus*; **EB**, *Equus burchelli*; **EP**, *E. przewalskii*; **HN**, *Hippotragus niger*; **KK**, *Kobus kob*; **OO**, *Ourebia ourebi*; **SC**, *Syncerus caffer*; **Am**, *Aepyceros melampus*; **Ce**, *Cervus elaphus*; **Oa**, *Ovis ammon*; **Rr**, *Rupicapra rupicapra*; **Rt**, *Rangifer tarandus*; **Ts**, *Tragelaphus scriptus*; **cc**, *Capreolus capreolus*; **cs**, *Cephalophus sylvicultor*; **db**, *Diceros bicornis*; **gc**, *Giraffa camelopardalis*; **gs**, *Gazella soemmerringi*; **lw**, *Litocranius walleri*; **sg**, *Sylvicapra grimmia*; **ov**, *Odocoileus virginianus*; **in capital letters**, grazing species *sensu lato*; **in lower case with a capital initial letter**, mixed feeding species *sensu lato*; **in lower case**, browsing species *sensu lato*; **◆**, species from Ravin de la Pluie (RPL); **◇**, species from Pentalo-phos (PNT); **◇**, species from Xirochori (XIR); **1**, *Ouzocerus gracilis*; **2**, *Protoryx* sp.; **3**, *?Palaeoryx* sp.; **4**, *Samotragus praecursor*; **5**, *Mesembriaceros melentisi*; **6**, *Prostrepsiceros vallesiensis*; **7**, *Ouzocerus pentalophosi*; **8**, *Protoryx* sp.; **9**, *Helladorcas geraadsi*; **N fs**, number of fine scratches; **N lp**, number of large pits; **N sp**, number of small pits; **N ws**, number of wide scratches.

N ws (breadth higher than 15 µm; Appendix). A fifth variable, the percentage of pits (% p = N p / (N p + N s)) is not integrated because it is dependent from the total number of pits (N p) and the total number of scratches (N s). The 490 wild-shot specimens from the “Ungulates” database are considered as active data whereas the fossil specimens are secondly included as supplementary ones.

RESULTS

The first axis explains 38.93% of the variance. The second and the third components represent 25.55 and 22.05% respectively. The fourth component is not exploited because the eigenvalue of this last component is too low to be significant (Table 1).

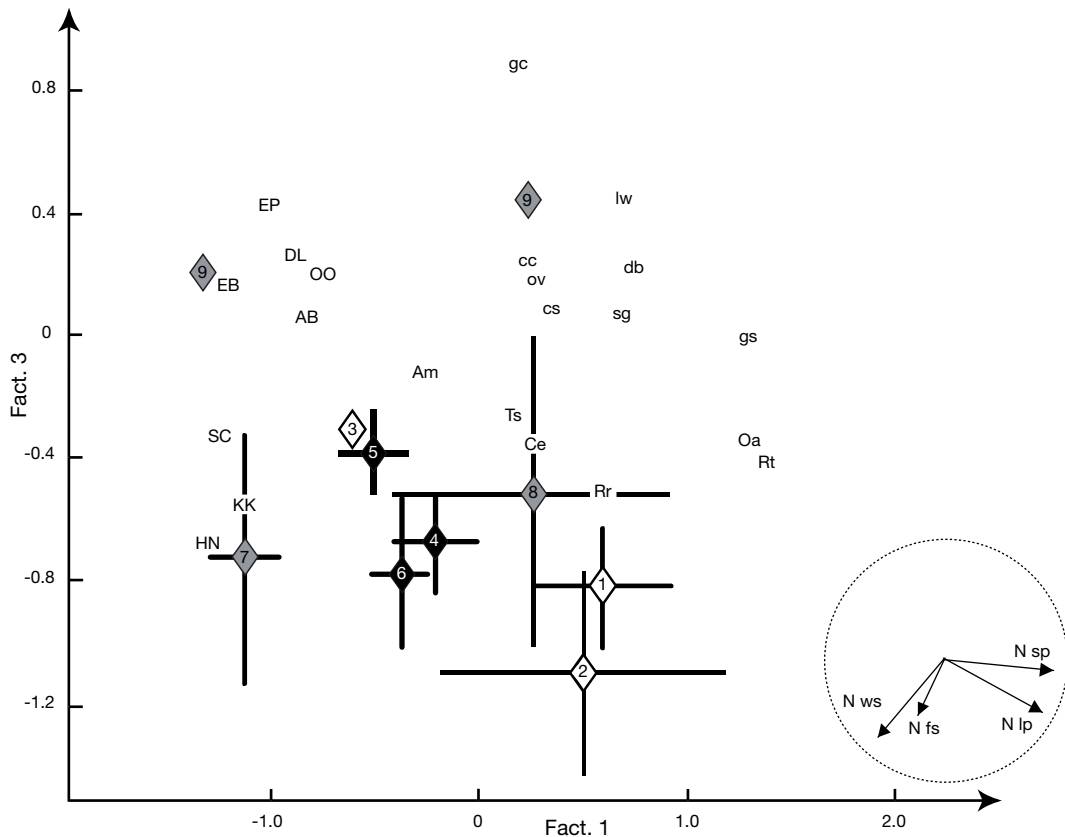


FIG. 3. — Principal components analysis (axes 1 and 3). For explanations and abbreviations, see legend in Figure 2.

RAVIN DE LA PLUIE

The three bovids (*Mesembriacerus melentisi*, *Samotragus praecursor*, and *Prostrepsiceros vallesiensis*) from Ravin de la Pluie plot close to *Aepyceros melampus* along the first component (Appendix; Fig. 2). Along the second and third axes, these bovids have coordinates similar to those of “meal by meal” mixed feeders and grazing species (Figs 2; 3). The dominance of fine scratches on shearing facets compared to the number of wide ones is pointed out by their coordinates on the second component. The low percentage of pits plus the high total number of scratches definitively reject browsing habits for these three species. Rather, it suggests that their food composition was rich in graminoids. The results of the microwear analysis agree with the ecomorphological analyses. For instance, *Mesembriacerus melentisi* has an orbit located posterior to the third upper

molar and a regular presence of a strong pillar on the upper molars. These skull features corroborate a non-browsing diet (Bouvrain 1975; Solounias & Dawson-Saunders 1988). The low ratio of pre-molar to molar lengths on one hand and the posterior position of the orbit of *Samotragus praecursor* on the other hand also suggest a probable adaptation to grazing habits (Bouvrain & Bonis 1985; Solounias & Dawson-Saunders 1988).

XIROCHORI

Regarding their molar microwear pattern, the three bovids (*Ouzocerus gracilis*, ?*Palaeoryx* sp., and *Protryx* sp.) from Xirochori are ranged from extant grazing to mixed feeding species (Figs 2; 3). The only specimen of ?*Palaeoryx* sp. has a molar microwear pattern that shows an abundance of scratches and a low pit percentage (Appendix; Figs 2; 3).

Although this indicates that this individual fed on graminoids during its few last meals, definitive judgments are not yet possible at this time about the feeding habits of this species in regard to the small sample size available. However, a previous ecomorphological analysis excludes browsing habits for *Palaeoryx* (Solounias & Dawson-Saunders 1988). *Ouzocerus gracilis* and *Protoryx* sp. have a coordinate similar to that of *Rupicapra rupicapra* along the first axis (Fig. 2). These two fossil species have negative coordinates along the two other axes (Figs 2; 3). This results from the high number of fine scratches and the lower amount of wide ones (Appendix). The XIR bovids have more pits than RPL ones. *Ouzocerus gracilis* and *Protoryx* sp. were probably mixed feeders as *Rupicapra rupicapra* and *Ovis ammon* are. The results on *Protoryx* sp. agree with previous dental microwear and ecomorphological analyses of *Protoryx* sp. from Samos and Pikermi (Solounias & Dawson-Saunders 1988; Solounias & Moelleken 1992).

PENTALOPHOS

The bovids from Pentalophos (*Ouzocerus pentalophosi*, *Protoryx* sp., and *Helladorcas geraadsi*) plot with extant grazing or mixed feeding species. *Ouzocerus pentalophosi* is close to *Equus przewalskii* on the first and second axes, and to *Syncerus caffer*, *Hippotragus niger* and *Kobus kob* on the third axis (Appendix; Figs 2; 3). Unlike *Ouzocerus gracilis* from XIR, the individuals of *Ouzocerus pentalophosi* fed mainly on graminoids during their last few meals. The microwear differences between both of these *Ouzocerus* species may suggest that *O. pentalophosi* was a pure grazer and *O. gracilis* a mixed feeder. But, they also could have been both mixed feeders. Given the small sample sizes available for analysis, however, definitive judgments are not yet possible. *Protoryx* sp. plots close to *Rupicapra rupicapra* and *Cervus elaphus* regarding on both PCA graphs (Appendix; Figs 2; 3). Although *Protoryx* sp. from PNT was also a mixed feeder, it slightly differs from the XIR one by a higher number of scratches. This may suggest that the last meals of the PNT individuals may have been richer in grasses or grass-like plants than those of XIR. Whatever their feeding differences, this is in accordance with ecomorphological

analysis and previous dental microwear analysis of *Protoryx* sp. from Pikermi and Samos that exclude browsing habits (Solounias & Dawson-Saunders 1988). One individual of *Helladorcas geraadsi* plots with extant grazers, whereas the second specimen has coordinates similar to mixed feeders on the first and second axes and similar to browsers on the third axis (Appendix; Figs 2; 3). The sample size is too small to specify their paleodiet. However, the ecomorphological features as the posterior orbit position as well as the reduction of the premolar length suggest adaptation to grazing habits (Solounias & Dawson-Saunders 1988; Bouvrain 1997).

DISCUSSIONS

C_3 , C_4 GRAMINOIDS, AND MICROWEAR SIGNATURE Solounias & Semprebon (2002) reveal that ungulates consuming C_3 graminoids (including mixed feeders and pure grazers) have usually more fine scratches than species foraging on C_4 graminoids. Merceron *et al.* (2004a) also notice these differences between extinct grazers from the late Miocene of Afghanistan and extant C_4 grazers from Africa. The present results also show that the extant taxa, *Equus przewalskii*, that consumes C_3 graminoids, have larger amounts of fine scratches compared to African grass-eaters as *Equus burchelli* (pure grazer) or *Tragelaphus scriptus* (mixed feeder). The dental microwear signature of the late Vallesian bovids from the Axios Valley would suggest that these ruminants fed on C_3 graminoids rather than C_4 ones. This agrees with previous stable isotopic and phytolith analyses. The stable isotope analyses definitively exclude the spread of C_4 graminoids in eastern Tethysian province during the late Miocene (Quade *et al.* 1994; Zazzo *et al.* 2002). However, phytolith remains from sediments show the presence of C_3 graminoids in two late Miocene localities Kemiklitepe B (Turkey) and Maragheh (Iran) from the north margin of Mediterranean basin (Strömberg & Werdelin 2004).

Although no quantitative analysis has hitherto established correlation between microwear signature and metabolic ways of graminoids, qualitative trends can be drawn. On one hand, ungulates consum-

ing C₃ graminoids have more fine scratches than those eating C₄ graminoids. On the other hand, the phytoliths inside the cell walls of graminoids differ in shape and concentration depending on the metabolic cycle of the plant. For instance, C₃ graminoids have thrice lower silica deposits in epidermal wall cells than C₄ graminoids. Moreover, C₃ graminoids have oval phytoliths whereas those on epidermis of C₄ ones usually have dumb-bell shape (Twiss *et al.* 1969; Twiss 1986, 1992; Lanning & Eleuterius 1989). Lanning & Eleuterius (1989) further point out that dicotyledonous Asteracea, which are associated with graminoids within the herbaceous layer, have fewer silica phytoliths, but more calcium deposits than C₃ and C₄ graminoids. Solounias & Semprebon (2002) conclude that the consumption of C₄ graminoids would imply higher wear rates of teeth because of a higher abrasiveness, resulting from the higher densities of phytoliths. Consequently, this would involve an under-estimation of the microwear feature densities because the phytoliths intensively abrade enamel microwear scars. Unlike, the consumption of C₃ graminoids may involve a lower wear rate and then would leave microwear scars (pits and scratches) on enamel surface for a longer period (Solounias & Semprebon 2002). Further works correlating microwear pattern of grazers and metabolic ways of graminoids will undoubtedly specify this point. The spin-off of a better understanding of correlation between microwear signature and metabolic type of graminoids will be helpful for reconstructing past environments and climates.

PALEOENVIRONMENT OF *OURANOPITHECUS MACEDONIENSIS*

Previous studies on the late Miocene faunal assemblages point out environmental differences from Western to Central to Eastern Europe (Bernor 1984; Bonis *et al.* 1992, 1999; Fortelius *et al.* 1996). Ecological indicators from diversity indexes analyses to body weight distributions of the large herbivorous mammals (Bonis *et al.* 1992; Fortelius *et al.* 1996) indicate open landscapes during the Vallesian (MN 9/10) from Eastern Europe to Anatolia. Correlation between hypsodonty index and relative humidity rate (Fortelius *et al.* 2002) indicates more open

landscapes in Southeastern Europe than in Western and Central Europe during the Vallesian.

Vesey-Fitzgerald (1963) describes recent plant communities and soil compositions along drainage lines (from headwater valley grasslands to low floodplain grasslands) in Central Africa. The author describes soils from floodplain grasslands as dominated by clays. This differs from the sediment content of the Nea Messimbria Fm, in which clayish sandy beds follow sandy bed rich in gravels as well (Bonis *et al.* 1988; Quade *et al.* 1994; Sen *et al.* 2000). This advocates many flooding periods with high water dynamic. This suggests similarities with soils from upstream portions along the drainage lines as Vesey-Fitzgerald (1963) recognized them. This author categorizes different plant communities associated with soils rich in sand particles such as riverine grasslands upper the floodplain along the drainage lines. Anyway, the author points out the dominance of grasses and grass-like plants within plant communities from high to low altitudes all along the river system (Vesey-Fitzgerald 1963). Also, according to the presence of a few carbonate nodules in the Nea Messimbria Fm, Quade *et al.* (1994) stipulate that rain precipitations were inferior to 1,000 mm per year. This agrees with the absence of dense forest similar to the recent equatorial and tropical ones over Northern Greece during the late Vallesian (White 1986).

The isotopic analysis of the carbonate nodules along the Nea Messimbria Fm points out that the C₃ vegetation dominated the environments along the Axios Valley during the Vallesian (Quade *et al.* 1994). Nevertheless, this is not incoherent with the dominance of grasses and grass-like plants. In fact, most of recent graminoids (including sedges, rushes and grasses) from Eurasian temperate latitudes have a C₃ metabolic pathway (Mateu Andrés 1993). In opposite to the specific evolution of C₄ African grasslands (McNaughton *et al.* 1985; Cerling *et al.* 1997), the Northern Mediterranean area was marked by the rise and the adaptation of sclerophyllous and xerophitic vegetations since the late Vallesian (Axelrod 1975; Agustí *et al.* 2003; Cherubini *et al.* 2003). The associated climax is the "sclerophyllous Mediterranean forest". This vegetal formation is defined as a forest where trees are sufficiently spread to

permit the development of important undergrowth vegetation, in opposite to the other forested ecosystems (White 1986; Demangeot 1996).

Previous molar and incisor microwear analyses on *Ouranopithecus macedoniensis* clearly suggest that this hominoid fed on hard-object items (Ungar 1996; King 2001). A new recent molar microwear analysis points out the similarities between the fossil hominoid and the extant species of *Papio*, and more particularly with *Papio hamadryas hamadryas*. This suggests that *Ouranopithecus macedoniensis* fed probably on roots, tubers, and graminoids in the same way that the Ethiopian hamadryas do (Merceron *et al.* 2005c). The dietary reconstructions of *Ouranopithecus macedoniensis* agree with the presence of landscapes with a low tree cover and a rich herbaceous layer.

Bovids constitute the largest part of late Vallesian mammals along the Axios Valley (Bonis *et al.* 1992). The present dental microwear analyses reports that these primary consumers were either grazers or mixed feeders, and then specify previous studies described above. The present study stipulates that the herbaceous layer along the Axios Valley was wealthy and rich in graminoids. Considering that the development of a herbaceous layer requires a low wooded cover, it undoubtedly excludes the presence of a dense forest (White 1986; Demangeot 1996). The presence of mixed feeders in XIR and PNT may indicate that the vegetation in both of these localities was probably richer in bushes and shrubs than at RPL. Further analyses including more specimens and other ungulate taxa exploiting adjacent ecological niches will specify habitat reconstructions along Axios Valley, and more particularly at PNT and XIR.

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APPENDIX

Statistic summary of the main variables of the dental microwear pattern of extant and extinct ungulates. Abbreviations: **m**, mean; **s.e.m.**, standard error of the mean. The extant species come from European museum collections as follows: Senckenberg Naturmuseum (Frankfurt), SMN (Stuttgart), MNHN (Paris), ONCFS (Chizé, France), IBGM-INRA (Toulouse, France). Abbreviations: **N fs**, number of fine scratches; **N lp**, number of large pits; **N sp**, number of small pits; **N ws**, number of wide scratches; **% p**, percentage of pits; **XIR**, Xirochori; **PNT**, Pentalophos; **RPL**, Ravin de la Pluie.

Diet Localities	Species	N	N ws		N fs		N lp		N sp		% p	
			m	s.e.m.	m	s.e.m.	m	s.e.m.	m	s.e.m.	m	s.e.m.
C ₃ grazer	<i>Equus przewalskii</i>	6	0.67	0.33	29.17	1.45	2.17	0.60	9.50	1.65	27.20	2.70
C ₄ grazers	<i>Equus burchelli</i>	9	2.11	0.56	18.67	1.46	3.56	0.73	5.89	1.78	28.90	3.60
	<i>Hippotragus niger</i>	13	2.85	0.41	24.85	1.41	4.00	0.97	10.23	1.73	32.30	2.90
	<i>Damaliscus lunatus</i>	14	1.50	0.39	21.14	1.38	3.86	0.55	8.86	1.68	33.70	2.60
	<i>Syncerus caffer</i>	24	2.63	0.30	21.96	1.45	3.67	0.35	9.58	1.19	33.80	1.90
	<i>Alcelaphus buselaphus</i>	28	1.54	0.31	24.50	0.90	3.46	0.51	12.86	1.17	37.10	1.70
	<i>Kobus kob</i>	26	2.73	0.32	23.62	0.86	3.89	0.49	13.00	1.34	37.40	2.30
	<i>Ourebia ourebi</i>	18	1.82	0.37	20.94	1.22	2.82	0.47	18.05	2.76	44.20	4.20
Seasonal mixed feeders	<i>Aepyceros melampus</i>	19	1.37	0.26	23.53	1.45	5.58	0.66	16.47	2.26	45.20	2.90
	<i>Tragelaphus scriptus</i>	18	1.72	0.51	16.50	1.43	8.33	0.98	16.00	2.15	56.20	2.60
"Meal by meal" mixed feeders	<i>Cervus elaphus</i>	47	1.45	0.20	24.94	0.91	5.51	0.47	31.40	1.94	56.70	1.70
	<i>Rupicapra rupicapra</i>	9	1.22	0.40	27.11	3.45	6.22	1.05	34.44	5.41	57.20	5.40
	<i>Ovis ammon</i>	9	0.67	0.24	26.33	3.64	7.11	2.78	43.78	9.58	58.30	9.10
	<i>Rangifer tarandus</i>	17	1.24	0.43	23.18	2.71	6.35	0.90	49.47	4.24	69.40	3.20
Fruit/leaf browsers	<i>Capreolus capreolus</i>	128	1.03	0.09	20.72	0.56	4.82	0.23	27.79	1.01	58.80	1.00
	<i>Odocoileus virginianus</i>	11	1.18	0.30	18.73	1.73	5.82	1.51	25.27	2.07	60.10	4.00
	<i>Cephalophus sylvicultor</i>	8	1.38	0.63	18.50	1.59	5.63	1.46	29.00	3.84	62.30	3.20
	<i>Sylvicapra grimmia</i>	24	1.06	0.24	19.88	1.08	6.04	0.75	33.10	2.56	63.50	2.40
	<i>Diceros bicornis</i>	10	1.20	0.50	16.45	1.84	6.05	1.10	33.45	5.22	66.00	4.80
Leaf browsers	<i>Gazella soemmerringi</i>	20	0.50	0.20	18.85	1.65	9.00	1.14	32.20	3.05	67.15	2.85
	<i>Giraffa camelopardalis</i>	16	0.81	0.28	14.25	1.25	4.00	0.75	25.31	3.18	64.00	3.40
XIR	<i>Litocranius walleri</i>	16	0.88	0.20	14.19	0.55	6.81	1.44	27.69	3.71	66.60	2.37
	<i>Protoryx</i> sp.	4	1.50	0.50	27.00	3.67	5.50	1.89	31.00	6.18	54.90	7.40
	? <i>Palaeoryx</i> sp.	1	1.00		37.00		3.00		12.00		28.30	
PNT	<i>Ouzocerus gracilis</i>	9	1.11	0.31	33.89	2.49	5.78	1.10	37.67	4.76	54.60	3.50
	<i>Protoryx</i> sp.	5	1.20	0.20	39.00	1.67	4.80	1.16	42.80	15.85	49.30	6.80
	<i>Helladorcas geraadsi</i>	2	1.00		25.00		3.00		18.50		43.40	
RPL	<i>Ouzocerus pentalophosi</i>	6	2.00	0.58	32.00	2.30	4.33	0.72	9.67	2.51	28.10	3.00
	<i>Samotragus praecursor</i>	31	1.48	0.28	31.26	1.21	5.93	0.75	20.17	1.91	42.30	2.50
	<i>Prostrepsiceros vallesiensis</i>	10	1.30	0.30	34.90	1.23	5.70	0.58	18.00	2.29	38.70	2.70
	<i>Mesembriacerus melentisi</i>	19	1.05	0.22	32.58	1.80	4.63	0.67	16.37	1.11	38.30	2.30