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Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian

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Abstract

The dental microwear pattern of fossil ungulates furnishes precise information on their feeding preferences and by extension on the dominant vegetation of past landscapes. Here, the molar microwear pattern of six bovid species from the Late Turolian “Dytiko” localities in Northern Greece is compared with that of twenty well-known extant ungulates (471 wild shot specimens). These extant species constitute the “UNGULATE” comparative database. This permits the precise correlation between food properties on the one hand and microwear pattern on the other. The shearing facet of second permanent molars was digitized in 256 gray levels using a tri-CCD camera. Scratches and pits were recorded and measured on a 0.09 mm² square on the center of the facets. Microwear variables of extant species were analyzed using principal component analysis. Data from fossil species were added as supplementary data. With the exception of one species, the fossil bovids have high numbers of scratches and pits. The comparisons with extant species suggest that the fossil species were either variable grazers or mixed feeders. These data support the presence of wooded or bushy vegetation with some grassy plants. Comparison with faunal, floristic, marine, and isotopic evidence comforts the existence of wooded landscapes in Northern Greece during the Messinian.

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Keywords: Messinian; Mediterranean; Ungulate; Molar microwear; Environment

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1. Introduction

In this study, we aim to characterize the environmental context in Northern Greece during the Messinian. During this period, evidence of intensive evaporitic deposition suggests arid conditions in the Mediterranean basin. Nevertheless, [Griffin \(2002\)](#)

shows some sedimentological changes within the evaporitic beds suggesting more humid conditions during the Latest Messinian. Dental microwear analysis can provide new insights regarding the paleo-vegetation of terrestrial environments through the paleodietary reconstruction of extinct ungulates (Merceron et al., 2004a).

Dental microwear results from the abrasion of teeth by food items which are consumed during the last days prior to the death of the animal (Solounias et al., 1988; Teaford and Oyen, 1989; Fortelius and Solounias, 2000; Merceron et al., 2004a,b). According to the properties of food and related items, microwear varies. For example, previous analyses based on electronic or optical microscopy revealed that browsing ungulates such as the roe deer (*Capreolus capreolus*) differ from grazers such as the sable antelope (*Hippotragus niger*) by having a higher percentage of pits on the enamel of shearing molar facets. Among browsing species, exclusive-leaf eaters such as the gerenuk (*Litocranius walleri*) differ from fruit/leaf browsers like the yellow-back duiker (*Cephalophus sylvicultor*) by virtue of a low number of scratches on the shearing facets of cheekteeth. The microwear pattern of mixed feeding species, such as the impala (*Aepyceros melampus*) shares similarities with that of either grazers or browsers depending on the last food items consumed. These dental microwear variations are correlated with seasonal and/or regional fluctuations in food availability. Some species, such as the ibex (*Capra ibex*) or the musk ox (*Ovibos moschatus*) are defined as “meal by meal” mixed feeders because their food consumed varies from grasses to leaves on a daily basis. Their dental microwear pattern is often characterized by a number of scratches comparable to the number of pits on the same dental facet (Solounias and Moelleken, 1992a, 1994; Solounias and Hayek, 1993; Solounias and Semprebon, 2002; Merceron et al., 2004a,b).

In this study, we propose an alternative and inexpensive method for studying microwear. This method consists of quantification of microwear from digitized photographs obtained with an optical stereomicroscope and a tri-CCD camera (Merceron et al., 2004a,b). In order to test the reliability of this alternative method, (i) 417 wild specimens from 20 extant ungulate species and (ii)

32 dental remains from the six bovid species of the Late Turolian of Northern Greece were investigated.

The dental microwear patterns of extinct and extant ungulates were integrated within a multivariate descriptive analysis. In this way, the dietary habits of extinct species can be inferred by comparisons with those of extant ungulates in the database. Beyond inferences regarding the food consumption of these Late Turolian bovids, quantification of their dental microwear is an exceptional tool for estimating the past vegetation and, by extension, past environmental conditions surrounding Dytiko in Northern Greece during the Messinian events.

2. Material

The fossil bovids studied here come from three nearby localities in the Axios valley of Northern Greece: Dytiko 1 (DTK), Dytiko 2 (DIT) and Dytiko 3 (DKO). These three localities are located into the Dytiko Formation, which overlays the Vathylakkos Formation. These three localities are correlated with the Late Turolian mammal age based on their faunal composition. In fact, the presence of the bovid *Protragelaphus theodori*, which is more derived than the related *P. skouzesi* from Pikermi, suggests a Late Turolian age. Moreover, the first occurrence *Hipparion periafricanum* in the Axios Valley at Dytiko also suggests a Late Turolian age (Bonis et al., 1989; Bonis and Koufos, 1999). The Late Turolian interval is included in the Messinian range (Steininger, 1999).

All specimens are housed in the Laboratory of Geology and Paleontology at the Aristotle University of Thessaloniki (Greece). The artiodactyls and especially the bovids represent more than half the number of large mammal specimens (Bonis et al., 1992a). Six species and 32 specimens were included in this dental microwear analysis (Table 1): 4 of *Palaeoreas lindermayeri*, 14 of *Dystychoceras macedoniensis*, 1 of *Palaeoryx* sp., 1 of *Gazella deperdita*, 10 of *Protragelaphus theodori* and 2 of *Hispanodorcus orientalis* (Bouvrain, 1978; Bonis et al., 1992a; Bonis and Koufos, 1999).

Table 1

Mean, minimum and maximum of microwear on shearing enamel facets of the second permanent molars of fossil bovids from the Dyitiko localities, Northern Greece

	N	N s			N p			N ws			N lp			% p		
		m	Min	Max	m	Min	Max	m	Min	Max	m	Min	Max	m	Min	Max
<i>Gazella deperdita</i>	1	34			46			0			6			57.5		
<i>Dystychoceras macedoniensis</i>	14	35.4	26	47	30.4	16.0	65.0	1.0	0	2.0	6.2	2.0	15.0	45.0	30.7	71.4
<i>Palaeoryx</i> sp.	1	35			39			1			8			52.7		
<i>Palaeoreas lindermayeri</i>	4	35.3	33	38	31.5	18	56	1.5	0	3	7.3	4	10	45.1	32.1	62.9
<i>Protragelaphus theodori</i>	10	33.4	23	46	53.8	29	69	1.0	0	4	8.0	3	12	61.2	42.5	71.0
<i>Hispanodorcas orientalis</i>	2	24.5	22	27	45.0	30	60	0	0	0	8.0	6	10	63.3	57.7	69.0

Number of scratches (N s), of pits (N p), of wide scratches (N ws), of large pits (N lp) and percentage of pits (% p).

The dental microwear of fossil species is compared to that of 471 wild shot specimens from 20 well-known extant ungulate species. This database, termed “UNGULATE,” is one of the largest databases ever-published (Appendix A). First, it is composed of 8 grazing species sensu lato: *Equus przewalskii*, *E. burchelli*, *Hippotragus niger*, *Damaliscus lunatus*, *Syncerus caffer*, *Alcelaphus buselaphus*, *Kobus kob* and *Ourebia ourebi* (Vesey-Fitzgerald, 1960, 1965, 1969, 1974; Stewart and Stewart, 1970; Dorst and Dandelot, 1972; Thomson, 1973; Grobler, 1974; Montfort and Montfort, 1974; Sinclair, 1977; Hoffman, 1989; Estes, 1991; Everett et al., 1992; Murray, 1993; Kingdon, 1997; Gagnon and Chew, 2000; Blake, 2002; King, 2002). Four mixed feeders, *Aepyceros melampus*, *Tragelaphus scriptus*, *Cervus elaphus* and *Rangifer tarandus* (Dorst and Dandelot, 1972; Jacobsen, 1974; Klein, 1982; Hoffman, 1989; Estes, 1991; Oleffe et al., 1993; Iason et al., 1996; Kingdon, 1997; Gagnon and Chew, 2000; Gebert and Verheyden-Tixier, 2001), and 8 browsing species sensu lato, *Litocranius walleri*, *Cephalophus sylvicultor*, *Sylvicapra grimmia*, *Gazella soemmerringi*, *Capreolus capreolus*, *Odocoileus virginianus*, *Giraffa camelopardalis* and *Diceros bicornis* complete this database (Gaare, 1968; Dorst and Dandelot, 1972; Halls, 1978; Leuthold, 1978a,b; Heymans and Lejoly, 1981; Hesselton and Monson Hesselton, 1982; Klein, 1982; Lumpkin and Kranz, 1984; Maillard and Picard, 1987; Hoffman, 1989; Estes, 1991; Cichowski, 1993; Oleffe et al., 1993; Tixier and Duncan, 1996; Kingdon, 1997; Ramirez et al., 1997; Grenier et al., 1999; Gagnon and Chew, 2000; Mysterud, 2000; Cransac et al., 2001).

3. Methods

The anterior lingual blade of the paracone and the posterior buccal blade of the protoconid on the second upper and lower permanent molars were considered (Fig. 1). These facets occlude during the shearing masticatory phase I (Kay and Hiiemae, 1974; Janis, 1990). Teaford and Walker (1984) point out no significant differences between the microwear patterns of upper and lower homologous molar facets. Thus, as in previous studies (Ungar, 1996; King et al., 1999; Merceron et al., 2004a,b), we include the data from both mandibular and maxillary molars in a single sample.

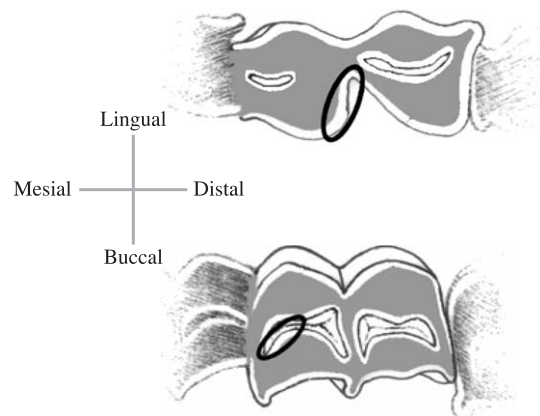


Fig. 1. Localization of shearing facets on second permanent lower (above) and upper (below) molars of ungulates (drawn by Sabine Riffaut).

Each molar was covered with an alcohol gel with neutral chemical properties which destroys glue and varnish on the enamel surface. After a few minutes, the molar facet was thoroughly cleaned with an ethanol solution (95%). Molds made from a polyvinylsiloxane material reaction were prepared in a formwork (Coltene President Microsystem®). The mold of the dental facet was oriented parallel with the maximum level of the poured resin—which constitute the cast's base (Fig. 2). The surface of the cast is then horizontal when the replica base is arranged on the platform under the stereomicroscope. Moreover, this casting procedure enables the deposition of a similar thickness of transparent resin throughout the mold. Thus, this protocol allows for a homogeneous light conditions along the cast. These steps also reduce the limitations of depth-of-focus throughout a large surface. The transparent epoxy resin was heated (30 °C, 1 h) and put in a vacuum bell jar (-10^5 Pa) in order to remove all bubbles.

For several decades, scanning electronic microscopy has been used to take photographs of enamel facets with high magnification (Walker et al., 1978; Solounias et al., 1988; Teaford, 1988; Solounias and Moelleken, 1992a,b). A recent study reveals that the use of optical microscopy at a low magnification level permits the distinction of dietary categories (Solounias and Semperebon, 2002). In this work, we propose an alternative method (Merceron et al., 2004a,b). This consists of the taking of high-resolution photograph (1 μm =1 px) with an optical stereo-microscope. This permits a repeatable protocol.

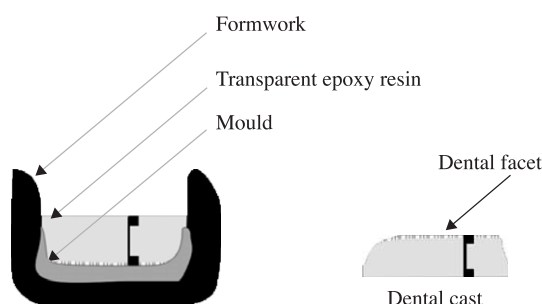


Fig. 2. Preparation of mould in a formwork for tilting horizontally the molar facets before the flowing of epoxy resin.

Table 2

Results of the principal components analysis of dental microwear pattern from twenty extant ungulate species

	Eigenvalue	% Eigenvalue	\sum Val. propres	\sum % Val. propres
1	2.49	62.1	2.49	62.1
2	0.64	16.0	3.13	78.2
3	0.63	15.7	3.76	93.9
4	0.24	6.1	4.00	100.0

	Axis 1		Axis 2		Axis 3	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
<i>N</i> s	-0.731	0.534	0.267	0.071	0.614	0.377
<i>N</i> p	0.847	0.717	0.043	0.002	0.420	0.176
<i>N</i> ws	-0.729	0.532	-0.652	0.426	0.142	0.020
<i>N</i> lp	0.838	0.702	-0.378	0.143	0.235	0.055

Eigenvalues, communities (*r*) and square communities (*r*²). *N* s—number of scratches, *N* ws—number of wide scratches, *N* p—number of pits, *N* lp—number of large pits.

% Eigenvalue—percentage of eigenvalue. \sum —sum.

The dental facets were digitized in 256 gray levels using an optical stereomicroscope ($\times 30$ on Leica MZ 125) connected to a spot CCD camera (Leica DC 300). Subsequently, each photograph was magnified up to 120 times for its treatment on computer monitor. Dental microwear was quantified using Optimas (6.5.2) software (Media Cybernetics®). A 0.09 mm² square was located around the half-way point between the top and the bottom of the shearing facet. Scratches and pits crossing the field area were both marked by only one observer (GM). When the size and the shape of microwear features were unable to be qualitatively differentiated, pits were distinguished from scratches following the minor/major axis ratio. A scratch has a minor/major axis ratio lower than 1/4 whereas a pit has a higher one (Grine, 1986). The breadth of scratches and the major axis of pits were measured to differentiate the large pits and the wide scratches. A pit is considered as large when its maximum diameter is 15 μm , and a scratch is considered wide if its breadth exceeds 15 μm (Merceron et al., 2004a,b).

Four variables are integrated in a principal components analysis (PCA): the number of scratches (*N* s), the number of pits (*N* p), the number of large pits (*N* lp), and the number of wide scratches (*N* ws). The 20 extant species represent the individual data and this permits the

development of a comparative framework. Fossil species were included as supplementary data. A fifth variable, the percentage of pits ($\%p = N p / [N p + N s]$) was not used because it is dependent on $N p$ and $N s$.

4. Results

The first axis explains 62.1% of the variance. The second and the third components represent respectively 16.0% and 15.7% of the variance. These three

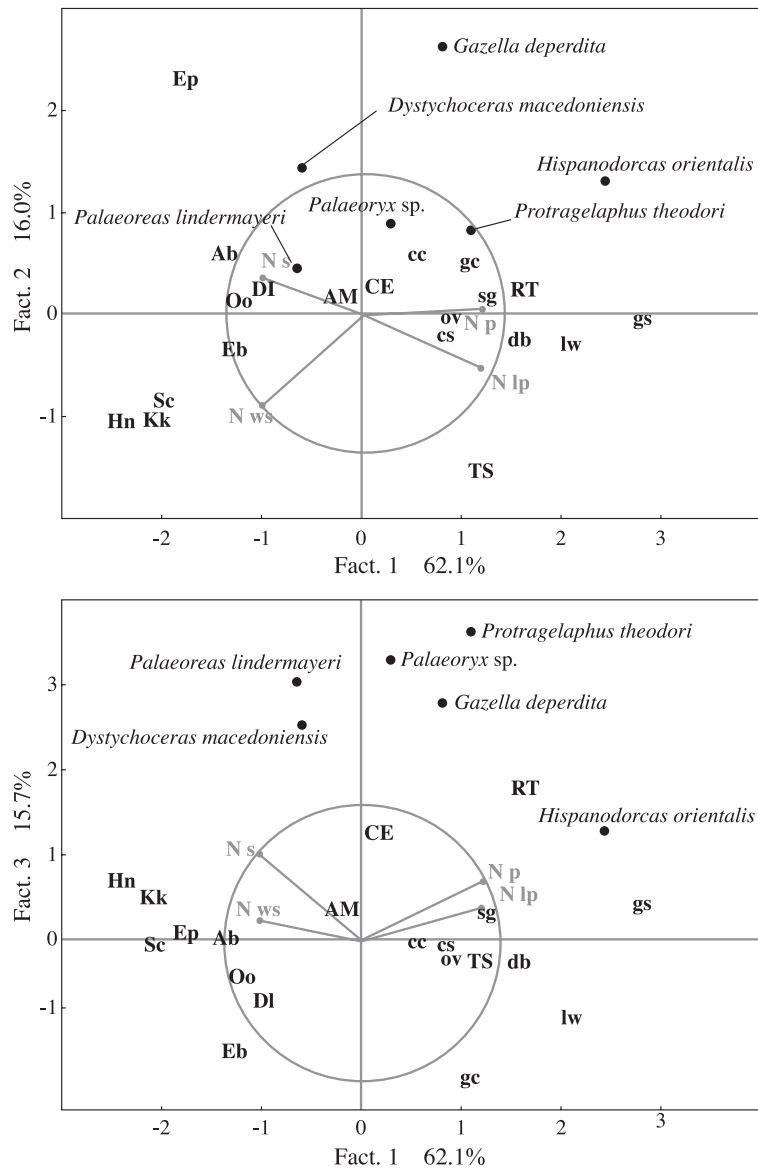


Fig. 3. Principal component analysis of extant species. The fossil bovids are included as added data. Xx—grazers; xx—browsers, XX—mixed feeders. AM—*Aepyceros melampus*, Ab—*Alcelaphus buselaphus*, cc—*Capreolus capreolus*, CE—*Cervus elaphus*, cs—*Cephalophus sylvicultor*, Dl—*Damaliscus lunatus*, db—*Diceros bicornis*, Eb—*Equus burchelli*, Ep—*Equus przewalskii*, gs—*Gazella soemmerringi*, gc—*Giraffa camelopardalis*, Hn—*Hippotragus niger*, Kk—*Kobus kob*, lw—*Litocranius walleri*, ov—*Odocoileus virginianus*, Oo—*Ourebia ourebi*, RT—*Rangifer tarandus*, sg—*Sylvicapra grimmia*, Sc—*Syncerus caffer*, TS—*Tragelaphus scriptus*.

axes explain more than 90% of the total variance (Table 2). The fourth component has a lower weight in the scattering of data, and therefore is not discussed.

The extant species are distributed along the first axis according to the positive weight of N_p and N_{lp} and the negative weight of N_s and N_{ws} . All extant grazing species differ from browsers sensu lato by a negative co-ordinate (Fig. 3). Among the browsing species, *Gazella soemmerringi* differs from the others species by a high co-ordinate on the first axis (Fig. 3). This is in accordance with the high N_p (Appendix A). Along the second axis, the extant species are mainly dispersed according to the negative weight of N_{ws} . Thus, the main divergence between the grass eaters is the high co-ordinate of *Equus przewalskii*, which is due to a low N_{ws} (Fig. 3; Appendix A). In contrast, *Tragelaphus scriptus* differs from browsers sensu lato and mixed feeders in having a low co-ordinate on this second component (Fig. 3; Appendix A). Along the third axis, the extant ungulates are mainly distributed according to the weight of N_s , and that of N_p to a lesser extent (Fig. 3; Appendix A). *Giraffa camelopardalis* and *Litocranius walleri* have a lower co-ordinate along this third axis, which is correlated with lower N_s than the other browsers (Fig. 3; Appendix A). Among the grazing species, the moderate weight of N_p is added to that of N_s . This explains why *Hippotragus niger* and *Kobus kob* have higher co-ordinates than *E. przewalskii*. The mixed feeders have various affinities with either grazers or browsers according to this component (Fig. 3). Although the N_s of *Cervus elaphus* is higher than that of *Rangifer tarandus*, this last cervid has a higher co-ordinate along the third axis because its higher N_p .

According to the first plane, *Palaeoreas linder-mayeri* is close to the extant grazing species (Fig. 3). One specimen has a high N_p , whereas the three other ones have a low one (Table 1). The $\%p$ is also similar to that of extant grazers such as *Alcelaphus buselaphus* (Table 1; Appendix A). *Dystychoceras macedoniensis* shares an intermediate co-ordinate on the first axis between *Aepyceros melampus* and *Damaliscus lunatus*, but it differs from these species in having a high co-ordinate on the second component (Fig. 3). *Dystychoceras macedoniensis* has a higher N_s than the most obligate grazers and a similar N_p with certain exclusive-leaf browsers

and fruit/leaf ones such as the roe deer (*Capreolus capreolus*; Table 1; Fig. 4A and B; Appendix A). The only specimen of *Palaeoryx* sp. is similar to fruit/leaf

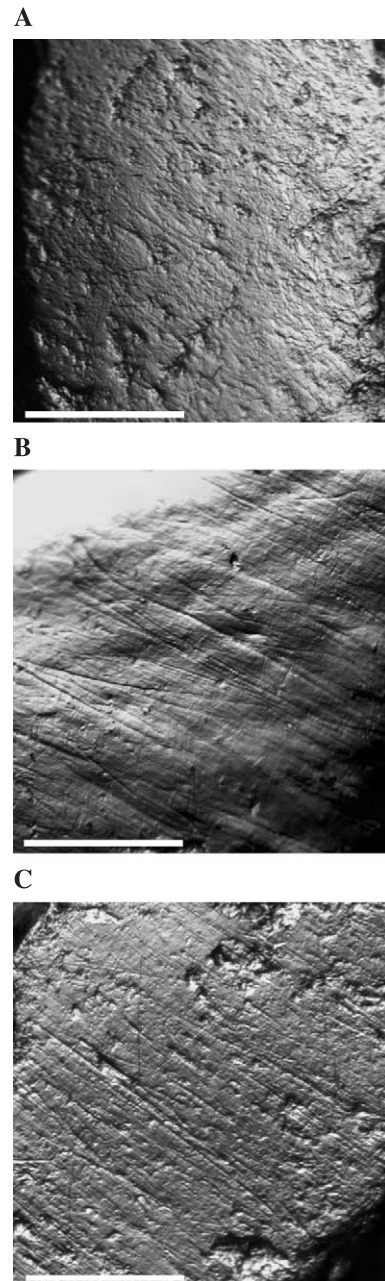


Fig. 4. Digitized photographs of shearing facets of the second molars of *Dystychoceras macedoniensis* (A and B) and *Protragelaphus theodori* (C). Scale bars=300 μ m.

browsers on the first plane of the PCA. According to the third component, this fossil bovid differs by having a higher co-ordinate. This indicates a higher N_s than that of the browsing species (Fig. 3; Table 1; Appendix A). The specimen of *Gazella deperdita* is within the browsing extant species plot according to the first axis whereas it is out of this cluster considering the second and the third components (Fig. 3). *Protragelaphus theodori* is plotted with the browsers on this first plane, and shows high co-ordinates on the third axis, which suggests highly scratched and pitted molar facets (Figs. 3 and 4C). *Protragelaphus theodori* shows strong affinities with *Rangifer tarandus* and *Gazella soemmerringi* according to N_p and the N_{lp} (Table 1; Appendix A). *Hispanodorcus orientalis* has a similar co-ordinate to that of *G. soemmerringi* according to the first axis (Fig. 3). This fossil bovid has a low N_{ws} and thus a high co-ordinate along the second axis (Fig. 3; Table 1). Along the third axis, this fossil species is close to *Cervus elaphus* (Fig. 3).

5. Discussion and conclusions

5.1. Extant species

The distribution of extant species is superimposed on their dietary habits. On the first plane, grazers mainly differ from browsers sensu lato by a lower numbers of pits and large pits. This is correlated with a lower percentage of pits (Fig. 3; Appendix A). *Equus przewalskii*, which mainly crops on C3 graminoids (grasses, sedges and rushes), differs from the African grazers in having a lower number of wide scratches (Fig. 3; Appendix A). Solounias and Semprebon (2002) revealed that the dental microwear pattern on the enamel shearing molar facets of C3 grazers is characterized by the abundance of fine scratches compared to C4 grazers. These microwear differences may be correlated with the concentrations and the form of biogenic silica phytoliths, which vary according to the metabolic pathway. In fact, C4 graminoids have about three more times silica cells on the epidermis than that of C3 ones (Kaufman et al., 1985). Moreover, the silica phytoliths of C4 grass and grass-like herbs are mostly dumb-bell shaped,

whereas those of C3 graminoids are primarily oval (Twiss et al., 1969; Twiss, 1986; Lanning and Eleuterius, 1989). Further experimental studies and dental microwear analysis on extant grazers from temperate latitudes will clarify the correlation between the metabolic pathways of graminoids and microwear patterns.

Among the browsers sensu lato, the difference in co-ordinates along the third axis between the exclusive-leaf browsers (*G. camelopardalis* and *Litocranius walleri*) and fruit/leaf browsers (*Capreolus capreolus*, *Odocoileus virginianus*, *Cephalophus sylvicultor*, *Sylvicapra grimmia*, *Gazella soemmerringi* and *Diceros bicornis*) results from a higher number of scratches for the latter. This results from the intake of fruits and seeds, whose stones and peels are more abrasive than leaf and pulp material. The inter-specific analysis using this large database clearly confirms the results of Solounias and Semprebon (2002).

Along the third axis, the high co-ordinate of *Rangifer tarandus* and *Cervus elaphus* results from a high number of scratches. This is correlated with a mixed diet and the regular consumption of grass and grass-like plants: up to 30% of the food composition in temperate latitudes. According to the first axis, *Aepyceros melampus* can be defined as a typical mixed feeder. In fact, this antelope eats fresh grasses and browses various foliage and fruits during the dry season. According to the first and the third axis, *Tragelaphus scriptus* falls within the fruit/leaf browsers. This species feeds on fresh grasses at the beginning of the wet season. The rest of the year, its diet varies from leaves to fruits. According to this analysis, *T. scriptus* feeds on grasses to a lesser extent than *A. melampus*.

Two extant species, *Rangifer tarandus* and *Gazella soemmerringi* share an intensive pitting of enamel molar facets. This high abrasion rate is correlated with the intake of hard food or exogenous items (Solounias and Semprebon, 2002). These authors reveal that this intensive pitting is found on the cheekteeth of certain suids and ruminants. In the case of certain suids such as *Potamochoerus*, the incidence of high pitting is explained by the regular intake of roots and soil particles. On the other hand, the intensive pitting on the cheekteeth of ruminants is recorded for species which inhabit open and arid (warm or

cold) environments. *Gazella soemmerringi* and *R. tarandus* (in this work), and *Llama vicugna*, *Camelus bactrianus*, *C. dromedarius* (Solounias and Semprebon, 2002) all inhabit this kind of environment. *Rangifer tarandus* frequents tundra and feeds mainly on lichens on the ground or bark on trees. *Gazella soemmerringi* favors the arid scattered scrubland and the grassy steppes of Ethiopia. *Llama vicugna* inhabits Andean arid grasslands whereas Old World camelids occupy dry to desert regions (Solounias and Semprebon, 2002). According to these authors, these environmental conditions facilitate the deposit and the adhesion to food material of dust and grit.

5.2. Extinct species

According to its co-ordinates on the PCA planes, *Palaeoreas lindermayeri* fed on grasses or grass-like plants. However, the number of pits is too important to imply an exclusively grassy diet and thus suggests that this antelope was either a variable grazer or a mixed feeder. In the same manner, *Dystychoceras macedoniensis* probably grazed. However, the high number of pits suggests either a variable grazing or a mixed diet for this bovid. The co-ordinates of the single specimen of *Palaeoryx* sp. on the first plane rejects without any doubt the exclusive consumption of grasses. Nevertheless, considering its high number of scratches, this specimen of *Palaeoryx* sp. fed on mixed diet (Table 1). According to its high number of scratches and its null number of wide scratches (Table 1), the single specimen of *Gazella deperdita* likely fed on various food items before its death. *Protragelaphus theodori* was not a grazer sensu lato. The high number of scratches is correlated with a certain amount of graminoids in the food composition. The numbers of pits and of large pits for *P. theodori* are similar to those of *Rangifer tarandus* and *Gazella soemmerringi*. Thus, *P. theodori* was probably a mixed feeder, which likely ingested exogenous hard particles. *Hispanodorcas orientalis* shares strong affinities with extant browsers and mixed feeders (Fig. 3). The specimens both have a high number of pits and large pits, which suggests the intake of hard particles. This indicates that these specimens fed on a mixed diet. The small size of the sample does not

enable a test regarding the intake of exogenous particles as was the case with *P. theodori* did it (Table 1; Appendix A).

5.3. Palaeoenvironmental reconstruction

In contrast to East Africa where the climatic trends implied the spread of grasslands during the Late Miocene (Cerling et al., 1997), the development of a deciduous forest in Spain began in the Lower Turolian replacing Vallesian evergreen forests (Agustí et al., 2003). These authors extrapolate this environmental trend throughout the Mediterranean basin (Agustí et al., 2003). This is synchronous with probably one of the more important falls in Mediterranean Sea level. In fact, Seidenkrantz et al. (2000) pointed out a first restriction between Atlantic and Mediterranean marine water is recorded at the Vallesian/Turolian limit. The evidence of a stronger event of water restriction is also revealed at 7.16 Ma, which marks the lowest Messinian (Seidenkrantz et al., 2000). Numerous disappearances of benthic foraminifera from the Metochia section in the island of Gavdos (Greece) and the decrease of carbon and oxygen isotope values support this strong fall in sea level (Seidenkrantz et al., 2000). These results are also revealed by the changes in diatoms in several sedimentary basins such as that of Pissouri in Cyprus (Pestrea et al., 2002). The faunal assemblages of the same Cypriot basin also indicate a trend from a lower circalittoral environment to closer one from the Latest Tortonian up to the Messinian salinity crisis (Merle et al., 2002).

The dental microwear analysis of fossil ungulates from the Late Turolian brings new insights regarding the environmental implications of these Messinian events. The PCA shows that four bovids were mixed feeders (*Protragelaphus theodori*, *Palaeoryx* sp., *Gazella deperdita* and *Hispanodorcas orientalis*), and that two others were either variable grazers or mixed feeders (*Palaeoreas lindermayeri* and *Dystychoceras macedoniensis*). The co-habitation in Dytiko surroundings of these species having intermediate dietary adaptations excludes the exclusive dominance of grasslands. This therefore suggests the presence of wooded landscapes. In the same way, the environment at Dytiko differed without any doubt from present dense-temperate or evergreen forests. In

fact, no bovid among these fossil species shows a typical molar microwear pattern for extant browsers *sensu lato* (e.g., *Cephalophus sylvicultor*). Moreover, the dominance of forested environments or of thicket bushlands would limit strongly the development of the herbaceous grassy undergrowth (White, 1986), whose existence is certified by the presence of mixed feeding species. These data suggest the alternation of wooded and bushy areas with some less spread grassy ones.

These results confirm and complete those based on the faunal data. In fact, the presence of the Tragulidae and the Cervidae at Dytiko suggests a closing of the environments from the Middle to the Late Turolian in Northern Greece. Moreover, the presence of the Chalicotherinae *Macrotherium macedonicum* also confirms this because this species was associated with the presence of trees. According to the body weight of the large herbivorous mammals, the faunas of the Dytiko localities show similarities with the faunal assemblages of recent Savannah woodlands (Bonis et al., 1992a,b, 1999; Bonis and Koufos, 1999). In the Silata locality from the Late Turolian of Chalkidiki, Vasileiadou et al. (2003) point out a spatial alternation of open and dry habitats with wooded areas around water holes. Their presence is revealed by many lignitic elements and numerous fresh-water mollusks. The rodent *Occitanomys* indicates some open and dry conditions in Silata whereas the Petauristid *Pliopetaurista* must be adapted to closed and forested environments (Vasileiadou et al., 2003).

The paleoenvironmental interpretations inferred based on the dental microwear pattern of the fossil bovids are also supported by the data of others. For example, the pollen assemblages from the DSDP marine site 380 (Deep Sea Drilling Project) in the Black Sea show forested environments dominated by subtropical taxa. This attests to warm and humid conditions in the Black Sea surroundings (Fauquette et al., *in press*). The changes in the sedimentologic composition within the evaporitic beds in the South-eastern Mediterranean confirm this increase in humid conditions during the Late Messinian (Griffin, 2002). The continental localities of Northern Greece reveal rich and diversified pollen assemblages from the Early to the Late Turolian. Karistineos and Ioakim (1989) point out wooded environments with the

increase of sclerophyllous vegetation (*Quercus* and *Alnus*) throughout the Late Miocene. Nevertheless, the authors reveal also the appearance of some xerophytic taxa (*Olea*, *Quercus ilex*-type) in the Serres basin.

The evidence of wooded and wet habitats with the existence of some environmental indicators of drier local conditions (in the Serres basin and in the Silata locality) during the Messinian events might be also have resulted from different climatic influences of the different European provinces. In Central Europe, the faunal assemblages suggest an opening of the habitats during the Turolian. In contrast, a slight closing of the Greek ones is indicated during the Late Turolian (Bonis et al., 1992a; Bonis and Koufos, 1999). This could result from the possible influence of the climatic conditions of one province on the other, which could explain the combination of humid conditions with some drier ones in Northern Greece. Further analysis of molar microwear of fossil ungulates from different European localities will enable a more complete description of the nature and extent of the environmental and climatic changes during the Messinian events.

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Appendix A. Summary statistical data of dental microwear on shearing molar facets of twenty extant species

Species	<i>N</i>	<i>N s</i>		<i>N p</i>		<i>N ws</i>		<i>N lp</i>		<i>% p</i>	
		<i>m</i>	S.E.	<i>m</i>	S.E.	<i>m</i>	S.E.	<i>m</i>	S.E.	<i>m</i>	S.E.
<i>Aepyceros melampus</i> ^a	19	24.89	1.41	22.05	2.77	1.37	0.26	5.58	0.66	45.15	2.87
<i>Alcelaphus buselaphus</i> ^b	28	26.04	0.78	16.32	1.38	1.54	0.31	3.46	0.51	37.15	1.72
<i>Capreolus capreolus</i> ^c	128	21.75	0.58	32.61	1.10	1.03	0.09	4.82	0.23	58.76	0.96
<i>Cephalophus sylvicultor</i> ^c	8	19.88	1.59	34.63	4.74	1.38	0.63	5.63	1.46	62.28	3.20
<i>Cervus elaphus</i> ^a	47	26.38	0.93	36.91	2.15	1.45	0.20	5.51	0.47	56.75	1.70
<i>Damaliscus lunatus</i> ^b	14	22.64	1.42	12.71	1.89	1.50	0.39	3.86	0.55	33.72	2.62
<i>Diceros bicornis</i> ^c	10	17.65	1.86	39.50	6.03	1.20	0.50	6.05	1.10	66.00	4.82
<i>Equus burchelli</i> ^b	8	20.25	1.16	8.38	1.91	1.88	0.58	3.50	0.82	27.23	3.64
<i>Equus przewalskii</i> ^b	6	29.83	1.49	11.67	2.09	0.67	0.33	2.17	0.60	27.22	2.71
<i>Gazella soemmerringi</i> ^c	20	19.35	1.72	41.20	3.04	0.50	0.20	9.00	1.14	67.15	2.85
<i>Giraffa camelopardalis</i> ^c	16	15.06	1.27	29.31	3.66	0.81	0.28	4.00	0.75	64.03	3.44
<i>Hippotragus niger</i> ^b	13	27.69	1.08	14.23	2.00	2.85	0.41	4.00	0.97	32.28	2.90
<i>Kobus kob</i> ^b	26	26.35	0.89	16.88	1.52	2.73	0.32	3.88	0.49	37.36	2.29
<i>Litocranius walleri</i> ^c	16	15.06	0.57	34.50	4.87	0.88	0.20	6.81	1.44	66.60	2.37
<i>Odocoileus virginianus</i> ^c	11	19.91	1.76	31.09	3.27	1.18	0.30	5.82	1.51	60.14	4.01
<i>Ourebia ourebi</i> ^b	18	22.76	1.09	20.86	3.07	1.82	0.37	2.81	0.47	44.17	4.17
<i>Rangifer tarandus</i> ^a	17	24.41	2.76	55.82	4.18	1.24	0.43	6.35	0.90	69.45	3.20
<i>Syncerus caffer</i> ^b	24	24.58	1.35	13.25	1.33	2.63	0.30	3.67	0.35	33.79	1.91
<i>Sylvicapra grimmia</i> ^c	24	20.94	1.18	39.15	3.09	1.06	0.24	6.04	0.75	63.54	2.41
<i>Tragelaphus scriptus</i> ^a	18	18.22	1.56	24.33	2.70	1.72	0.51	8.33	0.98	56.20	2.59

Mean (*m*) and standard error of the mean (S.E.) of the number of scratches (*N s*), of pits (*N p*), of wide scratches (*N ws*), of large pits (*N lp*) and percentage of pits (*% p*).

^a Mixed feeding species sensu lato.

^b Grazing species sensu lato.

^c Browsing species sensu lato.

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terrean basin and on

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