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The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls

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Abstract

Dental microwear of Late Miocene artiodactyls from Afghanistan can yield information on paleodiet and thus inferences can be drawn about their paleoenvironment. The "Molayan" locality lies at the border between the Greek–Iranian and Siwalik bioprovinces. Knowledge of the paleoenvironment will further our understanding of the faunal exchanges between these two provinces during the Late Miocene. Ninety-nine specimens of seven bovid and one giraffid species are considered. The number and diversity of the samples provide objective data, which enable the reconstruction of the paleoenvironment.

Prostrepsiceros aff. *vinayaki* and *Sporadotragus tadzhikistanicus* have similar dental microwear pattern, which suggests a "meal by meal" mixed feeding diet. *Phronetragus* aff. *secondus*, *Gazella* sp., and the giraffid *Palaeotragus* cf. *rouenii* can only be characterized as mixed feeders in a general sense. *Dorcadoxa porrecticornis* was an obligate grazer and the two species of *Tragoportax* were variable grazers. The analysis also brings out clear similarities between extinct grazers and *Equus przewalskii*, which is a C3 grazer. Isotopic evidence from previous studies supports the microwear data. Comparisons with data from the Late Miocene of the Potwar Plateau suggest strong environmental differences with the Afghan locality. When brought together, this disparate evidence about diet suggests an open and dry environment composed mainly of C3 grasses and evergreen bushes during the Late Miocene in Afghanistan.

Keywords: Microwear; Paleodiet; Paleoenvironment; Miocene; Afghanistan; Ungulates

1. Introduction

Dental microwear analysis is an exceptionally useful tool for characterizing the diet of paleofauna and consequently past environments. Extant ungulates can be divided into three main diet categories—browsers sensu lato, grazers sensu lato, and mixed feeders—on the basis of their feeding behavior (Hoffman, 1989). The browsers feed on leaves and fruits from various dicotyledonous species, whereas grazing species consume mainly on monocotyledonous graminoid plants (grasses, sedges, and rushes). The

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mixed feeders graze or browse according to the environmental conditions. Dental microwear results from the abrasion of teeth by food items 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., in press). According to the properties of food and related items, the microwear may vary (Fig. 1). For example, the dental microwear pattern on shearing molar facets of browsing ungulates (e.g. roe deer, *Capreolus capreolus*) differs from that of grazers (e.g. Burchell's zebra, *Equus burchelli*) by a higher percentage of pits (Solounias et al., 1988, 1993; Solounias and Semprebon, 2002). In fact, grasses and related plants leave numerous scratches on the teeth because of the high concentration of silica phytoliths in their cell walls (Mac Naughton et al., 1985; Robert and Roland, 1998). Among browsing species, leaf browsers such as the gerenuk (*Litocranius walleri*) differ from fruit/leaf browsers like the white-tailed deer (*Odocoileus virginianus*) by a lower number of scratches (Solounias and Semprebon, 2002). The dental microwear pattern of mixed feeders (e.g. impala, *Aepyceros melampus*) shows some similarities with that of either grazers or browsers according to their last food intakes (Solounias and Moelleken, 1992a, 1994; Solounias and Hayek, 1993). These dental microwear variations can be correlated with seasonal or/and regional fluctuations of food availability. Some species, such as the ibex (*Capra ibex*) or the muskox (*Ovibos moschatus*) are defined as 'meal by meal' mixed feeders because the composition of their food ranges from grasses to leaves on a daily basis (Solounias and Semprebon, 2002). Ungulates living in open and arid environments, such as the vicugna (*Llama vicugna*), show an intensive abrasion on molar facets. This is due to the important

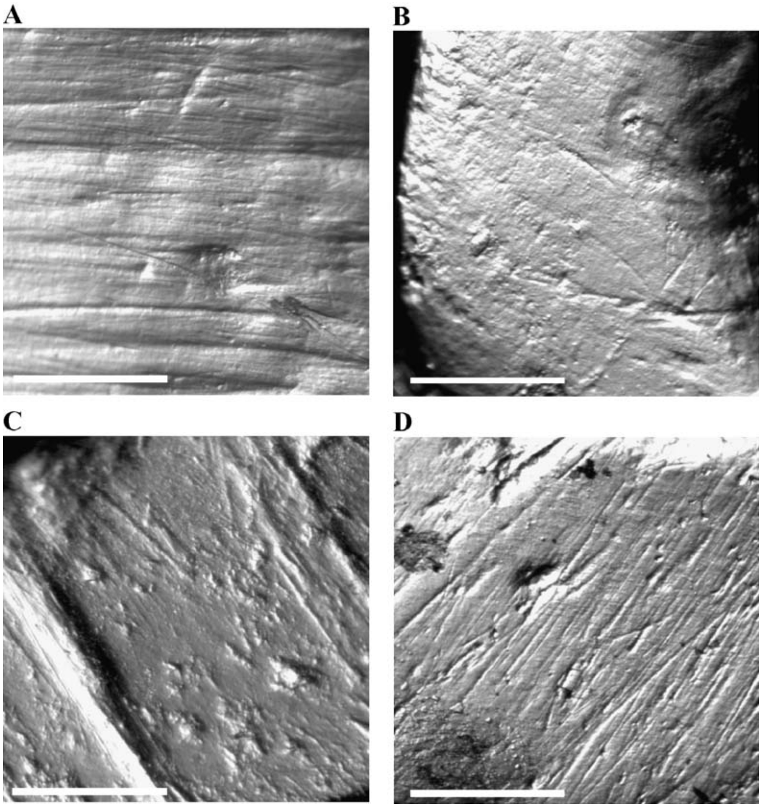

Fig. 1. Numerical photographs of molar shearing facets of extant species. (A) *Equus burchelli*; (B) *Litocranius walleri*; (C) *Rangifer tarandus*; (D) *Odocoileus virginianus*. Scale bars=300 μm.

intake of hard-food items such as exogenous grit particles (Solounias and Semprebon, 2002).

This study is a part of an attempt to reconstruct the paleoenvironment of the Turolian locality "Molayan", on the border between two distinct paleobiogeographical provinces: the Greek–Iranian and the Siwalik provinces. Faunal studies suggest a Middle Turolian age for this site (Brunet et al., 1981; Sen, 1998). Numerous ungulate families have been identified in this locality: Bovidae, Giraffidae, Equidae, Chalicotheridae, Rhinocerotidae, Gomphoteriidae, Deinotheriidae and Suidae (Heintz et al., 1978; Brunet et al., 1984). First, dental microwear analysis can yield new insights into the paleodiet of Afghan bovids and giraffids from the Late Miocene. This method consists in quantifying and analyzing the dental microwear of fossil specimens from Molayan, and compare it with that of extant ungulates. Second, the paleodiet of these ungulates may help inferring the floristic composition and the environment around the Molayan area during the Middle Turolian. In fact, if a large proportion of fossil species has a dental microwear pattern similar to those of browsers sensu lato, the vicinity of forested environments is suggested. Conversely, the presence of large and open grasslands is supported if a majority of specimens shares a similar microwear pattern with extant grazers. The Afghan bovids from Molayan are well diversified and 12 taxa have been distinguished: three species of Boselaphini (*Tragoportax amalthea*, *Tragoportax* nov. sp. and *Phronetragus* aff. *secondus*), one Reduncini (*Dorcadoxa porrecticornis*), one Caprini (*Sporadotragus tadzhikistanicus*), two Antilopini (*Gazella* sp. and *Prostrepsiceros* aff. *vinayaki*), one Ovibovinae (cf. *Plesiaddax* sp.), and four other indeterminate bovids (Bouvrain and Heintz, In press). Giraffidae are represented by only one species: *Palaeotragus* cf. *rouenii*.

2. Material

The fossil records are compared with data from 14 extant species (252 wild-shot and adult specimens) from collections housed in the Laboratoire Mammifères et Oiseaux at the Museum National d'Histoire Naturelle (Paris, France), the Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine (Poitiers, France), the Naturmuseum Senckenberg (Frankfurt, Germany) and the Staatliches Museum für Naturkunde (Stuttgart, Germany).

Several dietary categories are recognized from ecological data: grazers (sensu lato), mixed feeders (seasonal/regional and 'meal by meal'), and browsers (fruit/leaf and exclusive-leaf eaters) (Hoffman, 1989; Solounias and Semprebon, 2002). Grazers sensu lato are represented in our modern sample by 28 specimens of kongoni (*Alcelaphus buselaphus*), 24 African buffalo (*Syncerus caffer*), 14 topi (*Damaliscus lunatus*), 13 sable antelope (*Hippotragus niger*), 8 Burchell's zebra (*Equus burchelli*), and 6 Przewalski's horse (*Equus przewalskii*) (Vesey-Fitzgerald, 1969; Stewart and Stewart, 1970; Grobler, 1974; Sinclair, 1977; Hoffman, 1989; Estes, 1991; Murray, 1993; Kingdon, 1997; Blake, 2002; King, 2002). Eighteen specimens of bushbuck (*Tragelaphus scriptus*) and 19 ones of impala (*Aepyceros melampus*) compose the seasonal–regional mixed feeder category (Jacobsen, 1974; Hoffman, 1989; Estes, 1991; Kingdon, 1997). Fifty roe deer (*Capreolus capreolus*), 11 white-tailed deer (*Odocoileus virginianus*) and 8 yellow-backed duikers (*Cephalophus sylvicultor*) represent the fruit/leaf-browsing species (Halls, 1978; Heymans and Lejoly, 1981; Lumpkin and Kranz, 1984; Maillard and Picard, 1987; Hoffman, 1989; Estes, 1991; Tixier and Duncan, 1996; Kingdon, 1997; Ramirez et al., 1997; Grenier et al., 1999; Cransac et al., 2001). Seventeen reindeer (*Rangifer tarandus*) represent the browsers, which ingest hard-food and exogenous particles. Sixteen

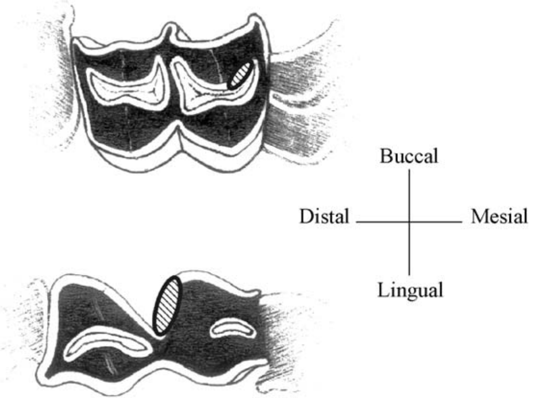

Fig. 2. Localization of shearing facets on second permanent lower (below) and upper (above) molars of ungulates (drawn by Sabine Riffault).

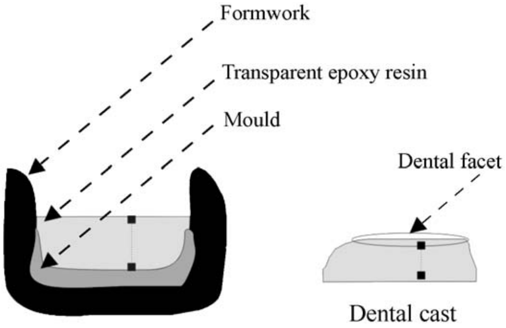

Fig. 3. Preparation of mould in a formwork in order to orientate the considered molar facets. Then, the dental facet is parallel to the level of epoxy resin poured out.

gerenuk (*Litocranius walleri*) compose the diet category of exclusive-leaf browsers (Gaare, 1968; Leuthold, 1978; Klein, 1982; Hoffman, 1989; Estes, 1991; Cichowski, 1993; Kingdon, 1997; Mysterud, 2000). There are few studies on the ecology of the Soemmerring's gazelle (*Gazella soemmerringi*). This species inhabits mainly evergreen bushland in hilly regions and sometimes low-lying grassy plains in Ethiopia (Kingdon, 1997). Dental microwear pattern of 20 specimens of the Soemmerring's gazelle is taken into consideration in order to specify the feeding behavior of this species.

Ninety-four Afghan fossil bovids housed in the Museum National d'Histoire Naturelle, Paris, France are examined: 17 *Dorcadoxa porrecticornis*, three *Gazella* sp., 5 *Phronetragus* aff. *secondus*, 11 *Prostrepsiceros* aff. *vinayaki*, 15 *Sporadotragus tadzhikistanicus*, 8 *Tragoportax* nov. sp., 22 *Tragoportax amalthea*, and 13 other *Tragoportax* remains (Bouvrain and Heintz, In press). Five specimens of *Palaeotragus* cf. *rouenii* are also included in this analysis.

Table 1
Means (M) and confidence interval at 95% (C.I.) of the three main variables species per species

		N	N_s		N_p		$\%p$	
			M	C.I.	M	C.I.	M	C.I.
Grazers sensu lato	*E. burchelli*	8	20.3	± 2.7	8.4	± 4.5	27.2	± 8.6
	E. przewalskii	6	29.8	± 3.8	11.7	± 5.4	27.2	± 7.0
	D. lunatus	14	22.6	± 3.1	12.7	± 4.1	33.7	± 5.7
	A. buselaphus	28	26.0	± 1.6	16.3	± 2.8	37.1	± 3.5
	H. niger	13	27.7	± 2.4	14.2	± 4.4	32.3	± 6.3
	S. caffer	24	24.6	± 2.7	13.3	± 2.8	33.8	± 3.9
Mixed feeders sensu lato	*A. melanpus*							
	Browser population	6	20.3	± 6.6	31.8	± 17.2	59.3	± 11.2
	Grazer population	13	27.0	± 3.0	17.5	± 3.7	38.6	± 3.9
	T. scriptus							
	Browser population	12	16.8	± 4.3	28.9	± 7.3	63.2	± 3.0
	Grazer population	6	21.2	± 5.9	15.2	± 2.6	42.3	± 3.8
Browsers sensu lato	*L. walleri*	16	15.1	± 1.2	34.5	± 10.4	66.6	± 5.0
	O. virginianus	11	19.9	± 3.9	31.1	± 7.3	60.1	± 8.9
	R. tarandus	17	24.4	± 5.9	55.8	± 8.9	69.4	± 6.8
	G. soemmerringi	20	19.3	± 3.6	41.2	± 6.4	67.2	± 6.0
	C. capreolus	50	19.2	± 1.4	25.5	± 2.4	56.1	± 2.6
	C. sylvicultor	8	19.9	± 3.8	34.6	± 11.2	62.3	± 7.6
Fossil species	*T. amalthea*	22	35.1	± 3.7	25.3	± 5.1	40.7	± 5.3
	T. nov. sp.	8	36.1	± 5.5	30.5	± 11.2	44.2	± 8.9
	Tragoportax undetermined	13	33.7	/	25.4	/	41.1	/
	D. porrecticornis	17	34.2	± 4.0	18.5	± 3.3	34.7	± 5.3
	S. tadzhikistanicus	15	27.3	± 3.8	33.5	± 10.2	52.1	± 9.2
	P. aff. *vinayaki*	11	28.4	± 5.5	30.4	± 8.6	50.1	± 9.3
	Gazella sp.	3	27.0	/	16.3	/	37.2	/
	P. aff. *secondus*	4	28.5	/	21.0	/	39.9	/
	P. rouenii	5	22.6	/	15.6	/	34.8	/

All specimens of cf. *Plesiaddax* and indeterminate bovids are not included in this study.

3. Methods

The study focuses on the second lower (M_2) and upper molars (M^2) because these teeth display an intermediate wear stage between the first and the third molar (Gordon, 1982). The paracone lingual and the protoconid buccal blades of the second upper and lower molars have a similar dental microwear pattern. In fact, both upper and lower molar facets are in occlusion together during the chewing–shearing phase (Fig. 2). Accordingly, data from lower and upper cheekteeth are combined into a single sample (Teaford and Walker, 1984; Janis, 1990).

A viscous and stripper gel (Syntilor®) with neutral chemical properties is applied on each molar. This alcohol gel dissolves all glues and varnishes on teeth, without causing any damage on the enamel and dentine surfaces. After a few minutes, the tooth is thoroughly cleaned with an ethanol solution (95%). Moulds are made with a polyvinylsiloxane material (Coltene President Microsystem®). All the moulds are included in a formwork (Coltene President Microsystem®), which permits to orientate horizontally the considered dental facet. This step reduces the limitations of depth of field throughout a large surface (Fig. 3). Transparent epoxy resin (In Epox®, ADAM Montparnasse) is previously heated (30 °C during 1 h). Then, the resin is put into a vacuum bell-jar (-10^5 Pa) during 10 min. These steps eliminate all the bubbles in the resin mixture before the casting. The polymerization of the resin is gently achieved at 20 °C during 72 h in order to help the free extraction of the last bubbles that have been incorporated during the flowing.

In this work, dental facets are digitized at 256 gray levels using a Spot CCD camera (Leica DC 300, Leica Microsystems®) connected to a stereo-light microscope at low magnification (30 × on a Leica MZ 125, Leica Microsystems®). Subsequently, each photograph is magnified up to 120 times for its treatment on computer monitor. Because a previous study (Gordon, 1982) reported some variations in dental microwear pattern along molar facets, a 0.09-mm^2 square is delimited about half-way up the enamel facet. This 0.09-mm^2 surface is chosen because it is always smaller than the smallest dental facet of the smallest ungulate.

An estimation of post mortem deterioration of extant and fossil teeth enables us to reject the altered teeth (King et al., 1999). Dental microwear is quantified using Optimas (v.6.5.2) software (Media Cybernetics®). All scratches and pits crossing this area are identified and, respectively, marked with a line and a point by only one observer (G.M) in order to limit the inter-observer error (Grine et al., 2002). Pits are distinguished from scratches by their minimum/maximum axis ratio. The formers have a ratio higher than 1/4, whereas scratches have a lower one (Grine and Kay, 1988). Maximum pit diameter and scratch width are measured in order to record the number of large pits and wide scratches. A pit is rated as 'large' if its maximum diameter exceeds 15 μm. A scratch is defined as 'wide' if its width exceeds 15 μm. These metric limits result from dental microwear comparisons of extant species such as *Equus przewalskii* and *Equus burchelli* on the one hand, and *Litocranius*

Table 2
Frequency of specimens showing more than two wide scratches (%W_s), four large pits (%L_p) and four cross scratches (%Cs_s)

		%W_s>2	%L_p>4	%Cs_s>4
Grazers *sensu lato*	*Alcelaphus buselaphus*	21	36	50
	Hippotragus niger	62	15	31
	Damaliscus lunatus	21	29	7
	Syncerus caffer	46	25	29
	Equus burchelli	25	25	25
	Equus przewalski	0	0	50
Mixed feeders	*Tragelaphus scriptus*			
	Browser population	17	92	33
	Grazer population	50	67	0
	Aepyceros melanpus			
	Browser population	0	83	69
	Grazer population	23	54	67
Browsers sensu lato	*Litocranius walleri*	0	69	37
	Rangifer tarandus	53	65	59
	Gazella soemmeringi	5	95	40
	Cephalophus sylvicultor	25	50	75
	Capreolus capreolus	6	29	34
	Odocoileus virginianus	9	55	45
Fossil species	*Dorcadoxa porrecticornis*	12	41	94
	Sporadotragus tadzhikistanicus	0	60	60
	Prostrepsiceros aff. *vinayaki*	9	73	72
	Tragoportax amaltheus	27	59	86
	Tragoportax nov. sp.	25	50	87

Table 3
Categorization of each species according to the frequency of specimens in each scratch ranges

			Scratch ranges		
			$N <= 17$	$17.5 < N < 29.5$	$N >= 30$
Grazers sensu lato	*Alcelaphus*	%	3.5%	75%	21.5%
	buselaphus	N	1	21	6
	Syncerus	%	12.5%	62.5%	25%
	caffer	N	3	15	6
	Damaliscus	%	21.5%	71.5%	7%
	lunatus	N	3	10	1
	Hippotragus	%	0%	77%	23%
	niger	N	0	10	3
	Equus	%	25%	75%	0%
	burchelli	N	2	6	0
	Equus	%	0%	67%	33%
	przewalski	*N*	0	4	2
Mixed feeders	*Tragelaphus scriptus*				
	Browser	%	58.3%	33.3%	8.3
	population	*N*	7	4	1
	Grazer	%	16.7%	83.3%	0%
	population	N	1	5	0
	Aepyceros melanpus				
	Browser	%	33.3%	50.0%	16.7%
	population	*N*	2	3	1
	Grazer	%	0%	84.6%	15.4%
	population	N	0	11	2
Browsers sensu lato	*Gazella*	%	25%	70%	5%
	soemmeringi	N	5	14	1
	Rangifer	%	23.5%	47%	29.5%
	tarandus	N	4	8	5
	Litocranius	%	87.5%	12.5%	0%
	walleri	N	14	2	0
	Odocoileus	%	18%	82%	0%
	virginianus	N	2	9	0
	Capreolus	%	40%	60%	0%
	capreolus	N	20	30	0
	Cephalophus	%	25%	75%	0%
	sylvicultor	N	2	6	0
Fossil species	*Prostrepsiceros.*	%	18.2%	27.3%	54.5%
	aff. *vinayaki*	N	2	3	6
	Sporadotragus	%	6.7%	60%	33.3%
	tadzhikistanicus	N	1	9	5
	Dorcadoxa	%	0%	23.5%	76.5%
	porrecticornis	N	0	4	13
	Tragoportax	%	0%	31.8%	68.2%
	amalthea	N	0	7	15
	Tragoportax	%	0%	12.5%	87.5%
	nov. sp.	*N*	0	1	7

walleri and *Rangifer tarandus* on the other hand. The number of pits (N_p), of scratches (N_s), of large pits (L_p), and of wide scratches (W_s) are recorded. For each specimen, the orientation of all scratches is superimposed on a circular diagram. Then, the number of cross scratches (Cs_s) whose direction are different from the main scratch's orientation, are recorded.

4. Statistical methods

The number of scratches (N_s), of pits (N_p), and the percentage of pits ($\%p = 100 * N_p/[N_p + N_s]$) are considered (Table 1). For each species, the percentages of specimens displaying more than two wide scratches, four large pits and four cross scratches on the studied dental surface are recorded (respectively abbreviated $\%W_s$, $\%L_p$, and $\%Cs_s$) (Table 2). These variables are

Table 4
Normality test (Kolmogorov–Smirnov test KS and Lilliefors corrections L) of the three main variables ($\%p$, N_s, N_p) for all samples with $N > 5$

	$\%p$		N_s		N_p	
	p_{KS}	p_L	p_{KS}	p_L	p_{KS}	p_L
Extant species						
Litocranius walleri	NS	NS	NS	< 0.05	NS	NS
Rangifer tarandus	NS	NS	NS	NS	NS	NS
Gazella soemmerringi	NS	NS	NS	NS	NS	NS
Capreolus capreolus	NS	NS	NS	NS	NS	NS
Cephalophus sylvicultor	NS	NS	NS	NS	NS	NS
Odocoileus virginianus	NS	NS	NS	NS	NS	NS
Tragelaphus scriptus	NS	< 0.05	NS	NS	NS	< 0.05
Aepyceros melampus	NS	NS	NS	NS	NS	< 0.05
Alcelaphus buselaphus	NS	NS	NS	NS	NS	NS
Syncerus caffer	NS	< 0.05	NS	NS	NS	NS
Damaliscus lunatus	NS	NS	NS	NS	NS	NS
Hippotragus niger	NS	NS	NS	NS	NS	NS
Equus burchelli	NS	NS	NS	NS	NS	NS
Equus przewalskii	NS	NS	NS	NS	NS	NS
Extinct species						
Prostrepsiceros aff. *vinayaki*	NS	NS	NS	NS	NS	NS
Sporadotragus tadzhikistanicus	NS	NS	NS	NS	NS	< 0.05
Dorcadoxa porrecticornis	NS	NS	NS	NS	NS	NS
Tragoportax amalthea	NS	NS	NS	NS	NS	NS
Tragoportax nov. sp.	NS	NS	NS	NS	NS	NS

NS: not significant.

Table 5
Results of the non-parametric Kruskal–Wallis ANOVA

	dl	*H*	*p*
N_s	18	148.6947	<0.05
N_p	18	159.5487	<0.05
$\%p$	18	196.9272	<0.05

adapted from those previously used by Solounias and Semprebon (2002).

Three scratch ranges are selected following the method of Solounias and Semprebon (2002) in order to distinguish each species according to the number of scratches. In the present study, the range limits are defined from the dental microwear pattern of well-known species. Although the methods of quantification and the levels of magnification are different in these two studies, it appears that the scratch range limits of this study are close to those previously defined by Solounias and Semprebon (2002). Therefore, the same scratch range limits have been chosen. Every specimens of each studied population are then assigned to one of the three categories: number of scratches lower than 17.5, higher than 29.5, or intermediate (Table 3). Solounias and Semprebon (2002) pointed out that leaf-browsing species belong mainly to the lowest scratch range, whereas grazing species fall into the middle or highest scratch ranges. Most fruit/leaf browsers are found in the first and the middle scratch ranges (Solounias and Semprebon, 2002).

The Kolmogorov–Smirnov non-parametric test with the Lilliefors correction, which is particularly useful for small samples (Sokal and Rohlf, 1998), rejects the normality for some distributions (see Table 4). The homogeneity of variances for the three variables is rejected among the samples according to the Levene test. Considering that these two assumptions of analysis of variances are not respected, the three variables (N_p, N_s, and $\%p$) are integrated in a non-parametric Kruskal–Wallis ANOVA and into a multiple comparison test of the rank (Tables 5 and 7) (Scherrer, 1984; Sokal and Rohlf, 1998).

The percentage of pits is not independent from the number of scratches and pits. Nevertheless, this variable is integrated in the analysis. In fact, some species may have a significant difference in the percentage of pits, whereas the number of pits or scratches is not significantly different among specific samples. In such a case, the percentage of pits is informative. This result is in accordance with the previous microwear studies, which revealed that the percentage of pits is a complementary informative source (Solounias et al., 1988; Ungar, 1996; King, 2001). The samples of *Gazella* sp.,

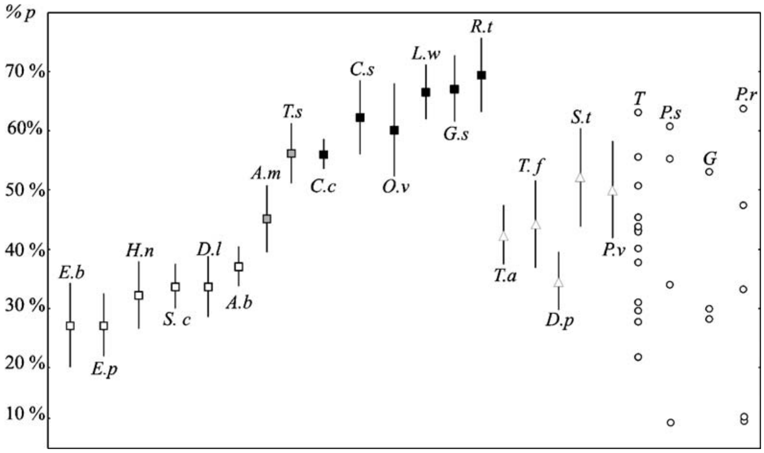

Fig. 4. Mean and confidence level at 95% of percentage of pits (calculated from variance of each sample) of all species. Species having five or less specimens and the undetermined *Tragoportax* are individually shown. White square: grazing species; gray square: mixed feeding species; black square: browsing species; white triangles: fossil species. *A.m*: *Aepyceros melanpus*; *A.b*: *Alcelaphus buselaphus*; *C.c*: *Capreolus capreolus*; *C.s*: *Cephalophus sylvicultor*; *D.l*: *Damaliscus lunatus*; *E.b*: *Equus burchelli*; *E.p*: *Equus przewalskii*; *G.s*: *Gazella soemmerringi*; *H.n*: *Hippotragus niger*; *L.w*: *Litocranius walleri*; *O.v*: *Odocoileus virginianus*; *R.t*: *Rangifer tarandus*; *S.c*: *Syncerus caffer*; *T.s*: *Tragelaphus scriptus*; *T.a*: *Tragoportax amalthea*; *T.f*: *Tragoportax* nov. sp.; *D.p*: *Dorcadoxa porrecticornis*; *S.t*: *Sporadotragus tadzhikistanicus*; *P.v*: *Prostrepsiceros* aff. *vinayaki*; *T*: *Tragoportax* undetermined; *P.s*: *Phronetragus* aff. *secondus*; *G*: *Gazella* sp.; *P.r*: *Paleotragus rouenii*.

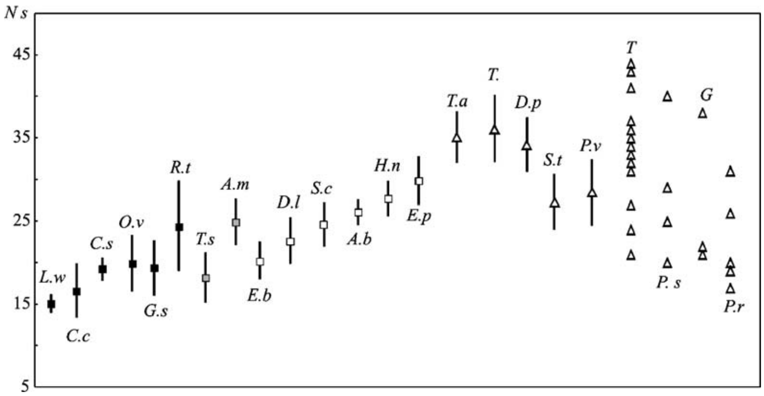

Fig. 5. Mean and confidence level at 95% of number of scratches (calculated from variance of each sample) of all species. Species having five or less specimens and the undetermined *Tragoportax* are individually shown. See abbreviations in Fig. 4.

Phronetragus aff. *secondus*, *Palaeotragus* cf. *rouenii* and the sample of indeterminate *Tragoportax* are not integrated in the analysis of variances.

5. Results

5.1. Dental microwear patterns of extant species

The extant browsers have a higher percentage of pits than the grazing species (Table 1; Figs. 1 and 4) that is in accordance with results of the previous analysis (Solounias and Moelleken, 1992a,b; Solounias and Hayek, 1993; Solounias and Semprebon, 2002). More precisely, *Litocranius walleri* and *Rangifer tarandus* both differ significantly from grazing species in having a higher percentage of pits (Tables 1 and 7, Figs. 1 and 4). Moreover, *L. walleri* is characterized by the lowest number of scratches on the shearing facets among the extant browsers from the database (Table 1; Figs. 1 and 6). *R. tarandus* differs from the latter species in having a variable, but significantly higher number of scratches (Tables 1, 3 and 7; Figs. 1 and 5). Conversely of *L. walleri*, more than half of the *R. tarandus*'s population have more than two wide scratches (Table 2; Fig. 1). Among the browsers sensu lato, the lowest percentage and number of pits are recorded for *Capreolus capreolus* (Table 1; Figs. 4 and 6). This cervid has also a low $\%W_s$ and the lowest $\%Cs_s$ and $\%L_p$ among

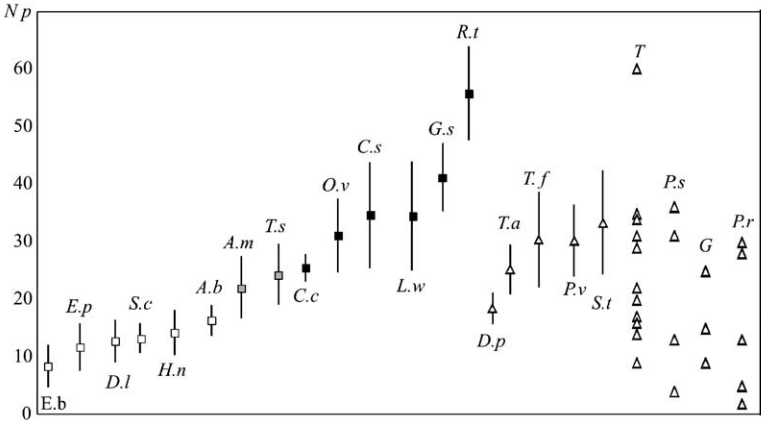

Fig. 6. Mean and confidence level at 95% of number of pits (calculated from variance of each sample) of all species. Species having five or less specimens and the undetermined *Tragoportax* are individually shown. See abbreviations in Fig. 4.

the browsers (Table 2). *Cephalophus sylvicultor* and *Odocoileus virginianus* show a similar dental microwear pattern with *C. capreolus* (Table 1; Figs. 1 and 5). *Cephalophus sylvicultor* is characterized by the highest %Cs_s among the browsers (Table 2). The majority of the population of these three fruit/leaf browsers fall into the intermediate scratch range. No specimen is found in the highest scratch range (Table 3). *Litocranius walleri* and the three previous fruit/leaf browsers differ from *R. tarandus* in having a lower number of pits (Table 1; Fig. 6).

The three main variables (N_p, N_s and %p) display a normal distribution for the population of *G. soemmerringi* (Table 4). This bovid differs significantly from the extant grazers in having higher percentage and number of pits (Tables 1 and 7; Figs. 4 and 6). Moreover, *G. soemmerringi* is characterized by the highest %L_p (Table 2). The number of scratches, which are mainly focused on lowest and intermediate scratch ranges, is close to those of fruit/leaf browsers (Tables 1 and 3; Fig. 5).

Table 6
Test of Student on percentage of pits showing the significant differences between dietary categories within the mixed feeders

	“Grazer” population M (%)	“Browser” population M (%)	t	p
Aepyceros melanpus	38.6	59.3	− 8.360	< 0.05
Tragelaphus scriptus	42.3	63.2	− 9.577	< 0.05

No significant differences are found among extant grazers in terms of percentage of pits, number of pits and scratches (Table 7). *Equus burchelli* and *Equus przewalskii* share the lowest percentage of pits. Nevertheless, the dental microwear pattern of these two equids is different. *Equus burchelli* has the lowest number of scratches and *E. przewalskii* the highest one among the extant grazers (Tables 1 and 3; Figs. 4 and 5). This is in agreement with their distribution within each scratch range (Table 3). The Eurasian Equidae differs also from African grazers in having lower %W_s and %L_p (Tables 1 and 2). *Alcelaphus buselaphus* has the highest percentage of pits and number of pits among the extant grazing species (Table 1, Figs. 4 and 6). *Hippotragus niger*, *Syncerus caffer*, and *Damaliscus lunatus* have percentage of pits lying between those of *A. buselaphus* and *Equus* species (Table 1; Fig. 4). The former species differs from the other grazers in having the highest %W_s. In opposite of the other grazing bovids, no *H. niger*

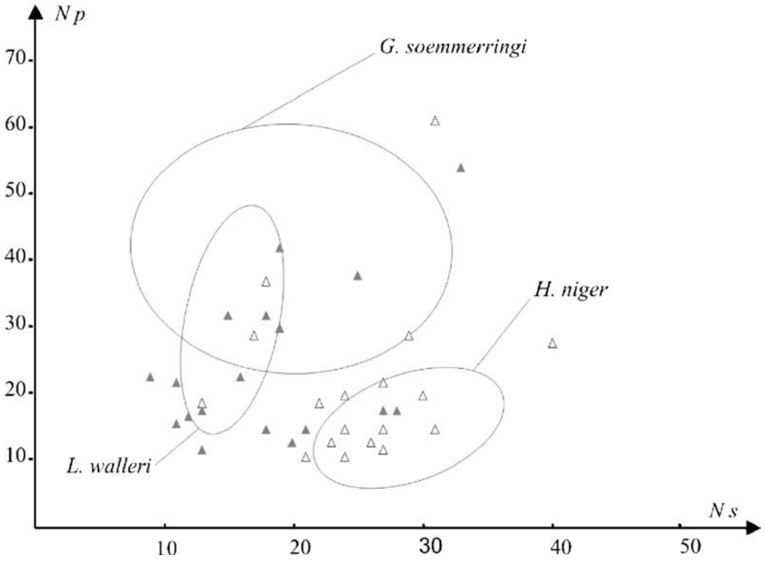

Fig. 7. Distribution of *Aepyceros melampus* (white triangles) and *Tragelaphus scriptus* (gray triangles) according to the number of pits (N_p) and scratches (N_s) on enamel shearing facets of the second permanent molars. The range ellipses (80%) of three extant species, *Litocranius walleri*, *Gazella soemmerringi*, and *Hippotragus niger* are superimposed on the graph for comparisons.

Table 7
Non parametric multiple comparisons of average ranks between extant and extinct species for the three main variables

%*p*																			
	A.m	*A.b*	*C.c*	*C.s*	*D.l*	*E.b*	*E.p*	*G.s*	*H.n*	*L.w*	*O.v*	*R.t*	*S.c*	*T.s*	*T.a*	*T.f*	*D.p*	*S.t*	*P.v*
	45.2	37.1	56.1	62.3	33.7	27.2	27.2	67.2	32.3	66.6	60.1	69.4	33.8	56.2	40.7	44.2	34.7	52.1	50.1
A.m^{a}																			
A.b	ns																		
C.c	ns	<0.05																	
C.s	ns	<0.05	ns																
D.l	ns	ns	<0.05	<0.05															
E.b	ns	ns	<0.05	<0.05	ns														
E.p	ns	ns	<0.05	<0.05	ns	ns													
G.s	<0.05	<0.05	ns	ns	<0.05	<0.05	<0.05												
H.n	ns	ns	<0.05	<0.05	ns	ns	ns	<0.05											
L.w	<0.05	<0.05	ns	ns	<0.05	<0.05	<0.05	ns	<0.05										
O.v	ns	<0.05	ns	ns	<0.05	<0.05	<0.05	ns	<0.05	ns									
R.t	<0.05	<0.05	ns	ns	<0.05	<0.05	<0.05	ns	<0.05	ns	ns								
S.c	ns	ns	<0.05	<0.05	ns	ns	ns	<0.05	ns	<0.05	<0.05	<0.05							
T.s	ns	<0.05	ns	ns	<0.05	<0.05	<0.05	ns	<0.05	ns	ns	ns	<0.05						
T.a^{b}	ns	ns	<0.05	ns	ns	ns	ns	<0.05	ns	<0.05	ns	<0.05	ns	ns					
T.f.^{b}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns				
D.p^{b}	ns	ns	<0.05	<0.05	ns	ns	ns	<0.05	ns	<0.05	<0.05	<0.05	ns	<0.05	ns	ns			
S.t^{b}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		
P.v^{b}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	

N_p

	A.m	*A.b*	*C.c*	*C.s*	*D.l*	*E.b*	*E.p*	*G.s*	*H.n*	*L.w*	*O.v*	*R.t*	*S.c*	*T.s*	*T.a*	*T.f*	*D.p*	*S.t*	*P.v*
	22.1	16.3	25.5	34.6	12.7	8.4	11.7	41.2	14.2	34.5	31.1	55.8	13.3	24.3	25.3	30.5	18.5	33.5	30.4
A.m[a]																			
A.b	ns																		
C.c	ns	ns																	
C.s	ns	ns	ns																
D.l	ns	ns	<0.05	<0.05															
E.b	ns	ns	<0.05	<0.05	ns														
E.p	ns	ns	ns	ns	ns	ns													
G.s	<0.05	<0.05	ns	ns	<0.05	<0.05	<0.05												
H.n	ns	ns	ns	ns	ns	ns	ns	<0.05											
L.w	ns	<0.05	ns	ns	<0.05	<0.05	ns	ns	<0.05										
O.v	ns	ns	ns	ns	<0.05	<0.05	ns	ns	ns	ns									
R.t	<0.05	<0.05	<0.05	ns	<0.05	<0.05	<0.05	ns	<0.05	ns	ns								
S.c	ns	ns	<0.05	<0.05	ns	ns	ns	<0.05	ns	<0.05	<0.05	<0.05							
T.s	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	ns						
T.a[b]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	ns	ns					
T.f[b]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns				
D.p[b]	ns	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	<0.05	ns	ns	ns	ns			
S.t[b]	ns	<0.05	ns	ns	<0.05	<0.05	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns		
P.v[b]	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns	ns	

(*continued on next page*)

Table 7 (*continued*)

N_s	*A.m*	*A.b*	*C.c*	*C.s*	*D.l*	*E.b*	*E.p*	*G.s*	*H.n*	*L.w*	*O.v*	*R.t*	*S.c*	*T.s*	*T.a*	*T.f*	*D.p*	*S.t*	*P.v*
	24.9	26.0	19.2	19.9	22.6	20.3	29.8	19.4	27.7	15.1	19.9	24.4	24.6	18.2	35.1	36.1	34.2	27.3	28.5
A.m[a]																			
A.b	ns																		
C.c	ns	<0.05																	
C.s	ns	ns	ns																
D.l	ns	ns	ns	ns															
E.b	ns	ns	ns	ns	ns														
E.p	ns	ns	ns	ns	ns	ns													
G.s	ns	ns	ns	ns	ns	ns	ns												
H.n	ns	ns	<0.05	ns	ns	ns	ns	ns											
L.w	<0.05	<0.05	ns	ns	ns	ns	<0.05	ns	<0.05										
O.v	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns									
R.t	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	ns								
S.c	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	ns	ns							
T.s	ns	<0.05	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns						
T.a[b]	ns	ns	<0.05	<0.05	<0.05	<0.05	ns	<0.05	ns	<0.05	<0.05	ns	ns	<0.05					
T.f.[b]	ns	ns	<0.05	<0.05	ns	<0.05	ns	<0.05	ns	<0.05	<0.05	ns	ns	<0.05	ns				
D.p[b]	ns	ns	<0.05	<0.05	ns	<0.05	ns	<0.05	ns	<0.05	<0.05	ns	ns	<0.05	ns	ns			
S.t[b]	ns	ns	<0.05	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns	ns	ns	ns		
P.v[b]	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns	ns	ns	ns	ns	

ns: non-significant.

[a] Abbreviations as follows: *A.m: Aepyceros melanpus*; *A.b*: *Alcelaphus buselaphus*; *C.c*: *Capreolus capreolus*; *C.s*: *Cephalophus sylvicultor*; *D.l*: *Damaliscus lunatus*; *E.b*: *Equus burchelli*; *E.p*: *Equus przewalskii*; *G.s*: *Gazella soemmerringi*; *H.n*: *Hippotragus niger*; *L.w*: *Litocranius walleri*; *O.v: Odocoileus virginianus*; *R.t: Rangifer tarandus*; *S.c*: *Syncerus caffer*; *T.s*: *Tragelaphus scriptus*; *T.a*: *Tragoportax amalthea*; *T.f*: *Tragoportax* nov. sp.; *D.p*: *Dorcadoxa porrecticornis*; *S.t*: *Sporadotragus tadzhikistanicus*; *P.v*: *Prostrepsiceros* aff. *vinayaki.*

[b] Fossil species.

specimen is found in the lower scratch range (Table 3). *Damaliscus lunatus* has a similar distribution to *E. burchelli* among the scratch ranges (Table 3). This bovid is characterized by the lowest %Cs_s (Table 2).

Tragelaphus scriptus and *Aepyceros melampus* display a typical distribution of seasonal or regional mixed feeders according to the numbers of scratches and pits. In fact, these populations are composed of specimens that show either a browser's dental microwear pattern or a grazer's one (Fig. 7). The *t*-test of Student indicates a significant difference according to the percentage of pits between the ‘‘grazer’’ and

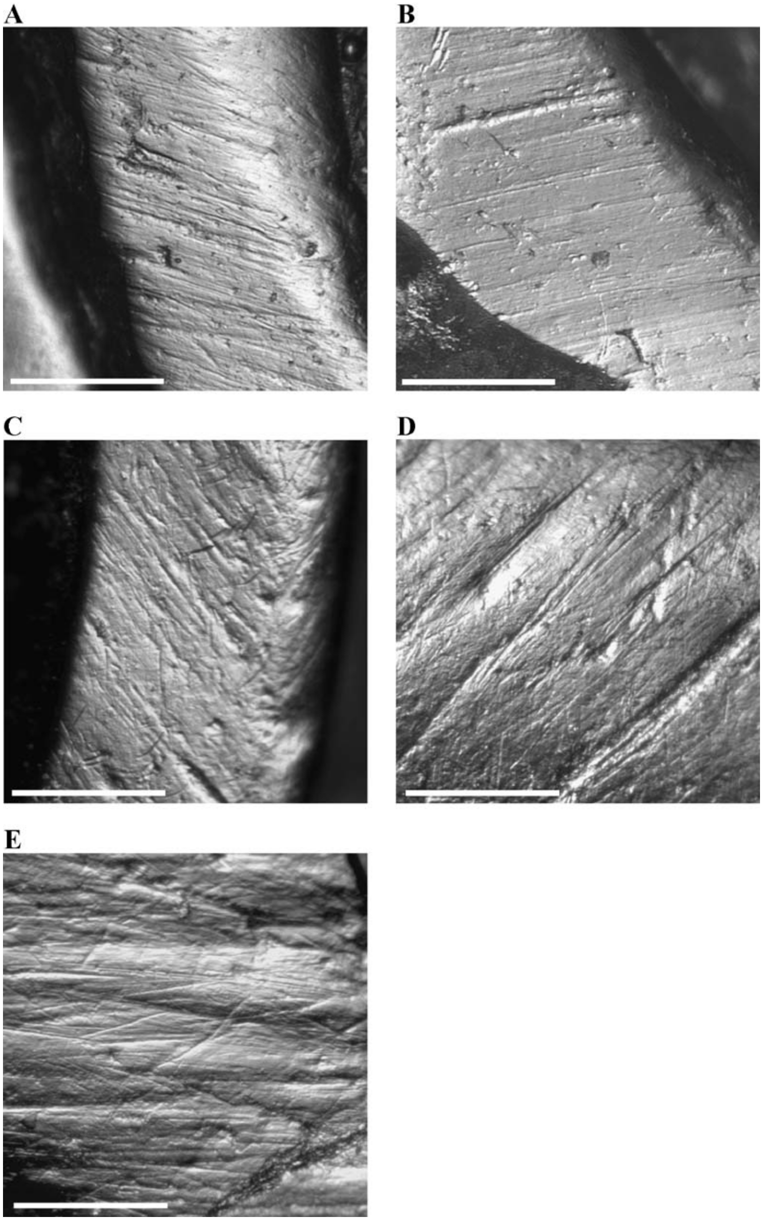

Fig. 8. Numerical photographs of molar shearing facets of fossil species. (A) *Dorcadoxa porrecticornis*; (B) *Prostrepsiceros* aff. *vinayaki*; (C) *Sporadotragus tadzhikistanicus*; (D) *Tragoportax* nov. sp.; (E) *Tragoportax amalthea*. Scale bars=300 μm.

"browser" clusters for each species (Tables 1 and 6). The grazer populations of these mixed feeders share a higher $\%W_s$ and a lower $\%L_p$ than the browser ones. Whatever grazing or browsing populations is chosen, *T. scriptus* has a lower number of scratches on shearing molar facets than *A. melampus* (Table 1).

5.2. Dental microwear patterns of extinct species

The percentage of pits of *Dorcadoxa porrecticornis* is not significantly different from that of extant grazers (Tables 1 and 7; Figs. 4 and 8). Moreover, *D. porrecticornis* has significant higher number of scratches and lower percentage of pits than *Litocranius walleri*, *Odocoileus virginianus*, *Capreolus capreolus* and *Cephalophus sylvicultor* (Tables 1 and 7; Figs. 1 and 8). All specimens are included in the middle and high scratch ranges (Table 3). All but one specimen have more than four cross scratches and some 12% of specimens have more than two wide scratches. Forty-one percent of the population of *D. porrecticornis* has more than four large pits (Table 2). Although there are not significant differences, this bovid differs from *Sporadotragus tadzhikistanicus* and *Prostrepsiceros* aff. *vinayaki* in having a lower percentage and number of pits (Tables 1 and 7, Figs. 4, 6 and 8).

Sporadotragus tadzhikistanicus and *Prostrepsiceros* aff. *vinayaki* have a similar dental microwear pattern. These fossil species have a slightly lower percentage of pits than the extant cervid *Capreolus capreolus* (Tables 1–3 and 7; Figs. 4–6, and 8). Both *S. tadzhikistanicus* and *P.* aff. *vinayaki* differ from *Dorcadoxa porrecticornis* in having a higher number of pits (33.5), a lower number of scratches (27.3), and a more scattered distribution throughout the three scratch ranges (Tables 1 and 3). *S. tadzhikistanicus* and *P.* aff. *vinayaki* are both characterized by a large part of their population, having more than four wide pits and four cross scratches. Conversely, the $\%W_s$ is low for these two species (Table 2). *S. tadzhikistanicus* differs from *P.* aff. *vinayaki* in having a more scattered distribution of number of scratches and pits (Fig. 9). In contrast to extant seasonal or regional mixed feeders, these species have both an intermediate molar microwear pattern between those of grazing and browsing ungulates (Fig. 9).

The percentage of pits of *Tragoportax amalthea* (40.7) and *Tragoportax* nov. sp. (44.2) is not significantly different from that of extant grazing bovids. Both *Tragoportax* species differ from *Litocranius walleri*, *Capreolus capreolus*, *Odocoileus virginianus*, *Gazella soemmerringi*, and *Cephalophus sylvicultor* in having a significant higher number of scratches

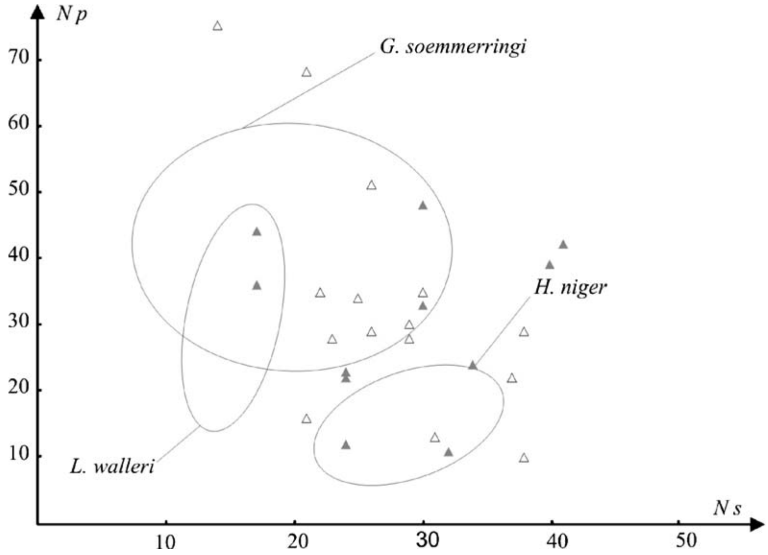

Fig. 9. Distribution of *Sporadotragus tadzhikistanicus* (white triangles) and *Prostrepsiceros* aff. *vinayaki* (gray triangles) according to the number of pits (N_p) and scratches (N_s) on enamel shearing facets of the second permanent molars. The range ellipses (80%) of three extant species, *Litocranius walleri*, *Gazella soemmerringi*, and *Hippotragus niger* are superimposed on the graph for comparisons.

(Tables 1 and 7; Figs. 5 and 8). *Tragoportax amalthea* differs from *Rangifer tarandus* in having a significant lower number of pits (Tables 1 and 7; Fig. 6). *Tragoportax* nov. sp. is not significantly different from extant species in regard to the percentage and the number of pits (Tables 1 and 7; Fig. 4). The two *Tragoportax* species differ from other extinct bovids by a higher $\%W_s$. More than 50 % of *Tragoportax* specimens have more than four large pits, and a high $\%Cs_s$ (Table 2).

The percentages of pits of the 13 indeterminate specimens of *Tragoportax* are found between those of the two determined samples of *Tragoportax* (Table 1; Fig. 4). The four specimens of *Phronetragus* aff. *secondus* display a large range of percentage of pits: 9.1% to 60.8% (Fig. 4). *Phronetragus* aff. *secondus* differs from *Tragoportax* species in having lower numbers of scratches and pits (Table 1). The genus *Gazella* is represented by three specimens. Two have a low percentage of pits and the third specimen differs in having a higher one (Table 1; Figs. 4–6). *Palaeotragus* cf. *rouenii* has a percentage of pits ranging from 9.5 to 64% (Fig. 4). The average numbers of scratches and pits vary. Nevertheless, these values are lower than these of all other extinct species (Table 1; Figs. 5 and 6).

6. Discussion

6.1. Extant species

The dental microwear pattern of extant species fluctuates according to the food items that were consumed prior the death of the animal (Solounias et al., 1988; Teaford and Oyen, 1989; Fortelius and Solounias, 2000). The grazing species differ from browsing ones in having a lower percentage of pits. The mixed feeders have a variable microwear pattern, which range from that of browsing to the one of grazing species. Within browsers, exclusive-leaf eaters have a lower number of scratches than fruit/leaf eaters. Our results are consistent with those of previous studies because all dietary categories have been clearly distinguished (Solounias et al., 1988, 2000; Solounias and Moelleken, 1992a; Solounias and Hayek, 1993; Caprini, 1998; Solounias and Semprebon, 2002).

The dental microwear pattern of the exclusive-leaf browser *Litocranius walleri* is closely correlated with a diet solely composed of leaves and flowers (Leuthold, 1978; Estes, 1991; Kingdon, 1997). The microwear data of *Rangifer tarandus* are due to a diet mainly composed of foliages and ground/tree lichens. The diet is sometimes completed by grasses. Thus, this cervid also ingests hard-food items, such as grit particles or bark pieces (Gaare, 1968). Like *Capreolus capreolus* and *Odocoileus virginianus*, *Cephalophus sylvicultor* differs from the exclusive-leaf browsers by a higher number of scratches. This is in accordance with the large amount of fruits and seeds in their food composition (Lumpkin and Kranz, 1984; Estes, 1991; Tixier and Duncan, 1996; Ramirez et al., 1997).

According to the latitudinal repartition of C3 and C4 plants, the Asian *Equus przewalskii* feeds on a larger amount of C3 grasses than the African grazers (Tieszen et al., 1979; Ehleringer et al., 1997). The Asian horse differs mainly from the African grazers in having a higher amount of fine scratches. Solounias and Semprebon (2002) point out a correlation between the abundance of fine scratches and the consumption of C3 grasses, due to the probable difference of phytolith size in C3 and C4 grasses (see also Lanning and Eleuterius, 1989; Mac Naughton et al., 1985; Runge, 1999). The C4 phytolith grasses would cause wider scratches, and that would lead to an underestimation of the numbers of scratches and pits. Therefore, a high number of scratches and a low $\%W_s$ may be characteristic of the consumption of C3 grasses. Thus, in the case of *E. przewalskii*, the narrowness of scratches can be correlated with a C3 grassy diet. Further experimental studies on captive ungulates with a controlled food composition will enable to determine precisely the correlation between C3 and C4 grasses and molar microwear pattern.

The African grazers share a lower percentage of pits. This points out the high abrasive characteristics of the grasses. The inter-specific differences of microwear pattern among C4 grazers are due to several feeding behavioral differences. Moreover, according to the plant species and the exploited tissues, the shape, size and concentration of phytoliths vary (Mac Naughton et al., 1985; Runge, 1999). Bell (1971) points out that the herds of Burchell zebra (*Equus burchelli*) graze at first the herbaceous layer during the migration. The herds of topi (*Damaliscus lunatus*) and wildebeest (*Connochaetes taurinus*) exploit secondly a shorter herbaceous layer. Finally, the kongoni (*Alcelaphus buselaphus*) feeds on the shortest herbaceous layer during the grass regrowth. According to these results, it is clear that these differences of feeding behavior are the main causes of the dental microwear pattern's fluctuations among the grazing ungulates.

The mixed feeding species show similar dental microwear pattern with that of either grazers or browsers. These data support the regional and seasonal variations of the dietary behavior of these bovids. The first sample of *Aepyceros melampus* is composed of specimens that fed on wide amount of grasses or related plants prior to their death. In contrast, the specimens from the second cluster have mainly browsed. The ecological data attest the large consumption of green grasses according to the environment and the season. This antelope supplements its diet with leaves, shoots, and seeds from pods (Dorst and Dandelot, 1972; Estes, 1991; Kingdon, 1997). In the same manner, it appears that the distribution of *Tragelaphus scriptus* across two clusters is correlated with the consumption of growing grasses during the wet season (Dorst and Dandelot, 1972; Jacobsen, 1974; Estes, 1991; Kingdon, 1997). The difference in scratch number between these species likely reflects a lower consumption of grasses for the bushbuck (*T. scriptus*).

The diet of *Gazella soemmerringi* is little known and can be specified on the basis of its dental microwear pattern (Estes, 1991). The high percentage of pits suggests a browsing diet sensu lato. The higher number of scratches indicates some differences with *Litocranius walleri* and shows similarities with the fruit/leaf browsers. The high number of pits and the high $\%L_p$ point out an intensive dental abrasion. *Gazella soemmerringi* inhabits mainly scattered, open grassland and shrubland of *Acacia* and *Commiphora* (Kingdon, 1997). Thus, hard-food items are undoubtedly seeds and hard fruits such as pods. To some extent, dust particles, which are abundant in open and arid environments certainly add scratches to the enamel surface (Solounias and Semprebon, 2002). Moreover, grit also causes additional pits in the enamel surface of *G. soemmerringi*.

6.2. Dietary reconstruction of extinct species

By comparison with extant grazers, *Dorcadoxa porrecticornis* appears to be an obligate grazer. In fact, the percentage of pits of this species is not significantly different to that of extant grazers. More specifically, the high number of scratches (distribution in the two higher scratch ranges) and the low frequency of $\%W_s$ indicate some similarities with *Equus przewalskii*. Therefore, this Afghan bovid was a grazer. These results are also confirmed by a recent isotopic and microwear study (Van Nelson, 2002). This latter study reveals that *D. porrecticornis* from the Siwaliks mainly browsed during the early Turolian and grazed at the end of the Middle Turolian.

The scattered distribution of the dental microwear pattern of *Sporadotragus tadzhikistanicus* suggests a mixed diet without any marked variations. The high number of scratches of *S. tadzhikistanus* associated with a low $\%W_s$ indicate the regular consumption of C3 grasses. The number of pits, which is lower than that of *Rangifer tarandus*, excludes the hypothesis of a browsing diet incorporating an important amount of hard-food items. Although the sample is smaller than that of *Capreolus capreolus* and *Litocranius walleri*, the wide distribution suggests a more varied diet than that of these extant species. Thus, *S. tadzhikistanicus* can be defined as a "meal by meal" mixed feeder.

The dental microwear of *Prostrepsiceros* aff. *vinayaki* is less variable than that of *Sporadotragus tadzhikistanicus*. This suggests a more grassy and more homogeneous diet. The low $\%W_s$ is consistent with the consumption of soft leaves or C3 grasses. The higher number of scratches cannot be explained by a browsing diet. It rather suggests a certain indeterminate amount of grasses in the food intake. The low number of pits indicates that this extinct species did not ingest hard-food items. Thus, *P.* aff. *vinayaki* can be regarded as a "meal by meal" mixed feeder.

The *Tragoportax* species, which are characterized by a slightly higher percentage of pits than extant grazing bovids, were probably variable grazers. These fossil species differ from *Sporadotragus tadzhikistanicus* and *Prostrepsiceros* aff. *vinayaki* in having lower percentage and number of pits and a higher number of scratches. Therefore, their diet likely included a larger amount of grasses. The dental microwear pattern of these two species is associated with higher $\%W_s$ than those of the other extinct bovids. This indicates the consumption of harder fibrous items, such as shoots or fruits. These results confirm the previous microwear analysis, which attributed to *Tragoportax* a mixed feeding and grazing diet in Samos and Pikermi during the Middle Turolian (Solounias and Hayek, 1993). A recent isotopic analysis reveals that *Tragoportax.* nov. sp. fed exclusively on C3 plants (Zazzo et al., 2002). The correlations between microwear and isotope data point out that the grasses in the food of *Tragoportax.* nov. sp. were C3 plants. Considering that there are no significant differences between the two fossil species, *Tragoportax amalthea* fed likely on a similar diet.

The presence of these two related species in the same area during the Middle Turolian raises many questions about the nature of their respective ecological niches. The dental microwear cannot help to distinguish dietary differences between these two *Tragoportax.* The length and width of upper molars and premolars do not allow to distinguish any size difference between these two species. Moreover, although the horned skulls of males of *Tragoportax* have several diagnostic features, the anatomy of the hornless female skulls is not diagnostic. In the same manner, no inter-specific differences on the appendicular skeleton have been found (Bouvrain and Heintz, In press). Nowadays, numerous cohabitations have been reported within the African wild game animals. Bell (1971) correlates the evolution of vegetal resources from season to season with the ecological requirements and the migration of ungulate herds. Each species exploits the vegetal resources according to the season and to its body-size (Bell, 1971). The extant grazing bovids *Damaliscus lunatus* and *Alcelaphus buselaphus* have a similar body size and cohabit in several geographical areas. Bell (1971) points out that *D. lunatus* grazes mainly high grasses, whereas *A. buselaphus* exploits a shorter herbaceous layer. The cohabitation of the two related *Tragoportax* in a same regional area is thus possible and indicates an exploitation of natural resources similar to those found by the African grasslands.

Two of the *Gazella* sp. specimens have a low percentage of pits. A third specimen has a higher one (Fig. 3). Two specimens of *Phronetragus* aff. *secondus* have less than 35% of pits, whereas two others have more than 55% of pits. This suggests that these two species have either a variable or a mixed diet. Nevertheless, the small size of the samples prevents us from concluding whether they were "meal by meal" or seasonal–regional mixed feeders.

The dispersed pit percentage distribution of *Palaeotragus* cf. *rouenii* clearly suggests that this giraffid was a mixed feeder. Previous dental microwear analysis of Palaeotraginae from Maragheh, Samos and Pikermi revealed that these giraffids were adapted to grazing or mixed diet (Solounias et al., 1988, 2000). Nevertheless, the small size of our sample prevents us from specifying whether they have a seasonal–regional or a "meal by meal" mixed diet throughout this region during the Middle Turolian.

6.3. Paleoenvironmental reconstruction

Bonis et al. (1992) define the Greek–Iranian–Afghan (GIA) province according to the faunal similarity between the Greek, Turkish, and Iranian faunas with those of the Afghan locality Molayan from the Middle Turolian of Afghanistan. The faunal assemblages from the Late Miocene localities of the Potwar Plateau, in the Siwaliks province, differ greatly from those of the GIA province by a higher diversity of Suina, Cervoidea and Primates. Moreover, the absence in the Potwar Plateau and the presence in Molayan of various taxa (Hyracoidea or Schizotheriinae) comfort the affinities with the Greek, Iranian, and Turkish localities (Heintz et al., 1981; Heintz and Brunet, 1982; Brunet et al., 1984; Bonis et al., 1992).

The differences concerning the Bovidae are smaller. In fact, the Late Miocene localities of the Potwar Plateau and Molayan have in common a low number of *Gazella*, a high diversity of Boselaphini (*Tragoportax* and *Phronetragus*), and the presence of Reduncini (*Dorcadoxa porrecticornis*). Nevertheless, the presence of Central Asian (*Sporadotragus tadzhikistanicus*) and Greek–Iranian related species (*Prosstrepsiceros* aff. *vinayaki* and *Tragoportax*) indicates several faunal influences (Bouvrain and Heintz, In press). Therefore, to reconstruct the paleoenvironment on the basis of the taxonomic affiliations is problematic. In fact, this region was likely an area of intensive faunal exchanges.

The high diversity of bovids (12 taxa) that exceeds those of all extant ecosystems as well as the mortality profiles of the *Tragoportax* specimens indicates that the mode of fossil accumulation was probably gradual rather than instantaneous (Bouvrain and Heintz, In press). In fact, the 'U-shape' mortality profile is characterized by a low proportion of subadult specimens. Moreover, among young specimens, all developmental dental stages from 3- to 24-month old are found in the fossiliferous level (Bouvrain and Heintz, In press). This is in agreement with the presence of numerous emersive surfaces in the fossiliferous level, which attest a gradual accumulation (Heintz et al., 1978). The cohabitation of ungulates having different dietary adaptation excludes a homogenous environment. A landscape where, an obligate grazer (*Dorcadoxa porrecticornis*), and two variable grazers (*Tragoportax amalthea* and *Tragoportax* nov. sp.) cohabited with two meal by meal mixed feeders (*Prostreppsiceros* aff. *vinayaki* and *Sporadotragus tadzhikistanicus*) likely displayed a wide variety of habitats. This Afghan environment was neither a uniform grass plain nor a forest. The dental microwear pattern of the *Tragoportax* species and *D. porrecticornis* implies that there were many open grassland areas. The presence of two variable grazers and two mixed feeders are evidence of scattered wooded or bushy vegetation. The *Gazella* species, *Phronetragus* aff. *secondus*, and *Palaeotragus* cf. *rouenii*, on the basis of their mixed feeding diet, confirm the reconstruction of this landscape.

Microwear data comparisons between the three fossil grazers and the extant ones emphasize the similarity with *Equus przewalskii*, suggesting the abundance of C3 grasses. These results are confirmed by isotopic data from molars of *Tragoportax* because the low values of δ^{13}C exclude the consumption of C4 grasses (Zazzo et al., 2002). The presence of grazers with mixed feeders is compatible with a C3-dominated environment. In fact, the molar microwear pattern of *Tragoportax* from Samos reflects a grazing diet whereas the δ^{13}C reveals the dominance of C3 vegetation. Conversely, the δ^{13}C values in mammalian tooth and in paleosols from the Upper Miocene of the Potwar Plateau (Siwalik province) point out an expansion of C4 grasses from the Late Vallesian up to the Middle Turolian (Barry et al., 2003). The palynological data of the sub-Himalayan region comfort the hypothesis of the expansion of grassy environments during the Turolian in the Siwalik province (Hoorn et al., 2000). The δ^{18}O values in mammal teeth from GIA localities reveal an increase of aridity from the Greek to the Afghan localities (Zazzo et al., 2002). In the Potwar Plateau, the paleosol δ^{18}O indicates also a strong seasonality with a dry period during the Turolian (Barry et al., 2003).

The cohabitation of grazers and mixed feeders and the results of the isotopic studies from Molayan suggest an evergreen sclerophyllous shrubland rather than a more closed environment. In fact, forested or ticket bushy environments limit strongly the development of the undergrowth herbaceous grassy layer. Moreover, aridity or strong seasonality is a restricting factor for the development of wooded and forested formations (White, 1986). These data are comforted by the floristic fossil record and by studies on paleosols. In fact, these results support the hypothesis of an expansion of the sclerophyllous vegetation along the Tethyan ecosystems from the Late Vallesian to the Late Turolian (Axelrod, 1975; Retallack, 1991). The presence of shrublands with a dominance of C3 plants is in accordance with the probable uneven topography of the landscape in Afghanistan and the raising of the Himalayan complex during the Late Miocene. In fact, the morphologic appendicular features of *Sporadotragus tadzhikistanicus*, such as the reduction of metapods, reveal an adaptation to a hilly landscape (Bouvrain and Heintz, In press). In contrast, the faunal assemblages from the Potwar Plateau inhabited extensive floodplains. This altitudinal difference may also explain the absence of C4 grasses in the Molayan area (Tieszen et al., 1979).

The correlation between dental microwear, morphological features and isotopic data clearly indicates an open, arid, and hilly environment, where evergreen sclerophyllous shrubs and C3 grasses made up the majority of the vegetation.

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