

# Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: Evidence from dental microwear and stable isotopes

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## Abstract

A multi proxy approach was performed to characterize vegetation in southwestern Bulgaria during the end of the Early and the Middle Turolian (8.7–7.0 Ma). This period was marked by eustatic fluctuations in the Mediterranean Sea that are well documented. In order to estimate the impact of these marine events on continental landscapes, dental microwear and stable isotope profiles in enamel were used to characterize feeding habits of extinct bovids, and in turn vegetation. Analyses were made on permanent molars of fossil bovids from two Late Miocene localities: Hadjidimovo-1 (Early/Middle Turolian) and Kalimantsi (Middle Turolian). Carbon isotopes profiles of *Tragoportax rugosifrons* and *Miotragocerus gaudryi* from the Hadjidimovo-1 indicate a pure C<sub>3</sub>-based diet for the two boselaphini. Large inter-individual differences in absolute  $\delta^{18}\text{O}$  values were found for *M. gaudryi* suggesting little reliance on drinking water due to a browsing diet. Dental microwear shows that none of the bovid species exclusively grazed. In Hadjidimovo-1, microwear evidence suggests mixed feeding habits for *Tragoportax rugosifrons*, *Gazella* sp., and *Palaeoreas lindermayeri* and a leaf browsing diet for *Miotragocerus gaudryi*. *Palaeoreas lindermayeri* from Hadjidimovo-1 has a bimodal pattern indicating that its feeding preferences were tied to seasonal food availabilities. At Kalimantsi, *Miotragocerus gaudryi* show variations between individuals whereas *Tragoportax* cf. *amalthea* was an exclusive browser. *Palaeoreas lindermayeri* and *Gazella* sp. were also mixed feeders in Kalimantsi. Our combined approach shows no evidence for dense forested environments during the Early and Middle Turolian, and then supports previous hypotheses based on faunal analyses. Our results rather suggest that southwestern Bulgaria was dominated by open wooded landscapes where C<sub>3</sub> graminoids grew in abundance among the herbaceous layer. Finally, microwear data suggest that the proportion of dicotyledons such as forbs, bushes or shrubs was probably higher in the plant communities of Kalimantsi than in those of Hadjidimovo-1.

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## 1. Introduction

From the Late Miocene to the Early Pliocene (~ 11.5–5.3 Ma; Van Couvering et al., 2000; Hilgen et al., 2000), the Mediterranean basin was marked by tectonic events and related eustatic consequences before the Messinian salinity crisis (Adams et al., 1977). Multidisciplinary approaches indicated tectonic causes for the succession of sea level fluctuations and subsequent environmental consequences on marine and continental ecosystems (Suc et al., 1995; Seidenkrantz et al., 2000; Blanc-Valleron et al., 2002; Merle et al., 2002; Duggen et al., 2003).

Paleontologists often associate faunal turnovers with climatic and environmental changes. This was also the case in the Mediterranean basin during the Late Miocene (Bonis et al., 1999). However, extinctions, dispersals and diversity rates throughout Europe and Anatolia during the Late Miocene may also be related to paleogeographic changes. Connections between Anatolia and Balkans, Africa and Central Asia might be the main factor explaining the Late Miocene faunal changes in Eastern Europe (Fortelius et al., 1996). Therefore, an approach independent of taxonomic inferences is necessary in order to reconstruct environmental dynamics.

Our aim is to characterize paleoenvironments and estimate environmental changes during the Late Tortonian in the northeastern margin of the Mediterranean basin. To reach this goal we reconstructed the dietary habits of Late Miocene bovids from Bulgaria using dental microwear and stable isotope analyses. In fact, reconstructing feeding preferences of fossil ungulates using both of these independent methods is an objective way of characterizing the plant communities of past environments.

### 1.1. Dental microwear and stable isotope analyses

Dental microwear patterns depend on the food composition of the last few meals (Teaford and Oyen, 1989). For instance, grazing ungulates have more scratches on molar shearing facets than browsing species because of the higher silica deposits on cell walls of graminoids (Solounias et al., 1988; Hayek et al., 1992; Solounias and Hayek, 1993). Recent comparative studies have gone further into detail about the microwear signature for living ungulates (Solounias and Semprebon, 2002; Semprebon et al., 2004; Merceron et al., 2004a,b, 2005a,b; Rivals and Semprebon, in press). Among grass-eaters (including grazers and mixed feeders), species from tropical latitudes feeding primarily on graminoids (including herbaceous monocotyle-

dons, grasses, sedges, and rushes) with a C<sub>4</sub> metabolic pathway, would show a different microwear signature than Eurasian species that graze on C<sub>3</sub> graminoids (Solounias and Semprebon, 2002; Merceron et al., 2004b). Among browsers, exclusive-leaf eaters differ from browsers that include fruits and seeds in their diet. Solounias and Semprebon (2002) also defined as “meal by meal” or “generalist”, mixed feeders that feed on a wide range of foods on a daily basis. These species have a microwear pattern which is usually characterized by large number of both pits and scratches. “Seasonal/regional mixed feeders” that are strongly tied to seasonality, have either a grazing or a browsing microwear pattern depending on the composition of their last meals (Solounias and Semprebon, 2002; Merceron et al., 2004b, 2005b).

Dietary reconstruction using carbon isotopes is based on the premise that the  $\delta^{13}\text{C}$  value of ingested food is recorded into biogenic apatite with an enrichment of about 14‰ (Cerling et al., 1997). In subtropical to tropical environments, plants rely primarily on two photosynthetic pathways that fractionate carbon to different degrees. Trees, shrubs and high-altitude graminoids use the C<sub>3</sub> photosynthetic cycle ( $\delta^{13}\text{C} = -25.0\text{‰}$ , on average), whereas low altitude graminoids use the C<sub>4</sub> photosynthetic cycle ( $\delta^{13}\text{C} = -12.1\text{‰}$ , on average). Based on these  $\delta^{13}\text{C}$  values, and the enrichment in biogenic apatite, ranges of C<sub>4</sub> plant proportion in diet can be calculated using a two end-member mixing model (Cerling et al., 2003).

In contrast to dental microwear pattern, stable isotope composition of tooth enamel records longer time-scale ecological and environmental information. In hypsodont teeth, enamel mineralization occurs basically from apex to cervix and is not remodeled once formed. Therefore, serial sampling along the growing axis allows for reconstruction of seasonal dietary and climatic changes that occurred during tooth growth (Fricke and O’Neil, 1996; Fricke et al., 1998a,b; Kohn et al., 1998; Sharp and Cerling, 1998). This approach was applied to *Tragoptax* sp. from Molayan (Middle Turolian of Afghanistan) and showed that the isotopic series extracted from unworn m2–m3 represents a continuous record lasting 12–15 months (Zazzo et al., 2002). Recent works have shown that full amplitude of short-term changes is likely not recorded in enamel because reservoir effects within the animal and time required to complete the enamel maturation process are responsible for some damping (Balasse, 2002; Kohn et al., 2002; Passey and Cerling, 2002). However this bias is expected to be constant within a single species and large intra-tooth variations measured in enamel of *Tragoptax* sp. from Molayan

suggest relatively fast maturing enamel (and therefore little damping) for this group.

Dental microwear and stable isotopic analyses provide different, but complementary information. Whereas it is not possible to decipher between grazing and browsing in a  $C_3$ -dominated vegetation using the stable isotope approach, dental microwear analysis may indicate the presence of graminoids within a  $C_3$  plant community (Franz-Odenaal and Solounias, 2004; Merceron et al., 2005a). Whereas dental microwear pattern provides information regarding the last food intakes, stable isotope profiles in tooth enamel give a continuous behavioral record (1–2 years) for each specimen (Boisserie et al., 2005).

### 1.2. The southwestern Turolian megafauna of Bulgaria

The fossil sites of Hadjidimovo-1 and Kalimantsi are among the richest Late Miocene localities of Europe (Spassov, 2002). The Hadjidimovo fossiliferous area is situated in the Mesta river valley near the town of Hadjidimovo (Gotse Delchev district) and the Bulgarian-Greek border (Fig. 1). The main locality Hadjidimovo-1, where more than 30 mammalian species have been reported, is located at the MN11/12 boundary ( $\sim 7.4$  Ma; Spassov, 2002). The fossiliferous area around the Kalimantsi village situated in the middle Struma basin covers a large region ( $\sim 6$  km<sup>2</sup>) of Late Miocene deposits

with more than 10 known fossil mammal localities (Fig. 1). The recent revision of their biochronology demonstrates that all Kalimantsi sites are of Turolian age (8.7–5.33 Ma). Kalimantsi-1 belongs to the newly established Gradishte lithocomplex, and is more likely to yield a fauna of Early Turolian age (8.7–7.4 Ma; Kostopoulos et al., 2003), while other Kalimantsi faunas (referred to the Strumyani genetic lithocomplex) are considered to belong to the Middle Turolian, MN 12 (7.4 to  $\sim 6.85$  Ma  $\pm 0.25$ ; Kostopoulos et al., 2003; Tzankov et al., 2005; Spassov et al., in press). A comparison of the age of these both localities, i.e. Hadjidimovo-1 and Kalimantsi, can be made with the faunal data. The biochronologic place of the Hadjidimovo-1 fauna is characterized by the presence of: *Mesopithecus* close to *M. delsoni*, a species belonging to MN11 (Koufos et al., 2003; Spassov et al., in press); *Palaeoreas lindermayeri* larger than the population from Pikermi (Geraads et al., 2003); *Hipparion mediterraneum* with archaic features in comparison to the Pikermian population (Hristova and Kovachev, 2005). All these faunal particularities demonstrate an age older than the typical MN12 faunas of Pikermi, probably about the MN 11/MN 12 boundary. The fauna from the Strumiani lithocomplex of Kalimantsi (i.e. from the upper horizons of the Kalimantsi Late Miocene deposits) is characterized by: *Mesopithecus* mostly close to *M. pentelicus*, a species belonging MN12 (Koufos et al., 2003); *Tragoportax cf. amalthea*

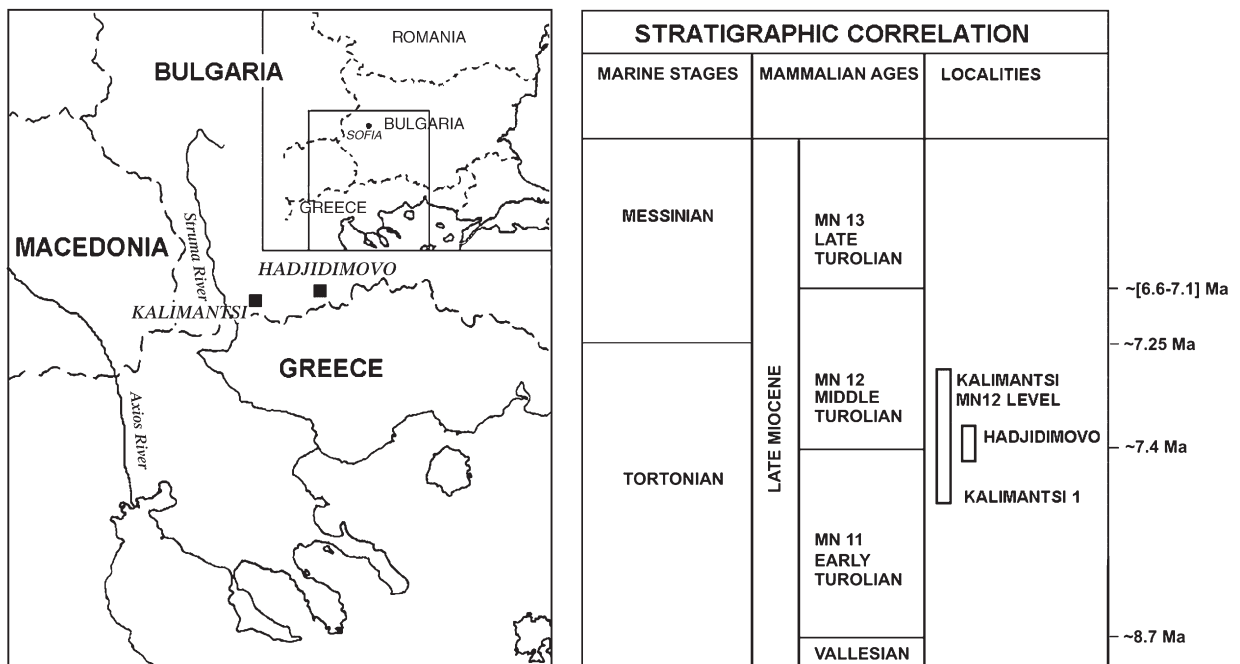


Fig. 1. Chronostratigraphic scale and map of South-Eastern Europe showing both age and locations of fossil localities in Southern Bulgaria.

probably identical with the Pikerminian species (Spassov et al., 2004), which is typical for the advanced stages of MN12; *P. lindermayeri* close to the Pikermin sample (Geraads et al., 2003); *H. mediterraneum* with more evolved features, close to the Pikermin sample or at stage between it and the Hadjidimovo one (Hristova and Kovachev, 2005). That is, the features of these Kalimantsi Middle Turolian fauna show close similarity with the typical MN12 localities of Pikermin.

## 2. Material

### 2.1. Microwear analysis

#### 2.1.1. Fossil material

All of the fossil specimens studied are stored in the Assenovgrad Museum, a paleontological division of the National Museum of Natural History, Sofia, Bulgaria. Four bovid taxa from the Hadjidimovo-1 collection were analyzed: *Tragoportax rugosifrons*, *Palaeoreas lindermayeri*, *Miotragocerus (Pikermicerus) gaudryi* and *Gazella* sp. *Miotragocerus* and *Tragoportax* have often been confused in the past, but Spassov and Geraads (2004) restrict *Tragoportax* mainly to *T. amalthea* and *T. rugosifrons*. Among the faunal assemblages assigned to Kalimantsi Middle Turolian localities, four bovids, *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri*, *Miotragocerus (Pikermicerus) gaudryi* and *Gazella* sp. were analyzed (Table 1).

#### 2.1.2. Comparative “UNGULATES” database

The dental microwear of fossil species was compared to that of 548 wild-shot specimens from 38 well-known extant ungulate species. This database, termed “UNGU-

LATES”, is one of the largest databases ever published (Appendix). It is nowadays composed of 11 grazing species *sensu lato*, nine mixed feeders *sensu lato*, and 18 browsing species *sensu lato*. Species were assigned to dietary category according to source bibliography (Appendix). In the case of *Gazella soemmerringi*, there was no information related to its dietary preferences. Considering the lack of data on its feeding behavior, this population of *G. soemmerringi* was therefore assigned to the leaf/fruit browser category on the basis of its dental microwear pattern. *Saiga tatarica* and *Ovibos moschatus* are assigned to “meal by meal” mixed feeders based on the fact that they graze and browse in open landscapes (Tener, 1965; Sokolov, 1974; Lent, 1988; Ihl and Klein, 2000).

### 2.2. Stables isotopes

The mandibles of five specimens from the tribe boselaphini (*Tragoportax* and *Miotragocerus*) were selected for carbon and oxygen isotope analyses (Table 2). Zazzo et al. (2002) showed that complete seasonal cycle was generally represented in the third molar of the bovid *Tragoportax*. However, we choose to also sample the second molar whenever it was available. At Hadjidimovo-1 the second (m2) and third (m3) molars from one specimen of *Tragoportax rugosifrons* and three specimens of *Miotragocerus (Pikermicerus) gaudryi* were sampled. At Kalimantsi only the third molar (m3) of one specimen of *Tragoportax* cf. *amalthea* was sampled. The isotope analyses were focused on both of these boselaphini, because they are widely distributed during the Late Miocene. Moreover, these taxa, and more specifically species belonging the genus *Tragoportax*,

Table 1

Summary statistics (mean *m* and standard error of the mean sem) of dental microwear variables for extinct bovids

Sites <sup>1</sup>	Species	<i>N</i>	% p		<i>N<sub>s</sub></i>		<i>N<sub>ws</sub></i>		<i>N<sub>fs</sub></i>		<i>N<sub>p</sub></i>		<i>N<sub>lp</sub></i>		<i>N<sub>sp</sub></i>	
			<i>m</i>	sem	<i>m</i>	sem	<i>m</i>	sem	<i>m</i>	sem	<i>m</i>	sem	<i>m</i>	sem	<i>m</i>	sem
HD	<i>Palaeoreas lindermayeri</i>	19	50.9	3.6	27.4 <sup>w</sup>	1.8	2.1	0.4	25.3	1.7	29.7	2.7	4.4	0.7	25.3	2.3
	Browsing population	8	63.2 <sup>u</sup>	4.0	19.3 <sup>u</sup>	0.8	1.1	0.6	18.1	0.7	35.5	3.9	4.3	1.3	63.2	4.0
	Grazing population	11	42.0 <sup>u</sup>	3.6	33.3 <sup>u</sup>	1.3	2.7	0.4	30.5	1.3	25.5	3.2	4.5	0.9	42.0	3.6
	<i>Tragoportax rugosifrons</i>	30	52.1 <sup>w</sup>	2.6	30.8	1.2	2.2	0.2	28.6	1.2	36.9	3.0	4.5	0.7	32.4	2.8
	<i>Miotragocerus gaudryi</i>	3	84.8		11.6		0.3		11.3		65.3		6.3		59.0	
	<i>Gazella</i> sp.	14	64.8	3.3	27.1	2.3	1.4	0.3	25.6	2.2	52.3	4.5	5.9	0.8	46.4	4.0
KAL	<i>Palaeoreas lindermayeri</i>	7	50.6	3.4	32.3	2.9	1.4	0.5	30.9	3.2	33.0	2.8	4.7	0.6	28.3	2.9
	<i>Tragoportax</i> cf. <i>amalthea</i>	9	68.4	1.1	18.1	1.5	0.9	0.5	17.2	1.4	39.2	3.4	3.7	0.8	35.6	3.1
	<i>Miotragocerus gaudryi</i>	3	50.8		26.0		0.7		25.3		27.7		4.3		23.3	
	<i>Gazella</i> sp.	8	56.2	5.8	26.8	3.4	1.3	0.5	25.6	3.3	36.8	5.9	4.8	0.6	31.9	5.8

<sup>1</sup>Sites: Hadjidimovo-1 (HD), Kalimantsi (KAL). <sup>w</sup>Significant Shapiro–Wilk test ( $p < 0.05$ ). <sup>u</sup>Significant Mann–Whitney test ( $p < 0.05$ ). % p Percentage of pits, number of scratches *N<sub>s</sub>*, of wide scratches *N<sub>ws</sub>*, of fine scratches *N<sub>fs</sub>*, number of pits *N<sub>p</sub>*, of large pits *N<sub>lp</sub>*, and of small pits *N<sub>sp</sub>*.

Table 2

Carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}_\text{c}$ ,  $\delta^{18}\text{O}_\text{p}$ ) isotope ratios of molar enamel bioapatite from late Miocene boselaphini from Bulgaria

Sample	Locality	Taxon	Tooth	Position (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}_\text{c}$ (‰)	$\delta^{18}\text{O}_\text{p}$ (‰)		
K 3879-1	Kalimantsi	<i>T. cf. amalthea</i>	M3	22.0	-11.3	24.4	16.1		
K 3879-2				20.0	-11.8	25.1	15.7		
K 3879-3				17.3	-11.8	26.4	17.2		
K 3879-4				15.5	-11.8	27.2	19.1		
K 3879-5				13.5	-11.6	28.1	20.0		
K 3879-6				12.5					
K 3879-7				11.5	-11.4	28.9	20.4		
K 3879-8				10.0					
K 3879-9				09.0	-11.1	28.1	20.5		
K 3879-10				08.0					
K 3879-11				06.5	-11.1	28.6	20.4		
K 3879-12				05.5					
K 3879-13				04.5	-11.2	28.0	19.2		
K 3879-14				03.0					
K 3879-15	01.5	-11.5	27.6	18.7					
HD 2507-1	Hadjidimovo	<i>T. rugosifrons</i>	M2	17.0	-12.7	26.6	17.4		
HD 2507-2				15.7	-12.4	26.1			
HD 2507-3				14.1	-12.6	25.8	16.2		
HD 2507-4				12.5					
HD 2507-5				10.9	-12.7	24.4	14.6		
HD 2507-6				09.5	-12.6	23.7			
HD 2507-7				08.1	-12.6	23.3	13.8		
HD 2507-8				06.8	-12.6	23.1			
HD 2507-9				05.3	-12.6	22.9	13.4		
HD 2507-10				03.8	-12.7	22.6			
HD 2507-11				02.3	-12.7	22.5			
HD 2507-12				00.8	-12.7	22.7			
HD 2507-13									
HD 2507-14					M3	21.5			
HD 2507-15						20.4	-12.1	23.1	14.5
HD 2507-16						17.6	-12.3	24.5	
HD 2507-17						16.8	-12.6	24.3	16.8
HD 2507-18						15.5	-12.3	25.9	17.7
HD 2507-19						13.3	-12.3	26.3	18.9
HD 2507-20						12.4	-12.3	26.6	
HD 2507-21						11.2	-12.3	27.8	19.8
HD 2507-22						09.2	-12.3	28.0	19.4
HD 2507-23						07.3	-12.2	27.5	19.4
HD 2507-24						04.8	18.7		
HD 2507-25				02.8	-11.6	25.2	17.5		
HD 2507-25				01.5	-11.6	24.9	16.9		
HD 2555-1	Hadjidimovo	<i>M. gaudryi</i>	M2	10.0	-11.5	31.3	22.4		
HD 2555-2				08.3	-11.4	31.2	21.8		
HD 2555-3				06.8	-11.5	30.5	21.5		
HD 2555-4				05.3	-11.3	29.9			
HD 2555-5				03.8	-11.2	29.3	21.0		
HD 2555-6				02.3	-11.3	29.3	20.1		
HD 2555-7				00.8	-11.0	28.8	20.1		
HD 2555-8					M3	10.3	-11.4	28.0	19.5
HD 2555-9						08.8	-11.6	28.5	19.4
HD 2555-10						07.3	-11.6	28.8	20.0
HD 2555-11						05.8	-11.5	28.5	20.3
HD 2555-12						04.5	-11.6	28.8	20.7
HD 2555-13						03.5	-11.6	29.4	20.9
HD 2555-14						02.5	-11.5	29.7	21.0
HD 2555-15						01.5	-11.5	29.9	21.7
HD 3588-1	Hadjidimovo	<i>M. gaudryi</i>	M2	12.5	-13.1	26.1	16.8		
HD 3588-2				11.5	-13.3	26.0			

(continued on next page)

Table 2 (continued)

Sample	Locality	Taxon	Tooth	Position (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{Oc}$ (‰)	$\delta^{18}\text{Op}$ (‰)
HD 3588-3				10.5	-13.4	25.8	15.4
HD 3588-4				09.5	-13.4	25.0	
HD 3588-5				08.5	-13.7	24.5	15.5
HD 3588-6				07.5	-13.1	24.3	
HD 3588-7				06.5	-13.1	24.0	14.9
HD 3588-8				05.5	-13.0	24.0	
HD 3588-9				04.3	-12.9	23.8	15.1
HD 3588-10				02.8	-12.3	23.9	
HD 3588-11				01.3	-12.8	23.7	15.5
HD 3588-12			M3	12.3	-12.4	24.2	15.2
HD 3588-13				11.0	-12.6	24.1	
HD 3588-14				09.5	-12.7	24.4	15.7
HD 3588-15				08.5	-12.8	24.2	
HD 3588-16				07.5	-12.7	24.8	15.8
HD 3588-17				06.5	-12.8	25.0	
HD 3588-18				05.5			16.6
HD 3588-19				04.5	-12.7	25.3	
HD 3588-20				03.5	-12.6	26.1	17.1
HD 3588-21				02.0	16.8		
HD 3828-1	Hadjidimovo	<i>M. gaudryi</i>	M2	13.3	-11.7	28.4	18.3
HD 3828-2				11.8	-11.6	27.4	
HD 3828-3				10.0			16.6
HD 3828-4				08.3	-11.8	26.2	
HD 3828-5				06.8	15.8		
HD 3828-6				05.3	-11.9	25.7	
HD 3828-7				03.8	16.0		
HD 3828-8				02.2			
HD 3828-9				00.8	16.2		
HD 3828-10			M3	12.8	-12.0	26.9	18.3
HD 3828-11				11.3	-12.0	26.8	18.9
HD 3828-12				09.8	-12.0	27.8	20.0
HD 3828-13				08.0	-12.0	28.1	20.2
HD 3828-14				06.3	-11.7	28.6	20.2
HD 3828-15				04.8	-11.8	28.4	20.3
HD 3828-16				03.3	-11.6	29.1	
HD 3828-17				01.8			20.3
HD 3828-18				00.5			20.7

m2, m3 = second and third lower molars.

Position of the samples is expressed as the average distance (in mm) from the cervical margin.

HD: Hadjidimovo-I; K: Kalimantsi.

are typical of Early and Middle Turolian mammalian ages throughout Eurasia.

### 3. Methods

#### 3.1. Microwear analysis

Preliminary researches of the dental microwear pattern of mammals were based on light microscopy (e.g. Walker, 1976). Later, most of the dental microwear studies regarding the fossil ungulates were based on scanning electronic microscopy (e.g. Solounias et al., 1988; Hayek et al., 1992). However, Solounias and 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 this approach by using high-quality digital images of dental surfaces before quantifying the dental microwear pattern with a semi-automatic method.

The protocol shown in Merceron et al. (2004a,b) was here applied for molding and casting steps, digitization of enamel facets and data extraction. Shearing facets of the permanent M2 were digitized at 256 grey 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<sup>®</sup>) connected to a light stereomicroscope (Leica MZ 125) at low magnification ( $\times 30$ ). Then, dental microwear was quantified in a 0.09 mm<sup>2</sup> square using Optimas v. 6.5.2 software (Media Cybernetics<sup>®</sup>) by one

of us (G.M.). Data was extracted and exported to statistical software (Statistica v. 6, Statsoft®). A Principal Components Analysis (PCA) was generated with extant specimens using four variables: number of fine scratches  $N_{fs}$  (width < 15  $\mu\text{m}$ ), small pits  $N_{sp}$  (major axis < 15  $\mu\text{m}$ ), large pits  $N_{lp}$  (major axis > 15  $\mu\text{m}$ ), and wide scratches  $N_{ws}$  (width > 15  $\mu\text{m}$ ) (Table 3). Numbers of pits ( $N_p = N_{sp} + N_{lp}$ ) and scratches ( $N_s = N_{ws} + N_{fs}$ ) as well as percentage of pits (% p =  $N_p / [N_p + N_s]$ ) were not integrated in this descriptive multivariate analysis because they are related to the previous variables. Fossil species were secondly included in the PCA as supplementary data. In order to reveal a probable non-normality, and then a possible bimodality of the distribution regarding the dental microwear pattern, the Shapiro–Wilk test was applied on each large sample for the three main variables:  $N_p$ ,  $N_s$ , and % p. If the normality was not upheld by this test, a non-parametric Mann–Whitney test was then applied to test the significance of differences if two sub groups had been recognized among the sample (Sokal and Rohlf, 1998).

### 3.2. Stable isotopes

Enamel samples were collected using a Dremel high-speed rotary tool with a diamond-impregnated bit from the top to the base of tooth crown. Each sample consists of horizontal 1 to 2-mm thick bands spanning the width of a lobe and most of enamel thickness. Between seven

and 11 samples and 12 to 15 samples were collected (but 12 and 13 samples were analyzed) for each tooth from *M. gaudryi* and *Tragoportax* sp., respectively. Samples were then split for carbonate and phosphate isotope analyses. Each sub sample was washed in 0.1 M acetic acid for twenty-four hours to remove exogenous carbonates and rinsed several times. Samples were then reacted for 4 min at 90 °C with 100% phosphoric acid in a Kiel III carbonate device interfaced to a Finnigan MAT 253 isotope ratio mass spectrometer in the Saskatchewan Isotope Laboratory, University of Saskatchewan. Analyses were normalized to the international standard NBS-19. Around 5–10 mg aliquots of enamel were necessary to isolate biogenic phosphate as  $\text{Ag}_3\text{PO}_4$  following the procedure of Lécuyer et al. (1993) that was slightly modified by one of us (A.Z.) for smaller samples. Measurements of  $^{18}\text{O}/^{16}\text{O}$  ratios from  $\text{Ag}_3\text{PO}_4$  were performed on a TC/EA coupled to a Delta+XL mass spectrometer in the Saskatchewan Isotope Laboratory, University of Saskatchewan. Results are reported as the mean of three replicate analyses from the same sample. Precision of  $\delta^{18}\text{O}$  measurements is  $\pm 0.3\text{‰}$ , based on repeated analyses of two standards (NBS120c and synthetic hydroxylapatite). Results are expressed using the standard ‰ notation where:

$$\delta^{18}\text{O}(\text{or } \delta^{13}\text{C}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 100$$

and  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{18}\text{O}/^{16}\text{O}$  (or  $^{13}\text{C}/^{12}\text{C}$ ) ratios in the sample and standard respectively. Standards are VPDB for carbon and VSMOW for oxygen. Oxygen values from carbonate are reported assuming the acid–calcite fractionation factor for calcite.

## 4. Results

### 4.1. Microwear analysis

#### 4.1.1. Hadjidimovo-1

Both patterns of the PCA clearly suggest that none of the species of bovids from Hadjidimovo-1 were grazers *sensu stricto* (Tables 1 and 3, Figs. 2–4, Appendix).

According to the first and second planes of the PCA (Figs. 2 and 3), *Palaeoreas lindermayeri* is close to seasonal mixed feeders like the living impala, *Aepyceros melampus*. The normality of the main variables ( $N_p$ ,  $N_s$  and % p) was tested with the Shapiro–Wilk application. The normality is not upheld for the distribution of the number of scratches ( $W=0.897$ ;  $p<0.05$ ; Table 1). The population of *P. lindermayeri* is distributed according to a balanced bimodality. In fact, two clusters can be significantly recognized using non-parametric Mann–Whitney test, which may indicate a probable dietary

Table 3  
Results of principal components analysis of dental microwear pattern of thirty-eight extant species that constitute the “UNGULATES” database

Eigenvalues				
Fact.	Eigenvalues	% eigenvalues*	$\Sigma$ eigenvalues	$\Sigma\%$ eigenvalues
1	1.558	38.96	1.558	38.96
2	1.036	25.92	2.595	64.89
3	0.861	21.52	3.456	86.42
4	0.543	13.57	4.000	100.00

\*% eigenvalues=percentage of eigenvalue;  $\Sigma$ =sum

	Communities $r$ and square communities $r^2$ between variables and axis					
	Fact. 1		Fact. 2		Fact. 3	
	$r$	$r^2$	$r$	$r^2$	$r$	$r^2$
$N_{ws}$	-0.565	0.319	0.434	0.188	-0.656	0.431
$N_{fs}$	-0.126	0.016	-0.884	0.782	-0.448	0.201
$N_{lp}$	0.728	0.531	0.251	0.063	-0.467	0.219
$N_{sp}$	0.832	0.693	-0.059	0.003	-0.104	0.011

Eigenvalues, communities  $r$  and square communities  $r^2$ .  $N_{fs}$ : number of fine scratches,  $N_{ws}$ : number of wide scratches,  $N_{sp}$ : number of small pits,  $N_{lp}$ : number of large pits.

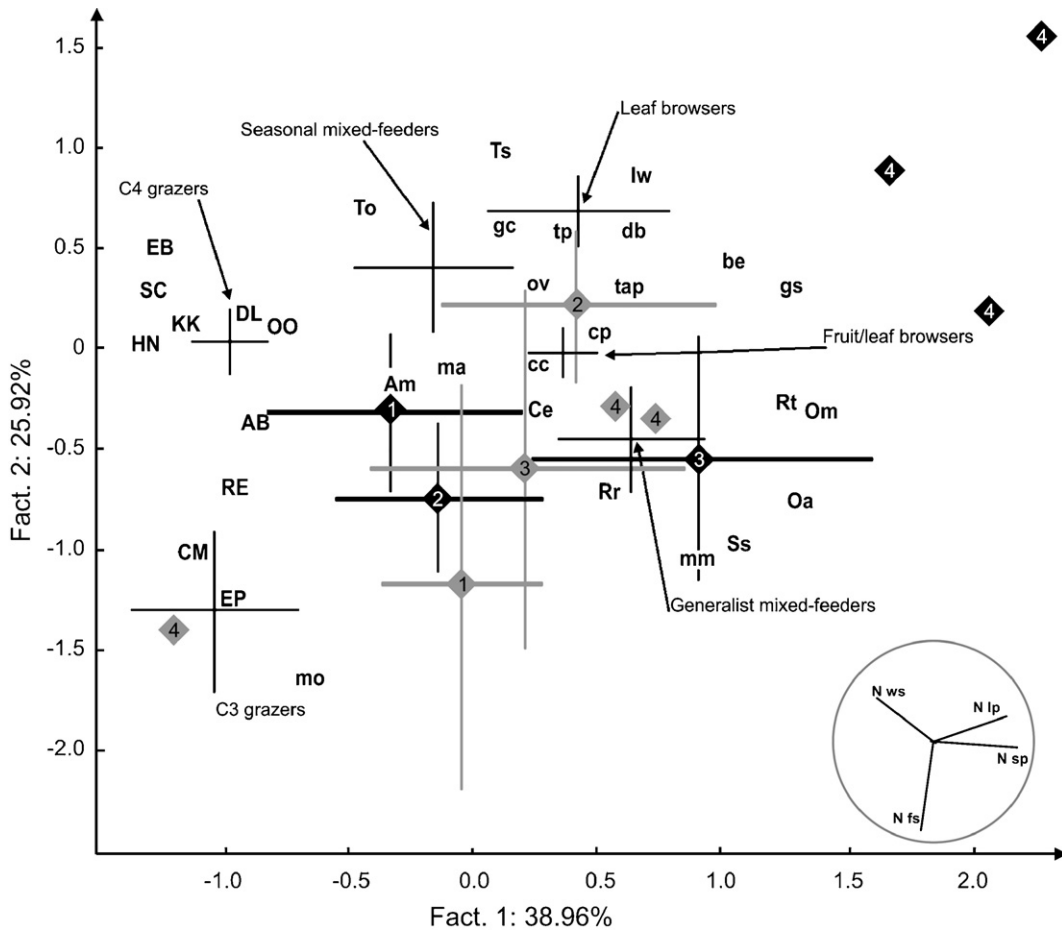


Fig. 2. First plane of the principal components analysis. Extant species are the active individuals of the PCA. Fossil species are included as supplementary data. Circle of correlation represents the strength of each variable. The mean and its confidence interval at 95% are shown for each diet category (C<sub>4</sub> and C<sub>3</sub> grazers, leaf browsers, fruit/leaf browsers, seasonal and generalist mixed feeders) on extant species, and for extinct species, except the specimens of *Miotragocerus gaudryi* from Hadjidimovo-1 and Kalimantsi, which are individually shown. Black diamonds: bovids from HD; Gray diamonds: bovids from KAL; 1. *Palaeoreas lindermayeri*, 2. *Tragoportax*, 3. *Gazella* sp., 4. *Miotragocerus*. Extant species from the “UNGULATES” database: EP *Equus przewalskii*, EB *E. burchelli*, SC *Syncerus caffer*, HN *Hippotragus niger*, KK *Kobus kob*, DL *Damaliscus lunatus*, OO *Ourebia ourebi*, AB *Alcelaphus buselaphus*, RE *Redunca redunca*, CM *Ceratotherium simum*, Am *Aepyceros melampus*, Ts *Tragelaphus scriptus*, To *Taurotragus oryx*, Ce *Cervus elaphus*, Rt *Rangifer tarandus*, Oa *Ovis ammon*; Rr *Rupicapra rupicapra*; Om *Ovibos moschatus*, Ss *Saiga tatarica*, cc *Capreolus capreolus*, ov *Odocoileus virginianus*, cp *Cephalophus* sp., sg *Sylvicapra grimmia*, lw *Litocranius walleri*, gc *Giraffa camelopardalis*, db *Diceros bicornis*, gs *Gazella soemmerringi*; mo *Moschus moschiferus*, mm *Muntiacus muntjak*, ma *Mazama americana*, tp *Tragelaphus strepsiceros*, tap *Tapirus* sp.

changes in correlation with seasonality (Table 1). A first cluster, which is composed of eight specimens, has a microwear pattern close to that of living fruit/leaf browsers such as *Odocoileus virginianus* or *Capreolus capreolus*. The other 11 specimens constitute the second group and show similarities with extant grazers. Nevertheless, the grazing individuals of *P. lindermayeri* differ from C<sub>4</sub> African grazers in having more fine scratches and more pits on shearing molar facets (Table 1).

According to the first axis, *T. rugosifrons* is close to *A. melampus* and *Taurotragus oryx*, which are both seasonal mixed-feeders (Fig. 2). In fact, the percentage

of pits plus the total number of scratches suggest that this fossil antelope was engaged in both browsing and grazing rather than specialized feeding preferences (Fig. 2). *T. rugosifrons* is also close to two leaf/fruit browsers, *Mazama americana* and *Moschus moschiferus*. However, *M. americana* has fewer scratches than *T. rugosifrons*. The small sample of the Moschidae ( $N=3$ ) strongly limits the reliability of the results regarding this extant taxon. Along the second and third axis, *T. rugosifrons* plots with seasonal mixed-feeders, and more particularly is closer to *A. melampus* (Figs. 2, 3). Similar to *P. lindermayeri* the normality of the distribution of *T.*



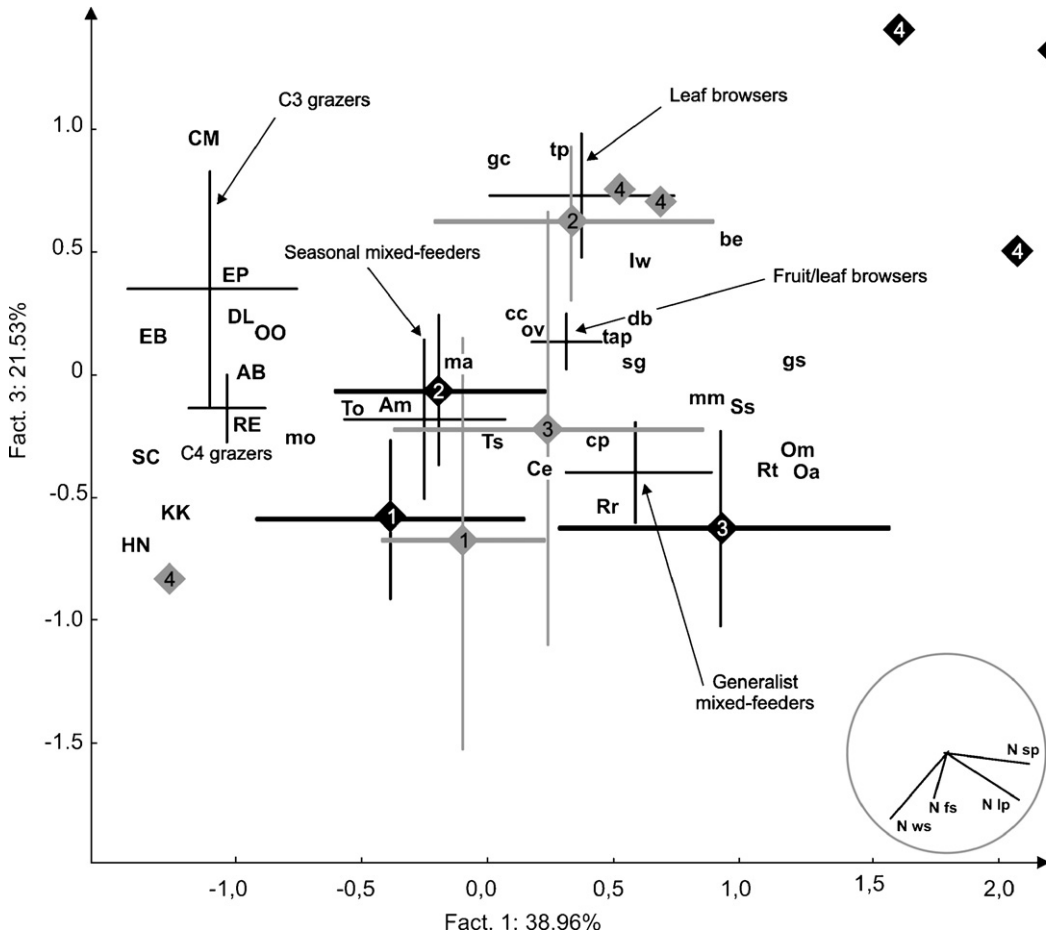


Fig. 3. Second plane of the principal component analysis. For abbreviations, see legends in Fig. 2.

*rugosifrons* according to the percentage of pits is not upheld ( $W=0.895$ ;  $p<0.05$ ; Table 1). The lack of normality does not however result from a balanced and typical bimodality.

*Gazella* sp. falls among browsers and generalist mixed-feeders along the first axis. Coordinates along the second and third axis indicate affinities with generalist mixed feeders such as *Rupicapra rupicapra* and *Ovis ammon* (Figs. 2, 3). The normality of the distribution for the main variables is upheld (Table 1). Thus, we conclude that *Gazella* sp. from Hadjidimovo-1 was a generalist mixed feeder.

The coordinates of the 3 individuals of *Miotragocerus* (*Pikermicrus*) *gaudryi* clearly indicate that, during the few days preceding their death, they fed only on dicots (Table 1, Figs. 2, 3).

4.1.2. Kalimantsi

As in Hadjidimovo-1, *P. lindermayeri* plots close to *A. melampus* according to the first axis (Fig. 2). The

differences between both populations of *P. lindermayeri* along the second and third axis result from the slightly higher numbers of both pits and scratches on enamel surfaces for the Kalimantsi population (Figs. 2, 3). Although the specimens are widely distributed, no reliable bimodality can be recognized according to the main variables because of the small sample size (Table 1). However despite this, *P. lindermayeri* from Kalimantsi can be assigned to the mixed feeder category.

In the first plane of the PCA, *Tragoptax* cf. *amalthaea* falls within browsers *sensu lato* (Fig. 2). The third axis points out stronger affinities with leaf browsers such as *Tragelaphus strepsiceros* (Fig. 3). This is in contrast with results from the *Tragoptax* population of Hadjidimovo-1 (Fig. 4).

*Gazella* sp. plots with seasonal and generalist mixed feeders. Therefore, this gazelle was probably engaged in both browsing and grazing (Table 1, Figs. 2, 3).

Two out of three analyzed specimens of *Miotragocerus gaudryi* plot close to generalist mixed feeders and

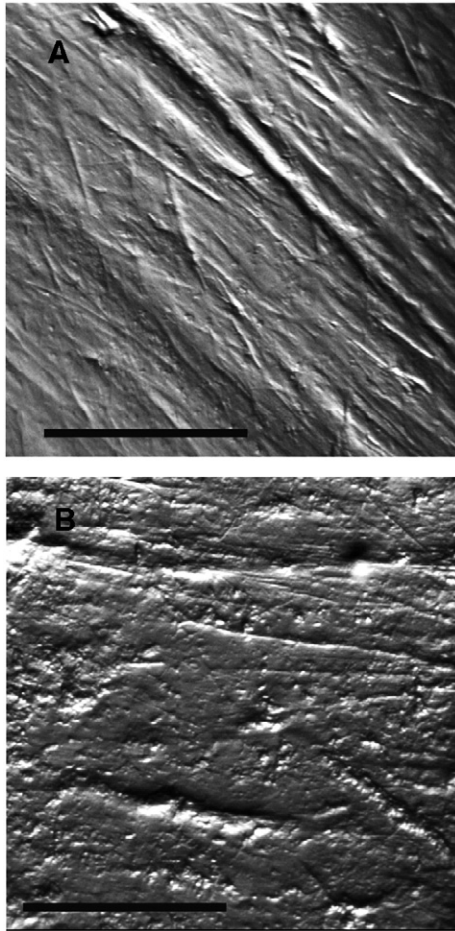


Fig. 4. Digitized photographs of the shearing molar facets of *Tragoportax rugosifrons* (A; HD 3702) and *Tragoportax cf. amalthea* (B; K3774). Scale bar=300  $\mu\text{m}$ .

browsers according to the first plane (Fig. 2). They plot with leaf browsers on the second plane of the PCA (Fig. 3). The third specimen plots with grazers. Given the small size of our sample ( $n=3$ ) it is difficult to infer if grazing was common for this taxon.

#### 4.2. Stable isotopes

Firstly, the lack of significant diagenetic alteration was tested by plotting  $\delta^{18}\text{Oc}$  versus  $\delta^{18}\text{Op}$  values following the methodology proposed in Zazzo et al. (2004) (Fig. 5). Fossil enamel samples plot very close to the empirical equilibrium line defined for modern mammals (Bryant et al., 1996; Iacumin et al., 1996). Moreover we found comparable oxygen isotope variabilities in carbonate and phosphate components from the same tooth. These results strongly suggest that neither  $\delta^{18}\text{Oc}$  nor  $\delta^{18}\text{Op}$ , and therefore the  $\delta^{13}\text{C}$

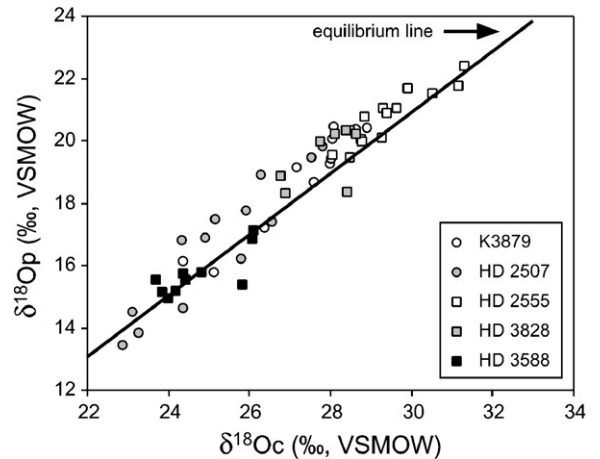


Fig. 5. Intra-tooth oxygen isotope composition of phosphate enamel ( $\delta^{18}\text{Op}$ ) reported as a function of the oxygen isotope composition of carbonate enamel ( $\delta^{18}\text{Oc}$ ) in Late Miocene boselaphini from Hadjidimovo-1 and Kalimantsi, Bulgaria. All samples plot close from the equilibrium line indicating that enamel oxygen isotope composition was not significantly altered.

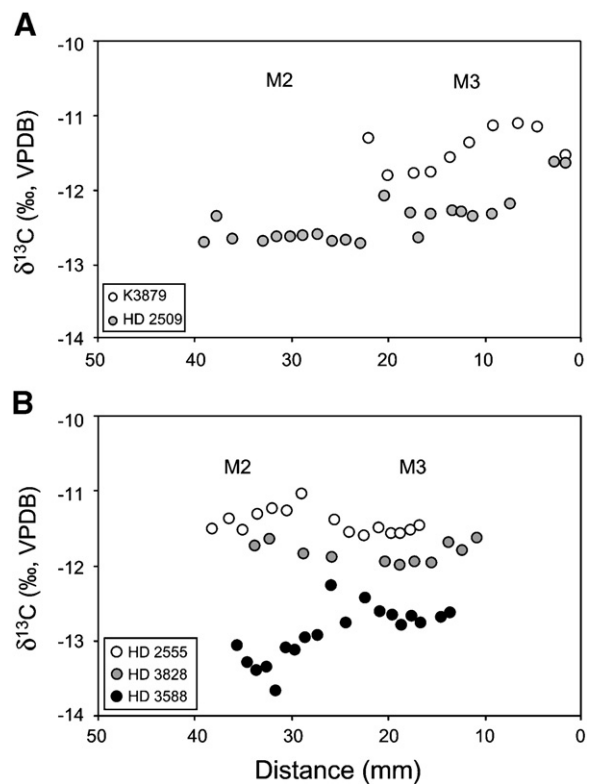


Fig. 6. Intra-tooth variations in carbon isotope composition ( $\delta^{13}\text{C}$ ) of *Tragoportax* (A) and *Miotragocerus gaudryi* (B) tooth enamel. Composite profiles are built assuming a 2 mm overlap between unworn m2 and m3 for *Tragoportax* and no overlap between unworn m2 and m3 for *Miotragocerus*. Isotope profiles for *M. gaudryi* were out of phase and were rescaled.

composition were significantly altered by diagenetic processes. Therefore stable isotope data can be interpreted as reflecting the primary environmental signal.

Individual values are plotted assuming that m2 forms before m3 with very little temporal overlap (0–2 mm) between the two teeth (Zazzo et al., 2002).  $\delta^{13}\text{C}$  values range from  $-11.0$  to  $-13.7\text{‰}$  and are indicative of a pure  $\text{C}_3$  diet for the two bovid taxa (Fig. 6). Small  $\delta^{13}\text{C}$  intra-individual variations were found ranging from  $0.4$  to  $1.4\text{‰}$  with no clear pattern of variation. On the contrary, large intra-tooth  $\delta^{18}\text{O}$  variations are observed in all specimens (Fig. 7). Distinct patterns are found between *Tragoportax* (Fig. 7A) and *Miotragocerus gaudryi* (Fig. 7B). Data for *Tragoportax* reveals sinusoidal variations, which we interpret as reflecting isotope seasonality. This pattern is characterized by a decrease in  $\delta^{18}\text{O}$  values from apex to cervix along the m2 and a bell-shaped pattern in m3, which reaches its maximum halfway up the tooth. The

wavelength is  $\sim 35$  mm, as estimated from one individual (HD 2507), implying that the vertical growth rate is  $\sim 3$  mm/month. This is slightly less than what was estimated for *Tragoportax* nov. sp. from Molayan (Zazzo et al., 2002). *M. gaudryi* exhibits a slightly distinct pattern, with decreasing  $\delta^{18}\text{O}$  values along the m2 and increasing  $\delta^{18}\text{O}$  values along the m3. We hypothesize that this difference could be explained by the fact that *M. gaudryi* m2–m3 require less than a complete year to form. This would be in keeping with the smaller size of the animal and lower crown height (Spassov and Geraads, 2004). Incomplete seasonal range recorded in *M. gaudryi* would also explain why intra-individual range in  $\delta^{18}\text{O}$  values remains consistently smaller than that recorded in *Tragoportax* from the same fossil site.

Little inter-individual difference in absolute  $\delta^{18}\text{O}$  values (less than  $1\text{‰}$ ) and intra-individual range (less than  $0.5\text{‰}$ ) were found between the two *Tragoportax* m3s at Kalimantsi and Hadjidimovo-1 (Fig. 7A). Large inter-individual differences in absolute  $\delta^{18}\text{O}$  values (more than  $4\text{‰}$ ) and intra-individual range (up to  $3\text{‰}$ ) were found between the three *M. gaudryi* specimens from Hadjidimovo-1 (Fig. 7B). Large inter-individual variability in *M. gaudryi* has another implication concerning the taphonomy. It suggests that dry years and those that were comparatively more humid are represented within the same quarry. Tooth wear suggests that the age at death was similar for the three specimens of *M. gaudryi*. Hence we conclude that the mode of carcass accumulation was likely not truly catastrophic and that the fossil specimens analyzed did not belong to one single herd.

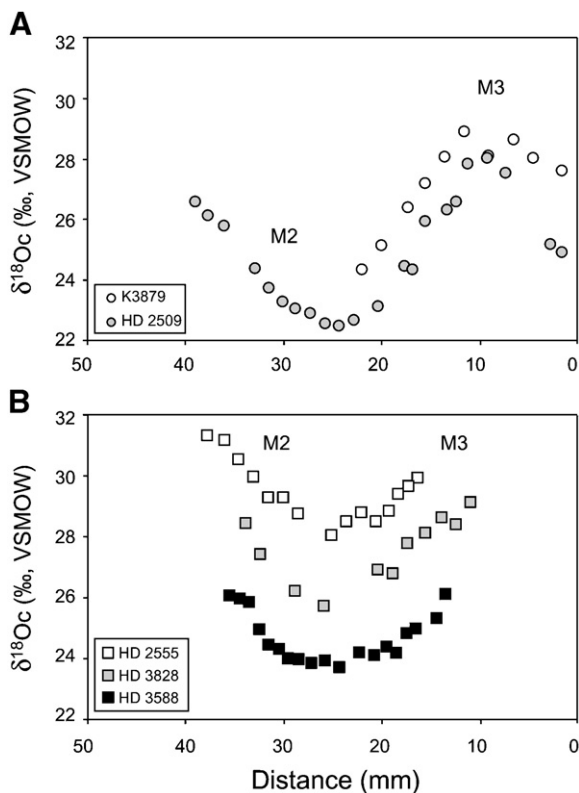


Fig. 7. Intra-tooth variations in oxygen isotope composition ( $\delta^{18}\text{O}$ ) of *Tragoportax* (A) and *Miotragocerus gaudryi* (B) tooth enamel. Composite profiles are built assuming a 2 mm overlap between unworn m2 and m3 for *Tragoportax* and no overlap between unworn m2 and m3 for *Miotragocerus*. Isotope profiles for *M. gaudryi* were out of phase and were rescaled.

## 5. Discussion

### 5.1. Boselaphini paleoecology

Hypotheses about the ecology and diet of the Late Miocene boselaphines *Tragoportax* and *Miotragocerus* (including *Pikermicetus* and *Dystyloceras*) have been based upon their preferential associations with other taxa, and upon their comparative anatomy. For instance, Bouvrain (1994) suggested that “*T. gaudryi*” (referred by us to *Miotragocerus*; see Material) lived in a more wooded environment, because it is more often associated with cervids and sometimes tragulids. Indeed, association of *Tragoportax sensu stricto* with the tragulid *Dorcatherium* is not common in Western Eurasia, and *Dorcatherium* is rare where they coexist (at Pikermi, Vathylakkos, Dityko) (Bonis and de Koufos, 1999). *Miotragocerus* is more often associated

with this tragulid, but most of the sites are Vallesian in age, and are located in Western Europe, so that it is difficult to decipher between chrono-geographical and ecological constraints. The two boselaphini taxa seldom co-occur in Europe at this time period. At Hadjidimovo-1 and Pikermi, they do co-exist, implying that they probably exploited different feeding resources within a same environment.

Enamel  $\delta^{13}\text{C}$  values are indicative of a pure  $\text{C}_3$  diet for both of these bovids. This result is not surprising considering the lack of significant  $\text{C}_4$  vegetation in Europe since the Miocene (Tieszen et al., 1979; Mateu Andrés, 1993; Quade et al., 1995). No discernable resource partitioning can be demonstrated between *Tragoportax* and *M. gaudryi* based on carbon isotope data, because intra-individual carbon isotope variability for *M. gaudryi* exceeds that observed between both genera. However, differences in inter-individual oxygen isotope variability between *Tragoportax* and *M. gaudryi* could be related to ecological differences. Large mammals (>100 kg) derive their water mostly from two sources: food and meteoric water. Water in plant roots and stems is isotopically similar to meteoric water, but leaf water is relatively enriched in  $^{18}\text{O}$  due to preferential evapotranspiration of the lighter  $^{16}\text{O}$  molecule (Gonfiantini et al., 1965; Dongmann et al., 1974; Epstein et al., 1977; Sternberg et al., 1989; Yakir, 1997). Therefore obligate drinkers are expected to have  $\delta^{18}\text{O}$  values depleted in  $^{18}\text{O}$  compared to mammals that derive most (or all) their water from plant sources (e.g. fruits, leaves). Grazing animals are often obligate drinkers, in part because grasses wither during the dry season, while many browsers are comparatively water-independent because leafy plants retain moisture and nutrients in all seasons (Ambrose, 1991). Indeed within a given ecosystem, Cerling et al. (1997) found that browsing giraffes are enriched in  $^{18}\text{O}$  compared with other herbivores, whereas hippopotamuses are significantly  $^{18}\text{O}$ -depleted (Bocherens et al., 1996). Likewise, Kohn et al. (1996) found that browsing and mixed-feeding herbivores tend to be enriched in  $^{18}\text{O}$  compared with grazing herbivores. Thus, according to its inter-individual  $\delta^{18}\text{O}$  variability, *M. gaudryi* could have been water-independent and relying on a browsing diet. Low inter-individual variability between *T. rugosifrons* and *T. cf. amalthea* suggests that the genus *Tragoportax* could have been an obligate drinker and hence a possible grass-eater (grazer or mixed feeder). However, this conclusion must be tempered by the very small sample size.

These results are supported by the dental microwear analysis on boselaphini of Hadjidimovo-1. In

fact, the dental microwear pattern of *M. gaudryi* specimens that have been analyzed for stable isotope analysis supports browsing habits. In the case of *T. rugosifrons*, the dental microwear analysis supports isotope inferences since this species grazed to a large degree. Microwear data indicates that *T. cf. amalthea* from Kalimantsi fed exclusively on dicotyledons before death. This hypothesis is consistent with oxygen stable isotope analysis, which demonstrates that this taxon probably fed on grasses. In fact, previous dental microwear analyses revealed mixed diet or grazing habits for *T. amalthea* in different eastern Tethysian Late Miocene localities (Solounias and Hayek, 1993; Merceron et al., 2004b, 2005b). Considering these large dietary preferences, the presence of an exclusive-leaf browsing population of *Tragoportax* in Kalimantsi is not surprising. Several hypotheses can explain this result: (1) taphonomic bias leading to an over-representation of the specimens browsing during dry seasons; (2) a strong pressure of competitors well adapted for grazing, such as *Ceratotherium*, *Hipparion mediterraneum* (evolved morph), which could push *Tragoportax* to exploit more browse; (3) a more wooded or bushy vegetation along the Struma valley than in the other eastern Tethys Turolian localities. The small sample size of *M. gaudryi* at Kalimantsi as well as large variations in its microwear pattern limits the dietary reconstruction based on dental microwear analyses. However, anatomical features and microwear analysis of *Tragoportax* and *M. gaudryi* from Hadjidimovo-1 support ecological partition between these species. For instance, tooth-rows of *T. rugosifrons* differ from *M. gaudryi* by their greater hypsodonty, relatively shorter premolar row, and more molarized p4 (Spassov and Geraads, 2004).

On the basis of stable isotope and microwear data, we assume that *M. gaudryi* has a faster dental growth and browsed more than *Tragoportax*. Our data suggests that both of the species of *Tragoportax* were engaged in both browsing and grazing. Considering its large range of feeding preferences, the genus *Tragoportax* could be a reliable palaeoenvironmental indicator.

## 5.2. Palaeoenvironmental implications

Assuming a 14‰ enrichment between food items and apatite (Cerling and Harris, 1997),  $\delta^{13}\text{C}$  value for the food source range from about  $-25$  to  $-27.5$ ‰ and are indicative of a 100%  $\text{C}_3$  diet for all boselaphini. This result is in keeping with the observed global pattern in which  $\text{C}_4$  biomass never became abundant in

Europe (Quade et al., 1994, 1995; Ehleringer et al., 1997). A number of studies have shown the distinction between  $C_3$  and  $C_4$  diets in fossil and modern herbivores, but little work has been done to study isotopic systematic in pure  $C_3$  environments (Franz-Odendaal et al., 2002; MacFadden and Higgins, 2004). Considering the  $\sim 1.5\%$  negative shift in the isotopic composition of the atmosphere in the last 150 years due to fossil fuel burning (Francey et al., 1999) these values are compatible with a “normal  $C_3$ ” ecosystem such as woodland or forest. They are not consistent with a diet derived from a closed canopy where the isotopic composition of the plants is shifted to more negative values and enamel  $\delta^{13}C$  values lower than  $-15\%$  are expected (Cerling et al., 2004). The presence of  $C_3$  dominated vegetation in the Turolian ecosystems in Bulgaria is consistent with the presence of  $C_3$  grasses and grass-like plants in this European region (Mateu Andrés, 1993). Because the presence of mixed feeders in both localities supports the presence of graminoids within a rich herbaceous layer, it also excludes the existence of a dense tree cover which would have limited the development of the herbaceous layer. This conclusion is in agreement with the carbon isotope data.

The dominance of open woodlands in Hadjidimovo-1 had been suggested by faunal analysis (Spassov, 2002). For instance, large size, long horns and sexual dimorphism of *Tragoportax* are perhaps slightly in favor of a more open habitat. Bouvrain (1994) described the outline of the premaxilla of *T. rugosifrons* from Vathylakkos as square, a feature that was found by Solounias and Dawson-Saunders (1988) to indicate grazing. However, from comparisons with modern forms, these authors classified boselaphini from Pikermi and Samos as browsers. Previous dental microwear analyses (Solounias and Hayek, 1993; Merceron et al., 2004b, 2005b) reconstruct *Tragoportax* as a grass-eater. This suggests that the skull morphology comparisons between extinct and extant antelopes may be biased because Late Miocene forms might simply not yet have evolved the derived features of present-day grass-eaters. Gentry (1974) found that the southern African boselaphini *Mesembriportax acrae* had relative lengths of long bones similar to those of the nilgai (*Boselaphus tragocamelus*) and the larger kudu (*Tragelaphus strepsiceros*), which could suggest an intermediate habitat showing the development of herbaceous, shrubby and bushy vegetation. However, Bouvrain (1994) noticed that the relative lengths of long bones of *T. rugosifrons* unambiguously point to a cursorial antelope. The size and proportions

of the metapodials of *T. rugosifrons* of Hadjidimovo-1 are similar to those of the wildebeest (*Connochaetes taurinus*), an open-country pure grazer (Spassov and Geraads, 2004, Tab. 3–4).

The ecological features of the Middle Turolian Kalimantsi faunal complex indicate a more advanced stage of the opening of tree cover, which agrees with faunal data (Spassov et al., in press). Such features of the Kalimantsi fauna include the more evolved *Hipparion* skull and teeth morphology towards grazing adaptation (Hristova and Kovachev, 2005), the lack of some forested elements existing in Hadjidimovo-1 like tapirs and cervids, and among rhinos, the dominance of *Ceratotherium*, a relative of the living white rhino (Geraads, Spassov, Kovachev, unpublished data).

While faunal and ecomorphological analyses suggest an opening of the tree cover in southwestern Bulgaria during the Turolian, the browsing habits of *T. cf. amalthea* would rather suggest the abundance of bushes and shrubs in the Kalimantsi surroundings. However, the mixed feeders (*Gazella* sp. and *P. lindermayeri*) demonstrate the presence of an abundant herbaceous vegetation, which excluded a dense tree cover. This suggests herbaceous, grassy and bushy vegetation in the Kalimantsi surroundings.

In spite of the presence of grass-eaters in both localities, African-like savanna environments should not be expected in Bulgaria during the Late Miocene. The African  $C_4$ -grasslands result from a specific co-evolution model between vegetation and herbivorous guild (Mac Naughton et al., 1985) that never happened in Eurasia. The dental microwear patterns of *T. rugosifrons*, as well as *Gazella* sp. and *P. lindermayeri* from both localities have more fine scratches than the present-day African mixed feeders. This may be due to the consumption of  $C_3$  graminoids whose silica deposits are less abundant than in  $C_4$  grasses (Twiss, 1986; Lanning and Eleuterius, 1989).

The presence of an herbaceous layer and the abundance of  $C_3$  graminoids are also supported by recent preliminary investigations on phytolith assemblages from sediments, which demonstrate the abundance of  $C_3$  graminoids in the eastern Mediterranean during the Late Miocene (Strömberg and Werdelin, 2004).

## 6. Conclusion

Carbon stable isotope analyses on boselaphini indicate a pure  $C_3$  environment in southwestern Bulgaria during the Early and Middle Turolian. Stable oxygen isotope analyses allow the ecology of these

boselaphini to be discerned, since *Tragoportax* may have been obligate drinkers in opposition to *Miotragocerus*. This should imply a diet more concentrated in graminoids for *Tragoportax*. This is consistent with dental microwear analysis on boselaphini of Hadjidi-movo-1, where *T. rugosifrons* fed mostly on grasses while *M. gaudryi* was a leaf browser. The population of *T. cf. amalthea* from Kalimantsi was only composed of specimens that browsed. However, these results agree with stable oxygen isotope analyses when all Eastern Tethysian populations of *Tragoportax amalthea* are plotted as a whole. In this case, *T. cf. amalthea* appears to have been a mixed feeder, which accommodated its diet depending on local conditions. Both isotopic and microwear analyses corroborate and specify hypotheses based on faunal analysis. Data demonstrates the presence of a rich herbaceous layer, which excludes undoubtedly dense forested habitats in both localities. Based on dental microwear analysis, the opening of landscapes throughout the Early and Middle Turolian seems to be non-existent or at least less important than faunal studies had suggested. This apparent contradiction invite us to include other taxa in the multi proxy approach combining microwear and stable isotope in order to characterize in objective ways the dynamics of

vegetation, and by implication of past environments in southwestern of Bulgaria in parallel with the eustatic Mediterranean fluctuations.

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### Appendix A

Summary statistics (mean  $m$  and standard error of the mean  $sem$ ) of dental microwear variables for extant species from the “UNGULATES” database. % p Percentage of pits, number of scratches  $N_s$ , of wide scratches  $N_{ws}$ , of fine scratches  $N_{fs}$ , number of pits  $N_p$ , of large pits  $N_{lp}$ , and of small pits  $N_{sp}$ .

Diet categories <sup>1</sup> and species	N	% p (%)		$N_s$		$N_{ws}$		$N_{fs}$		$N_p$		$N_{lp}$		$N_{sp}$	
		$m$	$sem$	$m$	$sem$	$m$	$sem$	$m$	$sem$	$m$	$sem$	$m$	$sem$	$m$	$sem$
Leaf browsers	28	68.4	3.4	15.5	1.2	0.8	0.3	14.8	1.3	38.1	7.2	5.4	1.2	32.7	6.2
<i>Tragelaphus strepsiceros</i>	8	66.6	3.9	14.9	1.5	0.6	0.3	14.3	1.4	31.9	4.5	4.5	0.8	27.4	3.8
<i>Boocerus euryceros</i>	4	71.9	4.1	16.6	1.7	0.8	0.5	15.9	2.0	48.0	12.3	5.0	1.5	43.0	11.2
<i>Litocranius walleri</i>	16	66.6	2.4	15.1	0.6	0.9	0.2	14.2	0.5	34.5	4.9	6.8	1.4	27.7	3.7
<i>Giraffa camelopardalis</i>	16	64.0	3.4	15.1	1.3	0.8	0.3	14.3	1.3	29.3	3.7	4.0	0.7	25.3	3.2
Leaf/fruit browsers	231	59.8	4.7	22.8	2.2	1.1	0.4	21.7	2.3	36.7	4.6	5.4	1.1	31.3	4.0
<i>Tapirus</i> sp.*	7	66.4	5.5	19.9	2.4	1.3	0.4	18.6	2.4	42.4	6.3	5.1	1.7	37.3	6.0
<i>Diceros bicornis</i>	10	66.0	4.8	17.7	1.9	1.2	0.5	16.5	1.8	39.5	6.0	6.1	1.1	33.5	5.2
<i>Gazella soemmerringi</i>	20	67.2	2.8	19.4	1.7	0.5	0.2	18.9	1.7	41.2	3.0	9.0	1.1	32.2	3.0
<i>Odocoileus virginianus</i>	11	60.1	4.0	19.9	1.8	1.2	0.3	18.7	1.7	31.1	3.3	5.8	1.5	25.3	2.1
<i>Mazama americana</i>	6	52.9	8.5	23.3	3.4	1.3	0.6	22.0	3.5	28.8	6.6	4.7	1.3	24.2	5.5
<i>Muntiacus muntjak</i>	8	64.4	3.5	28.0	2.7	0.8	0.3	27.3	2.6	51.1	3.9	4.0	0.8	47.1	3.6
<i>Moschus moschiferus</i>	3	37.4	11.6	34.0	5.0	1.0	1.0	33.0	6.0	21.3	7.8	3.0	1.7	18.3	6.4
<i>Capreolus capreolus</i>	128	58.8	1.0	21.8	0.6	1.0	0.1	20.7	0.6	32.6	1.1	4.8	0.2	27.8	1.0
<i>Sylvicapra grimmia</i>	24	63.5	2.4	20.9	1.2	1.1	0.2	19.9	1.1	39.1	3.1	6.0	0.8	33.1	2.6
<i>Cephalopus</i> sp.*	14	61.6	2.9	22.9	1.6	1.5	0.5	21.4	1.7	40.0	5.1	5.9	1.1	34.1	4.3
C <sub>3</sub> grazer															
<i>Equus przewalskii</i>	6	27.2	2.7	29.8	1.5	0.6	0.3	29.2	1.4	11.7	2.1	2.2	0.6	9.5	1.6

\**Tapirus* sample (*T. terrestris* N=5; *T. bairdi* N=2); *Cephalopus* sample (*C. sylvicultror* N=8; *C. dorsalis* N=1; *C. leucogaster* N=3; *C. callypigus* N=2).

## Appendix A (continued)

Species	N	% p (%)		N <sub>s</sub>		N <sub>ws</sub>		N <sub>fs</sub>		N <sub>p</sub>		N <sub>lp</sub>		N <sub>sp</sub>	
		m	sem	m	sem	m	sem	m	sem	m	sem	m	sem	m	sem
C <sub>4</sub> grazers	139	35.4	3.3	24.9	1.8	1.9	0.4	23.0	1.8	15.0	2.5	3.1	0.6	11.9	2.2
<i>Equus</i> sp.* “Zebra”	9	28.9	3.6	20.8	1.2	2.1	0.6	18.7	1.5	9.4	2.0	3.6	0.7	5.9	1.8
<i>Ceratotherium simum</i>	2	33.7	7.1	25.5	3.5	0.5	0.5	25.0	3.0	14.0	6.0	0.0		14.0	6.0
<i>Alcelaphus buselaphus</i>	28	37.1	1.7	26.0	0.8	1.5	0.3	24.5	0.9	16.3	1.4	3.5	0.5	12.9	1.2
<i>Damaliscus lunatus</i>	14	33.7	2.6	22.6	1.4	1.5	0.4	21.1	1.4	12.7	1.9	3.9	0.6	8.9	1.7
<i>Hippotragus niger</i>	13	32.3	2.9	27.7	1.1	2.8	0.4	24.8	1.4	14.2	2.0	4.0	1.0	10.2	1.7
<i>Kobus kob</i>	26	37.4	2.3	26.3	0.9	2.7	0.3	23.6	0.9	16.9	1.5	3.9	0.5	13.0	1.3
<i>Ourebia ourebi</i>	18	44.2	4.2	22.8	1.1	1.8	0.4	20.9	1.2	20.9	3.1	2.8	0.5	18.0	2.8
<i>Syncerus caffer</i>	24	33.8	1.9	24.6	1.4	2.6	0.3	22.0	1.5	13.3	1.3	3.7	0.3	9.6	1.2
<i>Redunca redunca</i>	5	37.8	3.0	28.2	4.5	1.6	0.5	26.6	4.6	17.4	3.0	2.8	0.7	14.6	2.6
Seasonal mixed feeders	41	53.2	3.8	21.1	1.5	1.9	0.4	19.3	1.6	25.5	3.8	6.0	1.0	19.6	3.2
<i>Aepyceros melampus</i>	19	45.2	2.9	24.9	1.4	1.4	0.3	23.5	1.4	22.1	2.8	5.6	0.7	16.5	2.3
<i>Tragelaphus scriptus</i>	18	56.2	2.6	18.2	1.6	1.7	0.5	16.5	1.4	24.3	2.7	8.3	1.0	16.0	2.1
<i>Taurotragus oryx</i>	4	58.3	6.0	20.3	1.7	2.5	0.5	17.8	2.1	30.3	6.0	4.0	1.4	26.3	5.2
Generalist mixed feeders	84	61.0	6.2	26.7	3.6	1.0	0.4	25.7	3.7	46.7	7.0	6.1	1.3	40.5	6.1
<i>Rangifer tarandus</i>	17	69.4	3.2	24.4	2.8	1.2	0.4	23.2	2.7	55.8	4.2	6.4	0.9	49.5	4.2
<i>Cervus elaphus</i>	47	56.7	1.7	26.4	0.9	1.4	0.2	24.9	0.9	36.9	2.2	5.5	0.5	31.4	1.9
<i>Rupicapra rupicapra</i>	9	57.2	5.4	28.3	3.2	1.2	0.4	27.1	3.4	40.7	6.0	6.2	1.1	34.4	5.4
<i>Saiga tatarica</i>	2	63.5	11.5	27.5	7.5	0.5	0.5	27.0	8.0	49.0	11.0	5.5	1.5	43.5	9.5
<i>Ovis ammon</i>	9	58.3	9.1	27.0	3.7	0.7	0.2	26.3	3.6	50.9	11.7	7.1	2.8	43.8	9.6
<i>Ovibos moschatus</i>	3	66.6	11.0	24.7	6.7	1.0	0.6	23.7	7.3	54.0	17.9	6.7	2.7	47.3	15.2

\**Equus* sp. “Zebra” sample (*E. burchelli* N=8, *E. grevyi* N=1).

<sup>1</sup>(Vesey-Fitzgerald, 1960, 1965; Wilson, 1966; Stewart and Stewart, 1970; Bell, 1971; Groves, 1972; Thomson, 1973; Grobler, 1974; Montfort and Montfort, 1974; Sokolov, 1974; Vesey-Fitzgerald, 1974; Sinclair, 1977; Leuthold, 1978, Leuthold, 1978; Ralls, 1978; Grubb, 1981; Lumpkin and Kranz, 1984; Stallings, 1984; Branan and Marchinton, 1985; Shackleton, 1985; Hillman, 1986; Mac Naughton and Georgiadis, 1986; Lent, 1988; Bowyer and Leslie, 1992; Murray, 1993; Oleffe et al., 1993; Hillman-Smith and Groves, 1994; Jong et al., 1995; Heroldova, 1996; Tixier and Duncan, 1996; Kingdon, 1997; Ramirez et al., 1997; Pereladova et al., 1999; Gagnon and Chew, 2000; Ihl and Klein, 2000; Mysterud, 2000; Cransac et al., 2001; Fedosenko and Weinberg, 2001; Gebert and Verheyden-Tixier, 2001; Blake, 2002; King, 2002; Awasthi et al., 2003; Bugalho and Milne, 2003; Namgail et al., 2004).

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