

华北晚中新世羚羊的食性与古环境 ——稳定碳同位素的证据

Benjamin H. PASSEY¹ Jussi T. ERONEN² Mikael FORTELIUS² 张兆群³

(1 美国犹他大学地质与地球物理系 盐湖城 84112)

(2 芬兰赫尔辛基大学地质系 赫尔辛基 FIN-00014)

(3 中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要:通过分析华北晚中新世保德期三个经典地点的羚羊牙齿釉质之稳定碳同位素,结合相同地点的单纯食叶者(鹿科)与食草者(三趾马)的数据,推断其食性取向。结果显示这些晚中新世生态系统中C₃植物占据主导地位,但也含有一小部分的C₄植物(可能小于30%)。高冠羚羊(*Gazella dorcadoides*类型)取食约20%的C₄植物,而中冠羚羊(*G. paotehensis*类型)与低冠羚羊(*G. gaudryi*类型)为纯C₃植物消费者。鹿科动物单纯取食C₃植物,而三趾马与*G. dorcadoides*类型的羚羊取食C₄植物的比例在统计上难以区分。碳同位素数据与*G. gaudryi*类型的食叶性以及*G. dorcadoides*类型以草食为主的观点相一致。参照这些类群的地理分布,当前的数据支持晚中新世黄土高原东南部处于相对于西北部更为封闭环境的观点。这种环境梯度的分布方向与模式可能是该地区东亚季风体系的早期信号。

关键词:华北,晚中新世,羚羊,碳同位素,食性

中图法分类号:Q915.5 文献标识码:A 文章编号:1000-3118(2007)02-0118-10

PALEODIETS AND PALEOENVIRONMENTS OF LATE MIOCENE GAZELLES FROM NORTH CHINA: EVIDENCE FROM STABLE CARBON ISOTOPES

Benjamin H. PASSEY^{*1} Jussi T. ERONEN² Mikael FORTELIUS² ZHANG Zhao-Qun³
(1 Department of Geology and Geophysics, University of Utah Salt Lake City, UT 84112, USA *corresponding author: passey@earth.utah.edu)

(2 Department of Geology, University of Helsinki Helsinki, P. O. Box 64, FIN-00014, Finland)

(3 Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing, 100044, China)

Abstract We use carbon isotopes in fossil tooth enamel to infer dietary preferences in Baodean (Late Miocene) gazelles from three classical localities in North China, along with putative browsers (Cervidae) and grazers (*Hipparion*) from the same localities. The results suggest that these Late Miocene ecosystems were dominated by C₃ vegetation, but contained a small fraction of C₄ vegetation (probably less than ~30%). We find that the higher-crowned gazelles (*Gazella dorcadoides*-type) consumed up to ~20% C₄ plants, whereas *G. paotehensis*-type gazelles (intermediate crown-height forms) and *G. gaudryi*-type gazelles (low-crowned forms) had essentially pure C₃ diets. Cervidae consumed pure C₃ vegetation, while *Hipparion* consumed some C₄ vegetation and is statistically indistinguishable from *G. dorcadoides*-type gazelles. The carbon isotope data are consistent with a primarily browsing diet in *G. gaudryi*-type

gazelles, and a larger fraction of graze in the diet of *G. dorcadoides*-type gazelles. Taken with the distributions of these taxa, the data support the established concept of relatively closed habitats in the south-east CLP (Chinese Loess Plateau) compared to the northwest CLP during the Late Miocene. The direction and pattern of this environmental gradient may be an early signature of the East Asian Monsoon system in this region.

Key words North China, Late Miocene, *Gazella*, carbonate isotope, paleodiet

1 Introduction

During the early part of the 20th century, extensive collections were made of fossil mammal faunas from the *Hipparion* red clay in the loess plateau of North China. The fossils came from dozens of localities (Fig. 1), many of which were ‘dragon bone’ mines from which fossils were extracted for traditional medicinal use. These often occurred in rich fossiliferous ‘pockets’ (Zdansky, 1923; see English translation by Jokela et al., 2005), with generally well-preserved and abundant material, much of which may represent instantaneous or accumulated mass death assemblages (Kurtén, 1952).

Workers suggested early on (Schlosser, 1903) that these localities could be separated into those with a forest-like faunal aspect, primarily located in the south, and those with steppe-like faunal aspects, located northward. Among others, Kurtén (1952) fully and classically developed these ideas, and further identified the geographic separation as a southeast to northwest pattern (Fig. 1) similar to the modern distribution of summer monsoon rainfall and the northwestward transition in North China from forest to steppe, and ultimately desert environments. These ideas are generally accepted today (e.g., Fortelius et al., 2002; Zhang, 2006) and are supported by independent proxy data such as plant macro- and micro-fossils (Sun and Wang, 2005).

The forest-like faunas in the southeast typically contain abundant deer, other presumed browsers like the giraffid *Honanotherium*, and the relatively low-crowned *Gazella gaudryi*. Kurtén (1952) termed these ‘gaudryi faunas’ and referred to localities with such faunas as ‘gaudryi localities’. The steppe-like faunas in the northwest typically contain higher-crowned forms such as the rhinocerotid *Chilotherium*, the ovibovoid *Urmiatherium*, and *Gazella dorcadoides*, and were termed by Kurtén ‘dorcadoides faunas’ and ‘dorcadoides localities’. Kurtén further recognized localities with elements of both types, which were termed ‘mixed localities’. Localities in the southeastern CLP are exclusively ‘gaudryi’ localities, whereas those in the northwest region near Baode are both ‘dorcadoides’ and ‘mixed’ localities (Fig. 1). Kurtén suggested that this region marked a transitional zone between two major ecological provinces, forest to the southeast and steppe to the northwest, with spatial ecological heterogeneity or a shifting boundary in time, or both, giving rise to the occurrence of both types of faunas.

This paper seeks to evaluate two related questions. First, do isotope data support the notion that the higher-crowned *G. dorcadoides* consumed more grass than the lower-crowned *G. gaudryi*? Second, are isotope data consistent with the idea of more humid, forested environ-

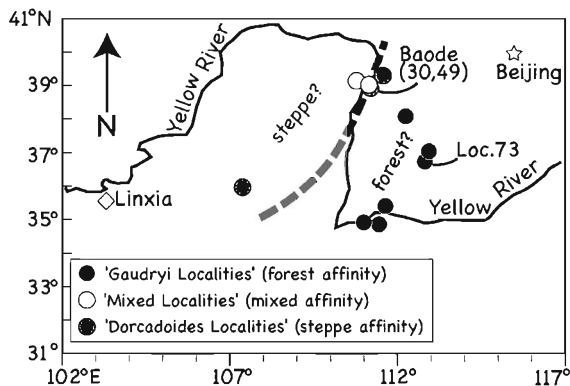


Fig. 1 Map showing study area and distribution of ‘gaudryi’, ‘mixed’, and ‘dorcadoides’ localities (after Kurtén, 1952)

ments to the southeast, and more arid, steppe-like environments to the northwest? In addition, are we able to address the question of whether the global Late Miocene C_4 vegetation expansion (Cerling et al., 1997) influenced North China. To answer these questions, we use carbon isotopes and focus on gazelles, equids, and cervids from three classic localities: Locality 30, a 'dorcadoides-type' locality near Baode, Shanxi Province; Locality 49, a 'mixed-type' locality also located near Baode, and Locality 73, a 'gaudryi-type' locality located near Wuxiang, Shanxi Province (Fig. 1).

Carbon isotopes reveal the extent to which an animal fed on plants using the C_3 photosynthetic pathway versus plants using the C_4 pathway. This is useful for paleodietary studies, because nearly all browse plants (e. g., trees, shrubs, and forbs) use the C_3 pathway, whereas graze plants (grasses, sedges) use either the C_3 or C_4 pathway. Within the graze plants, there is a very strong correlation between the percentage of species using the C_4 pathway, and growing-season (= rainy season) temperature, with higher temperatures favoring C_4 grasses (Ehleringer et al., 1997). Further, a very small fraction of browse plants utilize the C_4 pathway, less than 5% of species in most ecosystems, and these are more predominant in arid ecosystems. In continental Asian deserts, C_4 dicots in the families Chenopodiaceae and Polygonaceae may comprise a larger fraction of plant biomass (Pyankov et al., 2000).

Therefore, if there truly was a southeast-northwest environmental gradient in North China during the Late Miocene, such that habitats to the northwest were relatively open compared to those to the southeast, we might expect a minimized grazing potential in the southeast and C_3 -based diets in most herbivorous mammals there. Forest giving way to steppe to the northwest would permit more grazing, and if C_4 grasses were environmentally favored (e. g., due to warm rainy seasons, or sufficiently low atmospheric CO_2), we might expect a C_4 isotope signal in grazing herbivores, and possibly even in browsing herbivores eating C_4 dicots that are a minor component of some arid ecosystems. It should be stressed, however, that carbon isotopes cannot distinguish between C_3 grasses and C_3 browse. Therefore, findings such as those outlined above would support the concept of such an environmental gradient, but would not prove the existence thereof.

2 Methods

2.1 Fossil material

We analyzed fossil material housed in the Lagrelius Collection at the Museum of Evolution, Uppsala University, Sweden. At each locality, we analyzed *Gazella* specimens, along with *Hipparion* and Cervidae material. The latter two were sampled to provide putative grazing and browsing reference points that the *Gazella* results could be compared with. The Cervidae material includes specimens labeled as "Pliocervid" and *Cervocerus novorossiae* (= *Cervavitus novorossiae*).

Gazelles from the Late Miocene of north China are in need of revision and correlation with other Eurasian species. For this study we utilized the most recent assignments of the material in the Lagrelius collection, and grouped them into 3 'types' following Kurtén (1952). The '*G. gaudryi*-type' consists of specimens identified as *G. gaudryi* (Schlosser, 1903) and *G. sp.* (aff. *gaudryi*) (Bohlin, 1935). The '*G. paotehensis*-type' consists of those identified as *G. sp.* (? *paotehensis*) (Teilhard de Chardin and Young, 1931). Finally, the '*G. dorcadoides*-type' consists of those identified as *G. dorcadoides* (Schlosser, 1903) and *G. sp.* (? *dorcadoides*). The assignments utilized here are those from placards associated with the specimens when we sampled them during June 2005. We proceed with these assignments, recognizing that future revision may improve the results of the present study.

Kurtén (1952) reported tooth crown height measurements of gazelles in each group, and

the results are recast here in Fig. 2. Because we have access only to the average, standard deviation, and range of the data measured by Kurtén (1952), we do not perform statistical analysis of these data. However, on the basis of computing means and variances, Kurtén (1952) considered the difference in m3 height to be ‘certainly’ significant between *G. dorcadoides*- and *G. gaudryi*-types, ‘almost certainly’ significant between *G. dorcadoides*- and *G. paotehensis*-types, and ‘probably’ significant between *G. gaudryi*- and *G. paotehensis*-types (Kurtén, 1952:64). Visual inspection of the data in Fig. 2 largely supports these conclusions.

2.2 Stable isotope methods

The isotope delta (δ) notation is defined as, in the case of carbon isotopes, $\delta^{13}\text{C} = (R_s/R_{st} - 1) \times 1000$, where R_s is the $^{13}\text{C}/^{12}\text{C}$ ratio of the sample, and R_{st} is the $^{13}\text{C}/^{12}\text{C}$ ratio of a standard. Here the standard is PDB, and the carbon data are reported on the PDB scale. The units of δ are per mil (‰), which is essentially equivalent to parts per thousand deviation from the standard.

Enamel samples were removed from teeth by grinding with a diamond-impregnated drill bit and collecting the resulting powder over weighing paper. Samples were pretreated with 3% H_2O_2 and 0.1 M CH_3COOH buffer solution for 15 minutes each, with each step followed by several rinses in deionized water. Samples were reacted at 90°C in a common acid bath device, and the resulting CO_2 was analyzed in dual-inlet microvolume mode using a Finnigan MAT 252 mass spectrometer. All data were normalized to NBS-19 ($\delta^{13}\text{C} = 1.95\text{‰}$ PDB).

To calculate the percent C_4 vegetation in diet, we follow Passey et al. (2002) and use marine planktonic foraminifera data to estimate the $\delta^{13}\text{C}$ value of ancient atmospheric CO_2 . Data from Pagani et al. (1999) suggests a value for Late Miocene atmospheric CO_2 of $\sim -5.5\text{‰}$, using the foraminifera – atmospheric CO_2 fractionation factors discussed in Passey et al. (2002). Combined with fractionations between CO_2 and biomass of -16.7‰ and -4.7‰ for C_3 and C_4 plants, respectively, this gives end member values of -22.1‰ (C_3) and 11.4‰ (C_4) for Late Miocene vegetation. We use an enamel-diet fractionation of 14‰ (Cerling and Harris, 1999; Passey et al., 2005). Thus, a pure C_3 end member diet should be -8.4‰ , and a pure C_4 diet 3.7‰ , and we assume a linear mixing model such that $\% \text{C}_4 = 8.26 \times \delta^{13}\text{C} + 69.8$. These estimates are conservative, and should be viewed as the minimum possible fraction of C_4 vegetation in diet for each given $\delta^{13}\text{C}$ value.

2.3 Statistical approach

Our sample sizes are relatively small, and we utilize parametric and non-parametric statistics at the $\alpha = 0.05$ level. We use the unpaired t-test and Mann-Whitney test ($k=2$, where k is the

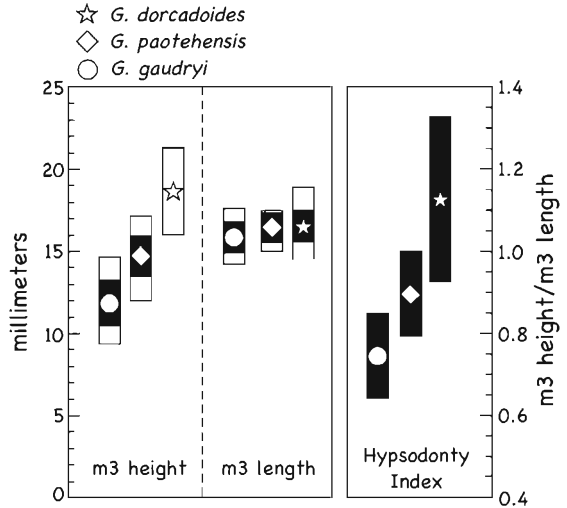


Fig. 2 Tooth crown heights and lengths, and hypsodonty index, for third lower molars of Baodean gazelles. The open circles, open diamonds, and stars show the mean values for *G. gaudryi*-type, *G. paotehensis*-type, and *G. dorcadoides*-type gazelles, respectively; the gray boxes show the standard deviation, and the white boxes show the total range of different individuals (data from Kurtén, 1952)

number of taxa being compared), or ANOVA followed by Fisher's PLSD, and the Kruskal-Wallis test followed by Dunn's Method ($k > 2$), to determine significant differences between and among populations. In the following discussions, we refer to pairs of samples as 'significantly different' when p-values are less than 0.05 for both the parametric and non-parametric tests, and 'likely different' when p-values are less than 0.05 for one of the tests.

3 Results

3.1 General ecosystem carbon isotope signal

Isotope data are reported in Table 1, and illustrated in Fig. 3. Carbon isotopes indicate C_3 -based diets for all taxa, ranging from pure C_3 vegetation for all cervids, *G. gaudryi*-type, and *G. paotehensis*-type gazelles, to 0 – 18% C_4 vegetation for *G. dorcadoides*-type gazelles, and 0 – 33% C_4 vegetation for *Hipparion*. While animal diets do not necessarily record the average photosynthetic pathway of biomass in an ecosystem, they are usually a good indicator of the dominant vegetation types. To this extent, the carbon isotope results suggest C_3 -dominated ecosystems in this region during the Late Miocene, complemented by a small but significant fraction of C_4 vegetation.

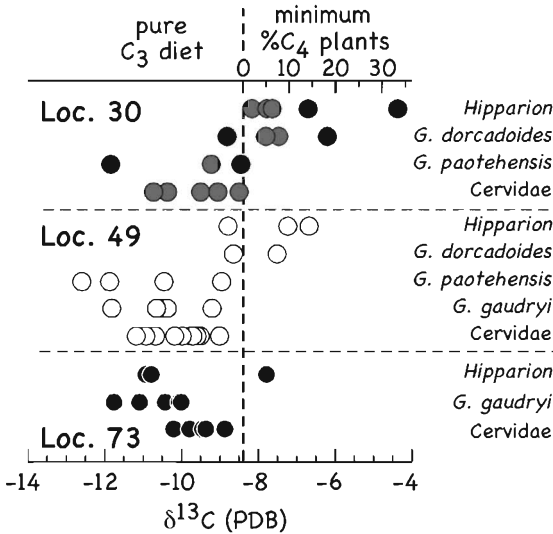


Fig. 3 Carbon isotope values of gazelles, cervids, and *Hipparion* from Localities 30, 49, and 73

3.2 Isotopic variation as a function of locality

Hipparion was sampled at each of the three localities, and has statistically indistinguishable carbon isotope values at Localities 30 and 49. ANOVA followed by Fisher's PLSD suggests a significant difference between Localities 30 and 73, while the non-parametric Kruskal-Wallis test indicates no difference. Therefore *Hipparion* likely consumed more C_4 vegetation at Localities 30 and 49 compared to Locality 73, but more data are needed to confirm this result. Cervids show no carbon isotope differences across the localities, and have $\delta^{13}C$ values consistent with pure C_3 diets at each. *G. dorcadoides*-type gazelle data are from Localities 30 and 49 only, suggest a minor component of C_4 vegetation in the diet at each, and display

no significant difference between the localities. *G. paotehensis*-type gazelles likewise were sampled at Localities 30 and 49 only. Carbon isotope values suggest pure C_3 diets, and do not differ significantly between the two localities. *G. gaudryi*-type gazelles, sampled at Localities 49 and 73, also have carbon isotope ratios consistent with a pure C_3 diet, and do not differ between localities. Therefore, with the possible exception of *Hipparion*, these taxa consumed the same relative proportions of C_3 and C_4 vegetation regardless of locality.

3.3 Isotopic variation as a function of taxonomy

There are a number of significant carbon isotope differences among taxa when all localities are considered together (Table 2). *Hipparion* and *G. dorcadoides*-type gazelles both consumed a measurable but small fraction of C_4 vegetation and are statistically indistinguishable. In contrast,

Table 1 Stable isotope compositions of Baodean fossil mammals

Taxon	Sample ID	material ¹⁾	$\delta^{13}\text{C}$	$\% \text{C}_4$ ²⁾	Taxon	Sample ID	material ¹⁾	$\delta^{13}\text{C}$	$\% \text{C}_4$ ²⁾
Locality 30 – “dorcadooides”					Locality 49 – “mixed”, continued				
<i>Gazella dorcadooides</i>	M11487	R m3	-8.8	0	<i>H. hippidioides</i>	M256	cheek	-7.3	10
	M11490	L M3	-7.5	8	<i>H. plocodus</i>	M263	L DP2	-6.7	15
	M11493	R P4	-7.8	5	<i>H. platyodus</i>	M3824	L p2	-8.8	0
	M11502	L M3	-6.2	18	<i>Cervavitus novorossiae</i>	M9136	L m3	-9.5	0
	mean		-7.6 ± 1.1			M9143	L M3	-10.0	0
<i>G. sp. (? paotehensis)</i>	M11320	L m3	-11.9	0		M9144	R M2	-9.6	0
	M11345	R m3	-8.5	0		M9146	R m2	-11.2	0
	M11344	R m3	-9.3	0		mean		-10.1 ± 0.8	
	mean		-9.9 ± 1.8		Pliocervid indet.	M9790	R M3	-9.8	0
Pliocervid indet.	M9826	R m3	-9.5	0		M9791	L M3	-9.8	0
	M9820	L m3	-10.4	0		M9798	L M3	-9.7	0
	M9813	R M3	-8.5	0		M9799	R M3	-10.2	0
	M9824	R m3	-9.1	0		M9802	L M3	-10.7	0
	M9828	R m3	-10.7	0		M992	L m3	-10.9	0
	mean		-9.7 ± 0.9			M993	L m3	-9.0	0
<i>Hipparion fossatum</i>	M304	L P2	-7.8	5		mean		-10.0 ± 0.6	
	M303	L M3	-4.4	33	Locality 73 – “gaudryi”				
	M3822	R m3	-7.7	6	<i>G. gaudryi</i>	M11185	L M3	-10.0	0
	mean		-6.6 ± 1.9			M11189	R M3	-11.1	0
<i>H. platyodus</i>	M343	L m3	-6.7	14		M11196	R m3	-11.8	0
<i>H. ptychodus</i>	L30 Hipp-3	cheek	-8.2	2		M11197	R m3	-10.4	0
						M11202	R m3	-10.1	0
						mean		-10.7 ± 0.7	
Locality 49 – “mixed”					<i>H. ptychodus</i>	M350	R P2	-7.8	5
<i>G. dorcadooides</i>	M11473	R M3	-8.7	0		M352	CHEEK	-10.9	0
	M11480	R M1	-7.5	8		M354	unknown	-10.8	0
<i>G. sp. (? paotehensis)</i>	M11327	L M3?	-11.9	0		mean		-9.8 ± 1.8	
	M11328	L M3	-9.0	0	<i>C. novorossiae</i>	M9444	R M3	-10.2	0
	M11331	L m3	-10.5	0		M9445	L M3	-8.9	0
	M11332	R m3	-12.6	0		M9452	L M3	-9.5	0
	mean		-11.0 ± 1.6			M9455	L M3	-9.8	0
<i>G. gaudryi</i>	M11264	R M3	-9.2	0		M9457	R M3	-9.4	0
	M11269	L m3	-10.5	0		mean		-9.6 ± 0.5	
	M11270	R m3	-11.8	0					
	M11271	R M3	-10.4	0					
	M11275	L m3	-10.7	0					
	mean		-10.5 ± 0.9						

Note: $\delta^{13}\text{C}$ values are relative to PDB ± values given as 1 σ .

1) R, L, right and left, respectively; m, p, lower molar and premolar; M, P, upper molar and premolar; cheek, CHEEK, lower and upper cheek teeth; D, deciduous.

2) Minimum estimate of the percent C_4 vegetation in diet. See Methods section.

Hipparion consumed significantly more C_4 vegetation than did *G. paotehensis*-type and *G. gaudryi*-type gazelles, and likely consumed more than the cervids. Likewise, *G. dorcadooides*-type ga-

zelles consumed significantly more C_4 vegetation than all of the other taxa exclusive of *Hipparion*. There are no significant carbon isotope differences among *G. paotehensis*-type, *G. gaudryi*-type, and cervidae.

Table 2 Significant differences between taxa ($\alpha=0.05$) for all localities grouped together

$\delta^{13}C$	<i>Hipparion</i>	<i>G. dorcadoides</i>	<i>G. paotehensis</i>	<i>G. gaudryi</i>
<i>Hipparion</i>	–			
<i>G. dorcadoides</i>	ns	–		
<i>G. paotehensis</i>	a, b	a, b	–	
<i>G. gaudryi</i>	a, b	a, b	ns	–
Cervidae	a	a, b	ns	ns

Note: a. Taxa are significantly different based on ANOVA followed by Fisher's PLSD.

b. Taxa are significantly different based on Kruskal-Wallis followed by Dunn's method.

ns. not significantly different according to either method.

When localities are considered individually (Table 3), the same general patterns are observed according to ANOVA followed by Fisher's PLSD, whereas the nonparametric Dunn's method rarely indicates significant differences between pairs of species, despite the fact that the Kruskal-Wallis test often suggests that significant differences exist. In particular, this is true of the differences between *Hipparion* and *G. paotehensis*-type, *G. gaudryi*-type, and Cervidae, and of the differences between *G. dorcadoides*-type and *G. paotehensis*-type, *G. gaudryi*-type, and Cervidae. This may be an artifact of small sample sizes and the extremely conservative nature of Dunn's method (Dunn, 1964), and we consider these pairs to be likely different in $\delta^{13}C$.

Table 3 Significant differences between taxa ($\alpha = 0.05$) for each locality taken separately

$\delta^{13}C$	<i>Hipparion</i>	<i>G. dorcadoides</i>	<i>G. paotehensis</i>	<i>G. gaudryi</i>
<i>Hipparion</i>	–			
<i>G. dorcadoides</i>	[ns], (ns), { – }	–		
<i>G. paotehensis</i>	[a], (a), { – }	[a], (a), { – }	–	
<i>G. gaudryi</i>	[–], (a), { ns }	[–], (a), { – }	[–], (ns), { – }	–
Cervidae	[a, b], (a), { ns }	[a], (a), { – }	[ns], (ns), { – }	[–], (ns), { ns }

Note: Loc. 30 = [], Loc. 49 = (), Loc. 73 = { }.

a. Taxa are significantly different based on ANOVA followed by Fisher's PLSD.

b. Taxa are significantly different based on Kruskal-Wallis followed by Dunn's method.

ns. not significantly different according to either method.

4 Discussion

4.1 Carbon isotopes and hypsodonty in gazelles

G. gaudryi-type and *G. paotehensis*-type gazelles have $\delta^{13}C$ values that are consistent with pure C_3 diets, whereas *G. dorcadoides*-type gazelles are significantly enriched in ^{13}C compared to these taxa, and have values indicating a small C_4 dietary component. These results indicate that *G. gaudryi*-type and *G. paotehensis*-type gazelles were either browsers, mixed feeders, or C_3 grazers that avoided C_4 vegetation. *G. dorcadoides*-type gazelles, on the other hand, have $\delta^{13}C$ values consistent with mixed feeding and consumption of C_4 grass, or of pure grazing on C_3 and C_4 grasses, with the C_3 grasses comprising the bulk of its diet. It is also possible that *G. dorcadoides*-type gazelles were pure browsers that consumed a small fraction of C_4 dicots. Tooth crown height information alone (Fig. 2) suggests that the relative proportion of graze (or abrasive foods in general) was greatest in *G. dorcadoides*-type, least in *G. gaudryi*-type, and intermediate in *G. paotehensis*-type gazelles. This information, combined with carbon isotope data, is consistent with the interpretation of *G. gaudryi*-type gazelles as primarily browsers, and *G. dorcadoides*-type gazelles as mixed feeders or

grazers. *G. paotehensis*-types, while having higher-crowned teeth than *G. gaudryi*-type gazelles, do not appear to have consumed more C_4 vegetation than that species. It may therefore have been a browse-dominated mixed feeder that avoided consumption of C_4 vegetation. These dietary interpretations are the most parsimonious in terms of agreeing with the traditional interpretations of tooth crown height and carbon isotopes. However, data from additional methods, such as microwear or mesowear analysis, will be needed to evaluate the possibility of C_3 grass in the diets *G. gaudryi*-type and *G. paotehensis*-type, and C_4 browse in the diet of *G. dorcadoides*-type gazelles.

In East Africa today, the sympatric gazelles *G. granti* and *G. thomsonii* may be good analogs for the relationship between *G. gaudryi*-type and *G. dorcadoides*-type gazelles. Tooth crown heights and mesowear analysis suggest that both *G. granti* and *G. thomsonii* are mixed feeders (Janis, 1988; Fortelius and Solounias, 2000). These classifications have been investigated using stable isotope analysis, and the results suggest that Grant's gazelle is a browse-dominated mixed feeder (~22% grass), and that Thomson's gazelle is a graze-dominated mixed feeder (~68% grass) (Cerling et al., 2003). These diets are broadly similar to diets consistent with isotope data for *G. gaudryi*-type, and *G. dorcadoides*-type gazelles, respectively. For *G. gaudryi*-types, a 22% grass diet would, in a setting where nearly all grasses are C_3 , be consistent with a nearly pure C_3 isotope signal. For *G. dorcadoides*-types, on the other hand, a 68% grass diet would probably result in a minor but resolvable C_4 carbon isotope signal. For instance, if 25% of grasses during Locality 30 and 49 times were C_4 , then the total fraction of C_4 vegetation in the diet of a 68% grass-eater would be 17%. This value is consistent with the carbon isotope results from *G. dorcadoides*-type gazelles. For a 22% grass-eater, the total fraction of dietary C_4 vegetation would be only 6%, and this is consistent with carbon isotope data from *G. gaudryi*-type gazelles, especially since the % C_4 estimates given in Table 1 and Fig. 3 are minimum values.

4.2 North China and the global Late Miocene C_4 expansion

Wang and Deng (2005) studied carbon isotopes of fossil mammals from a 25 million year fossiliferous sedimentary sequence in Linxia. Those herbivores consumed essentially pure C_3 vegetation during the entire record, although one Pleistocene *Equus* individual appears to have had significant C_4 vegetation in its diet. These results were interpreted to suggest that the East Asian summer monsoon, which today allows for the existence of C_4 vegetation in the Loess Plateau, was relatively weak until ~2–3 million years ago.

The results presented here show unambiguous evidence of C_4 vegetation in Late Miocene ecosystems in the Loess Plateau. Why is C_4 vegetation present at Baode during the Late Miocene, but not at Linxia? A simple explanation invokes the pattern of summer monsoon precipitation in North China. The summer monsoon precipitation is greatest to the south and east, and it decreases in intensity to the north and west. Therefore, a Late Miocene summer monsoon system may have been strong enough to provide sufficient summer precipitation for C_4 vegetation at Baode, but not at Linxia, which lies much further to the west (Fig. 1). An alternative explanation may reside in paleoelevation: Linxia currently resides ~1900 m, whereas Baode resides at ~1000 m. If Linxia was significantly higher than Baode during Late Miocene time, then it is likely that growing-season temperatures were lower at Linxia, and this would favor C_3 vegetation.

4.3 Late Miocene environment and ecosystems in the Chinese Loess Plateau

Hypsodonty of fossil mammalian herbivores has long been used as an indicator of browsing versus grazing preference, and thereby as a proxy for ancient vegetation types and climates. In North China, there is a clear difference in average hypsodonty between localities in the southeast, and those in the northwest. This pattern was recognized by early workers (Schlosser, 1903; Kurtén, 1952), and is supported by recent re-analyses (Fortelius et al., 2002; Fortelius and Zhang, 2006). The widely accepted interpretation is that environments in the southeast were sig-

nificantly more humid and forested than those in the northwest.

Carbon isotope data presented here show that relatively low-crowned *G. gaudryi*-type gazelles and cervids consumed pure C_3 vegetation, and therefore may have been primarily browsers. In contrast, high-crowned *G. dorcadoides*-type gazelles and *Hipparion* consumed C_4 vegetation, and therefore likely had significant fractions of graze in their diets. Intermediate-crowned *G. paotehensis*-type gazelles consumed pure C_3 vegetation. These findings alone say nothing about spatial environmental patterns in North China during the Late Miocene, but taken with the geographical distributions of these taxa, they provide significant insight. *G. gaudryi*-type gazelles are the dominant gazelles in southeastern localities, and these localities also have higher relative occurrences of cervids compared to localities in the northwest (Kurtén, 1952). *G. dorcadoides*-type gazelles are never found in the southeastern localities, and are restricted to occasional appearance (and sometimes dominance, as at Locality 30) at localities in the northwest. *Hipparion* enjoys a cosmopolitan distribution. Therefore, the emergent pattern is one of lower-crowned, C_3 -feeders dominating southeastern localities, and higher-crowned, C_4 -feeders present at, and often dominating, northwestern localities. *Hipparion*, although the data are few, likely consumed less C_4 vegetation in the southeastern locality 73 compared to the northwestern localities 49 and 30. These results are supportive of the idea of relatively forested environments in the southeastern CLP during Baodean time, giving way to progressively open, steppe or forest-steppe environments in the northwestern CLP. To be conservative, though, it should again be noted that carbon isotopes do not distinguish between C_3 grass and C_3 browse. It is possible then, despite the observed hypsodonty patterns, that *G. gaudryi*-type, *G. paotehensis*-type gazelles, and cervids were not exclusive browsers. Indeed, carbon isotopes are consistent with pure C_3 grass diets for these taxa, and such an inference would imply very different vegetational and climatic patterns during Baodean times. While this interpretation is non-parsimonious with respect to the usual interpretation of hypsodonty, and with respect to non-faunal proxies of climate during Late Miocene time in China (Sun and Wang, 2005), additional data such as microwear and mesowear of teeth will be needed to evaluate its possibility.

5 Conclusions

The main findings of this study can be summarized as follows:

1) Baodean ecosystems in the Chinese Loess Plateau were dominated by C_3 vegetation, but contained a small but significant fraction of C_4 vegetation, as evidenced by up to ~20% C_4 vegetation in the diets of higher crowned gazelles, and up to ~30% in the diets of *Hipparion*. Thus, C_4 vegetation was present in North China by the end of Late Miocene time, consistent with C_4 vegetation distributions on other continents by this time.

2) The lower crowned *G. gaudryi*-type and *G. paotehensis*-type gazelles consumed pure C_3 diets, whereas the higher-crowned *G. dorcadoides*-type gazelles consumed some C_4 vegetation. The isotope evidence is consistent with the traditional view based on tooth morphology that *G. dorcadoides*-type gazelles consumed more grass than *G. gaudryi*-type and *G. paotehensis*-type gazelles. Further agreement between stable isotopes and morphology is shown by the finding that cervids consumed pure C_3 diets, whereas *Hipparion* regularly consumed C_4 vegetation.

3) The stable isotope data are wholly consistent with the idea that environments in the southeast CLP were more humid and forested than environments in the northwest CLP during Late Miocene time. However, the isotope data do not require such an interpretation, as it is possible that the C_3 signal in the lower-crowned taxa derives from C_3 grasses rather than C_3 browse. Additional morphological study, focusing on mesowear and microwear, may help to evaluate this possibility.

Acknowledgements We thank Prof. John Peel for access to and assistance with the collections in the Museum of Evolution, Uppsala University, and Prof. Thure Cerling for provision of mass

spectrometry facilities at the University of Utah. The Geological Society of America provided travel funding to BHP. This work was supported by the Academy of Finland and National Geographic Society grants to MF, NSFC to ZZQ (40672010).

References

- Bohlin B, 1935. Cavicornier der *Hipparion*-Fauna Nord-Chinas. *Palaeont Sin, Ser C*, **9**(4): 9 – 164
- Cerling T E, Harris J M, 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*, **120**: 347 – 363
- Cerling T E, Harris J M, MacFadden B J et al., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature*, **389**: 153 – 158
- Cerling T E, Harris J M, Passey B H, 2003. Diets of East African bovidae based on stable isotope analysis. *J Mammal*, **84**(2): 456 – 470
- Dunn O J, 1964. Multiple comparisons using rank sums. *Technometrics*, **6**: 241 – 252
- Ehleringer J R, Cerling T E, Helliker B R, 1997. C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia*, **112**: 285 – 299
- Fortelius M, Eronen J, Jernvall J et al., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol Ecol Res*, **4**: 1005 – 1015
- Fortelius M, Solounias N, 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. *Am Mus Novit*, (3301): 1 – 36
- Fortelius M, Zhang Z Q, 2006. An oasis in the desert? History of endemism and climate in the late Neogene of North China. *Palaeontogr Abt A: Paläozool, Stratigr*, **227**: 131 – 141
- Janis C M, 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. In: Russel D E, Santorio J P, Signogneau-Russel D eds. *Teeth Revisited: Proceedings of the VII International Symposium on Dental Morphology. Mém Mus Natl Hist Nat, Ser C (Paris)*, **53**: 367 – 387
- Jokela T, Eronen J, Kaakinen A et al., 2005. Translation of Otto Zdansky's "the localities of the *Hipparion* Fauna of Baode County in northwest Shanxi" (1923). *Palaeont Electron*, **8**(1), 3A: 1 – 10. http://palaeo-electronica.org/palaeo/2005_1/jokela3/issue1_05.htm
- Kurtén B, 1952. The Chinese *Hipparion* Fauna. *Comment Biol, Soc Sci Fennica*, **13**: 1 – 82
- Pagani M, Freeman K H, Arthur M A, 1999. Late Miocene atmospheric CO₂ concentrations and the expansion of C₄ grasses. *Science*, **285**: 876 – 879
- Passey B H, Cerling T E, Perkins M E et al., 2002. Environmental change in the Great Plains: an isotopic record from fossil horses. *J Geol*, **110**: 123 – 140
- Passey B H, Robinson T F, Ayliffe L K et al., 2005. Carbon isotope fractionation between diet, breath CO₂, and bioapatite in different mammals. *J Archaeol Sci*, **32**: 1459 – 1470
- Pyanikov V I, Gunin P D, Tsoog S et al., 2000. C₄ plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. *Oecologia*, **123**: 15 – 31
- Schlosser M, 1903. Die fossilen Säugethiere Chinas nebst einer odontographie der recenten antilopen. *Abh K Bayer Akad Wiss*, **22**: 1 – 221
- Sun X J, Wang P X, 2005. How old is the Asian monsoon system? Palaeobotanical records from China. *Palaeogeogr, Palaeoclimatol, Palaeoecol*, **222**: 181 – 222
- Teilhard de Chardin P, Young C C, 1931. Fossil mammals from Northern China. *Palaeont Sin, Ser C*, **9**(1): 1 – 66
- Wang Y, Deng T, 2005. A 25 m. y. isotopic record of paleodiet and environmental change from fossil mammals and paleosols from the NE margin of the Tibetan Plateau. *Earth Planet Sci Lett*, **236**: 322 – 338
- Zdansky O, 1923. Fundorte der *Hipparion*-Fauna um Pao-Te-Hsien in NW-Shansi. *Bull Geol Surv, China*, **5**: 69 – 82
- Zhang Z Q (张兆群), 2006. Chinese Late Neogene land mammal community and the environmental changes of East Asia. *Vert PalAsiat (古脊椎动物学报)*, **44**(2): 133 – 142