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ORIGINAL PAPER

Stable carbon isotope reconstructions of diet and paleoenvironment from the late Middle Pleistocene Snake Cave in Northeastern Thailand

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Abstract Thailand's geographical location in the tropics and almost complete, relatively uninterrupted forest cover makes it valuable for paleodiet and paleoclimate research. We present the first dietary and environmental reconstructions in Northeastern Thailand, using stable isotope abundances in mammalian tooth enamel from the late Middle Pleistocene locality, Tham Wiman Nakin (Snake Cave), which reflect a much higher (over 70%) than modern (13%) occurrence of C4 plants. Bovids and cervids appear to have had almost entirely a C4 plant diet. Carnivores consumed a mixture of C3 (suids) and C4 (bovids, cervids) consumers. Rhinoceroses and orangutan appear to have maintained their preference through time for forested or open C3 environment, respectively. $^{13}C/^{12}C$ from bone bioapatite, horn and hair of modern Southeast Asian mammals almost exclusively demonstrate C3 vegetation dominance. C4 consumption is rare in analysed modern species and it could be related to anthropogenic influences such as ingestion of domestic crops or livestock. Interesting implications emerge in the C4 vegetation distribution in southern Eurasian ecosystems, indicating that Southeast Asia, south of the Tibet, could be part of the global C4 vegetation spread, which occurred around 7 Ma. However, the C4 percentage in ecosystems varied geographically. Despite modern reversal towards C3 habitats due to factors such as increasing CO_2, we think that anthropological influences may be responsible for habitat and dietary changes in extant species. Bovids demonstrate the most significant shift in diet and habitat through time, from C4-dominated open habitats to C3-dominated habitats indicative of dense forest understory.

Keywords Thailand · Serow · Middle Pleistocene · C4 spread

Introduction

Stable isotope analyses of tooth enamel have been shown to be a good proxy for reconstructing terrestrial paleoenvironments, e.g., climates and vegetation, providing valuable information regarding the presence of C3 and C4 vegetation in ecosystems and the degree of canopy cover versus openness in habitats. Thailand is particularly interesting for paleoenvironmental analyses. Modern Thailand consists of uninterrupted tropical forests (Woodruff 2003) dominated by C3 vegetation. However, previous analyses on global and simultaneous spread of C4 plants in low and middle latitudes during the latest Late Miocene (Cerling et al. 1997) suggest a measurable abundance of C4 plants in Thailand during the Pleistocene.

Northern Thailand is a mountainous area with variable altitude, changing from lowlands of 200 m to high peaks over 2,500 m (e.g., the peak of Don Inthanon). This habitat is covered by semi-evergreen forest, dominant dry evergreen (more widespread during the Pleistocene glaciations)

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and extensive deciduous forests, mixed with teak (*Tectona grandis*) in the northwest and dry dipterocarp in the northeast (Lekagul and McNeely 1977). In the north of the country, the forests experience higher seasonal variability in precipitation and temperature (Chaimanee 2007). It appears that the ancestral forest species of the dipterocarp rain forest were already adapted to seasonal climate (Chaimanee 1998).

Despite numerous studies on paleoenvironment and fossil mammal communities of Thailand, few have so far employed isotopic paleoreconstructions. Unequally documented Middle Pleistocene fossil record in Southeast Asia is mostly concentrated in the Indochinese province, which includes Northern Thailand (Chaimanee 1998; Tougard 2001; Tougard and Montuire 2006). Thus, our focus was to perform isotopic paleoreconstructions as well as to look at the differences in species habitats and diets from the present, since no comparison data for modern Southeast Asian ecosystems exist in the literature.

We studied the late Middle Pleistocene locality of Tham Wiman Nakin (also known as the Snake Cave, hereafter, TWN), situated at low altitude in Northeastern Thailand in the Kon San district of Chaiyaphum Province (Fig. 1). The cave occurs in a tropical forest on a floodplain on the southwestern side of a hill about 10 m above the surrounding areas. TWN is dated by U/Th to be older than 169,000 ± 11,000 years ago (Esposito et al. 2002), which is consistent with the site occurring in the deposits of the age of the Saalian Glaciation (129,000–300,000 years ago) in the range of marine oxygen isotope stage OIS6.

We analysed stable carbon isotope relative abundances in the carbonate fraction of enamel bioapatite in fossil terrestrial mammals from the late Middle Pleistocene TWN cave, since collagen is usually not preserved in fossil mammals from this period in this region. In modern mammals we analysed carbon stable isotope signatures, examining either the carbonate fraction of bone bioapatite or keratin of hair and horns.

Fig. 1 The geographical location of the locality of Tham Wiman Nakin (TWN or the Snake Cave)

^{13}C abundances, diet and habitat

Carbon isotopic compositions in herbivores reflect the source of carbon in their diet, indicating the photosynthetic pathways and thus, the proportions of C3 and C4 vegetation in their habitat as well as the degree of canopy closure versus openness in wooded habitats. C4-plants are generally herbaceous (grasses and some cereal crops such as maize, millet and sorgho) and adapted to hot growing seasons (above 20°C, monsoon system) usually in tropical, low-latitude biomes (Bender 1968; Smith and Epstein 1971). C3 plants are the trees in all tropical, temperate and boreal biomes and the herbaceous plants (grasses) in temperate and cold or cool high-altitude regions with cool growing seasons (Vogel et al. 1978). Both types of plants are ^{13}C-depleted relative to atmospheric CO_2, the source of inorganic carbon and exhibit different isotopic signatures. C4 are more ^{13}C-enriched than C3-plants (Cerling et al. 1997; Cerling and Harris 1999; Lee-Thorp and van der Merwe 1987; Lee-Thorp et al. 1989; Kohn and Cerling 2002; Bocherens and Drucker 2007). The δ^{13}C values of C4 plants range between −9‰ and −17‰, with a mean of −13‰ (Bender 1968; Smith and Epstein 1971; Vogel et al. 1978). The δ^{13}C values for C3 plants range between −34‰ and −23‰, with a mean of −26‰ (Smith and Epstein 1971; van der Merwe and Medina 1989).

In forest environments, differences in δ^{13}C composition can result in a vertical δ^{13}C gradient known as the canopy effect, where the understory plants and the forest floor (often referred to as the bottom of the canopy) are depleted in ^{13}C compared to the top of the canopy (e.g., van der Merwe and Medina 1991). This effect occurs because of the mixture of atmospheric CO_2 with CO_2 depleted in ^{13}C from respiration, decomposition of organic matter and recycling of already-depleted organic carbon within an enclosed heavily wooded environment at the ground surface in comparison to woodland and more open forest environments with higher evapotranspiration (e.g., Schleser and Jayasekera 1985; Gebauer and Schulze 1991). Because of the canopy effect, a single species (e.g., pigs, porcupine) feeding on plants from different tree elevations can exhibit up to a 5‰ difference in δ^{13}C value. The canopy effect has also been observed in pure C3 environments between the herbivores feeding in a heavily enclosed wooded environment and more open forest environments with higher evapotranspiration (e.g., Drucker et al. 2003; Feranec and MacFadden 2006; Drucker et al. 2008; Drucker and Bocherens 2009).

Enamel bioapatite carbon isotope enrichment varies among herbivores, carnivores and omnivores relative to ingested forage. The herbivores usually exhibit +14‰ enrichment for the $\delta^{13}C$ values of carbonate from bioapatite in bone and enamel relative to the plant food consumed (Lee-Thorp et al. 1989; Cerling and Harris 1999; Passey et al. 2005). In carnivores as well as in pigs, primates and some rodents, the enrichment is +9‰ for bone and enamel apatite relative to their diet (Lee-Thorp et al. 1989; Koch 1998; Bocherens 2000; Cerling et al. 1999; Kohn and Cerling 2002; Bocherens and Drucker 2007). In hair and horns, there is +3.1‰ enrichment (Cerling and Harris 1999). Hair can record significant variations in diet over several days due to quick changes in blood chemistry (Kohn and Cerling 2002).

Grazers with a diet consisting of pure C4 grasses are expected to have $\delta^{13}C$ apatite values ranging from −4‰ to +4‰, whereas grazers or browsers with pure C3 diets should display values from −15‰ to −10‰ (Cerling et al. 1997; MacFadden et al. 1999; Cerling and Harris 1999; Feranec 2007). Roughly, carnivores feeding on species in C4 habitats are expected to have $\delta^{13}C$ apatite values more positive than −6‰ and in C3 habitats more negative than −16‰. In large herbivores, the enamel value as high as −8‰ can be still explained by pure C3 diets and is a suggested conservative threshold for herbivores, corresponding to a dietary intake of −22‰, which is within the range of observed values for pure C3 ecosystems (Cerling et al. 1997; MacFadden et al. 1999). This conservative 'cut-off' value, corrected for primates and carnivores, produces a threshold of −13‰.

We take into account the isotopic change in carbon composition of atmospheric CO_2 when comparing isotope composition oscillations between fossil and modern faunas. Since the beginning of the industrial revolution in 1850, $\delta^{13}C$ has decreased approximately from −6.5‰ to −8‰ due to fossil fuel combustion and deforestation (Marino and McElroy 1991), and this trend is continuing.

Since we analysed not only enamel carbonate but also hair and horns, we converted our carbon isotopic results into diet $\delta^{13}C$ values, according to the above mentioned differences, expressed in the following formulas (Table 1):

$$\delta^{13}C_{\mathrm{hair/horn}} = \delta^{13}C_{\mathrm{diet}} + 3.1 \text{ (for herbivores and carnivores)}$$
$$\delta^{13}C_{\mathrm{bioapetite}} = \delta^{13}C_{\mathrm{diet}} + 14 \text{ (for large herbivores)}$$
$$\delta^{13}C_{\mathrm{bioapetite}} = \delta^{13}C_{\mathrm{diet}} + 9 \text{ (for carnivores, pigs, rodents, primates)}$$

We also calculated an approximate crude percentage of C4 plants in a diet based on the formula from Koch et al. (1998), using the mean $\delta^{13}C$ values for C3 plants −26‰ and C4 plants −13‰, where C4%=($\delta^{13}C_{\mathrm{enamel\ obtained}}$−$\delta^{13}C_{\mathrm{enamel\ C3\ feeder}}$)/($\delta^{13}C_{\mathrm{enamel\ C4\ feeder}}$−$\delta^{13}C_{\mathrm{enamel\ C3\ feeder}}$)× 100%.

This calculation is, however, extremely sensitive to the fractionation between diet and apatite (or diet–hair), depending on the species and can apparently produce negative and over 100% results (see 'Discussion' section). Despite the fact that because of ecological preferences in the diet of animals, the calculations of C4% in diet from mammalian teeth can underestimate ecosystem C4 abundance, they still give a general idea of the C4 flora presence.

Material and methods

Fossil enamel was obtained from French–Thai expeditions to Southeast Asia since 1985, led by Professor J.-J. Jaeger. All samples analysed belonged to the adult individuals of ungulates, rodents, carnivores and primates, and each was identified to the family or species level (Table 1). The bone apatite, hair and/or horn samples of analysed modern adult mammals were obtained in Southeast Asia after 2000 (Table 1). Thus, the modern isotope values were corrected +1.5‰ to account for the recent changes in atmospheric $\delta^{13}C$ values compared to the Pleistocene animals.

Preparation of samples for isotope analyses

Enamel samples were mechanically separated from dentine and either ground to a finer condition in an agate mortar or directly drilled with a rotary tool equipped with a diamond-coated drill tip. The uppermost surface of the bone or tooth was removed before sampling, usually by drilling. Samples of approximately 20 mg were analysed. The fossil and modern enamel powder samples were pre-treated following the method described by Bocherens et al. (1996). Enamel powders were first reacted with 2.5% sodium hypochlorite NaOCl for 20 h at 20°C to oxidise organic residues and rinsed twice with distilled water. They were subsequently treated with 1 M buffer acetic acid-calcium acetate (pH= 4.75) for 20 h at 20°C to remove exogenous carbonate without losing a lot of bone mineral (Koch et al. 1998) and finally rinsed with distilled water three times and dried at 70°C overnight. Then the treated powders were reacted with 100% anhydrous orthophosphoric acid H_3PO_4 at 70°C for 90 min to produce CO_2.

The isotopic analysis was performed using a continuous flow (CF) system, the ThermoFisher Scientific GasBench II coupled to an isotopic ratio mass spectrometer MAT 252, at the University of Tübingen, Germany (Institut für Geowissenschaften, Abteilung Geochemie). This system is optimal for fossil enamel carbonate analysis because of having an integrated chromatographic column and allowing for the analysis of the gas evolved from the reaction with orthophosphoric acid ten times instead of once as with the

Table 1 The $\delta^{13}C$ values from enamel apatite of fossil TWN species and apatite, horn and hair of modern samples converted into the diet $\delta^{13}C$ values

Taxon	Common name	Part	Origin	$\delta^{13}C$	$\delta^{13}C$ diet
Fossil					
Rhinoceros		Enamel	Tham Wiman Nakin	−14.4	−28.4
Rhinoceros		Enamel	Tham Wiman Nakin	−14.7	−28.7
Rhinoceros		Enamel	Tham Wiman Nakin	−14.9	−28.9
Rhinoceros		Enamel	Tham Wiman Nakin	−15.1	−29.1
Rhinoceros		Enamel	Tham Wiman Nakin	−15.2	−29.2
Sus scrofa	Wild pig	Enamel	Tham Wiman Nakin	−7.9	−15.9
Sus scrofa	Wild pig	Enamel	Tham Wiman Nakin	−8.6	−16.6
Sus scrofa	Wild pig	Enamel	Tham Wiman Nakin	−13.0	−21.0
Sus scrofa	Wild pig	Enamel	Tham Wiman Nakin	−13.1	−21.1
Sus scrofa	Wild pig	Enamel	Tham Wiman Nakin	−13.8	−21.8
Bovidae		Enamel	Tham Wiman Nakin	2.8	−11.2
Bovidae		Enamel	Tham Wiman Nakin	0.9	−13.1
Bovidae		Enamel	Tham Wiman Nakin	−0.6	−14.6
Bovidae		Enamel	Tham Wiman Nakin	−2.4	−16.4
Bovidae		Enamel	Tham Wiman Nakin	−2.9	−16.9
Cervidae		Enamel	Tham Wiman Nakin	0.6	−13.4
Cervidae		Enamel	Tham Wiman Nakin	−0.9	−14.9
Cervidae		Enamel	Tham Wiman Nakin	−2.2	−16.2
Cervidae		Enamel	Tham Wiman Nakin	−3.7	−17.7
Cervidae		Enamel	Tham Wiman Nakin	−6.8	−20.8
Hystrix	Porcupine	Enamel	Tham Wiman Nakin	−5.5	−13.5
Hystrix	Porcupine	Enamel	Tham Wiman Nakin	−8.3	−16.3
Hystrix	Porcupine	Enamel	Tham Wiman Nakin	−9.4	−17.4
Hystrix	Porcupine	Enamel	Tham Wiman Nakin	−11.7	−19.7
Hystrix	Porcupine	Enamel	Tham Wiman Nakin	−12.9	−20.9
Carnivore	Hyena	Enamel	Tham Wiman Nakin	−4.1	−12.1
Carnivore	Hyena	Enamel	Tham Wiman Nakin	−6.1	−14.1
Pongo pygmaeus	Orangutan	Enamel	Tham Wiman Nakin	−13.1	−27.1
Modern				Uncorrected	Corrected +1.5
Elephas maximus	Elephant	Apatite	Western Thaïland (Huai Kra Kheng)	−11.4	−23.9
Elephas maximus	Elephant	Apatite	Eastern Thaïland (Khao Soi Dao)	−18.4	−30.9
Rhinoceros sondaicus	Javan rhino	Apatite	Thaïland (Kanchanaburi)	−18.0	−30.5
Rhinoceros sondaicus	Javan rhino	Hair	Thaïland (Kanchanaburi)	−25.6	−27.2
Bos gaurus	Gaur	Apatite	Thaïland	−5.9	−18.4
Capricornis sumatraensis	Serow	Apatite	Laos	−15.9	−28.4
Capricornis sumatraensis	Serow	Horn	Western Thaïland (Thung Yai)	−25.1	−26.7
Capricornis sumatraensis	Serow	Horn	Western Thaïland (Thung Yai)	−25.0	−26.6
Capricornis sumatraensis	Serow	Horn	Laos	−24.7	−26.3
Capricornis sumatraensis	Serow	Horn	Laos	−25.5	−27.1
Muntiacus muntjak	Barking deer	Hair	Thaïland	−24.2	−25.8
Cervus unicolor	Sambar deer	Apatite	Western Thaïland (Huai Kha Khaeng)	−3.0	−15.5
Cervus sp.	A deer	Apatite	Thaïland	−8.0	−20.5
Hystrix sp.	Porcupine	Apatite	Western Thaïland (Thung Yai)	−18.6	−25.1
Felis sp.	Wild cat	Apatite	Thaïland	−16.5	−23.0
Viverra zibetha	Indian civette	Apatite	Singapore	−12.3	−18.8
Panthera tigris	Tiger	Apatite	Singapore	−10.0	−16.5
Pongo pygmaeus	Orangutan	Apatite	Singapore	−16.2	−28.7

Table 1 (continued)

Taxon	Common name	Part	Origin	δ^{13}C	δ^{13}C diet
Hylobates lar	Gibbon	Apatite	Thaïland	−16.0	−28.5
Trachypithecus phayrei argenteus	Phayre's langur	Apatite	Singapore	−16.4	−28.9
Macaca nemeshina nemeshina	Pigtailed macaque	Apatite	Singapore	−16.8	−29.3
Macaca nemeshina nemeshina	Pigtailed macaque	Apatite	Singapore	−16.3	−28.8
Macaca nemeshina leonine	Pigtailed macaque	Apatite	Singapore	−16.7	−29.2

Multiflow system from Micromass (e.g., Tütken et al. 2007). Therefore, the CF system offers a more sensitive discrimination and separation of gaseous compounds and purification of CO_2 before it enters the mass spectrometer, thus allowing to identify the real signal (Bocherens et al. 2009). The carbon isotopic analyses were normalised to the international standard NBS-19.

Hair was pre-treated using the cleaning protocol described by Urton and Hobson (2005). Isotopic analysis was performed using a CHN-elemental analyzer (Eurovector) coupled to a VG Optima continuous-flow ratio mass spectrometer used for $^{13}C/^{12}C$ measurements in the Institut des Sciences de l'Evolution (Université Montpellier 2, France).

Carbon isotopic ratios $^{13}C/^{12}C$, expressed as the delta value, are calculated as follows: $\delta^{13}C = \left[\left({}^{13}C/{}^{12}C_{\mathrm{sample}}/{}^{13}C/{}^{12}C_{\mathrm{standard}}\right) - 1\right] \times 1000$. The standard is the marine carbonate Vienna PeeDee Belemnite for carbon. For $\delta^{13}C$ samples, the analytical error is 0.1‰.

Statistical analysis

We used both parametric and non-parametric tests with α= 0.05. Since analysis of variance (ANOVA) is robust enough to handle departures from normality and unequal variances and the distribution in our samples did not significantly depart from normal to affect *t* test statistics, we incorporated it to see the differences in means among species within and between the modern and fossil samples. However, we also confirmed all results using non-parametric test of Wilcoxon to see the differences in medians between fossil and modern samples, and Kruskal–Wallis (analogous to ANOVA) among species because they make no assumptions about the sample distributions (normality), since Shapiro–Wilk test indicated that they are not normally distributed and the variances are not equal. To identify the sources of significant differences in these multiple comparisons, we used post hoc Tukey tests.

Results

Pretreatment was used for all our fossil and modern samples and the results do not show any evidence of diagenetic contamination. $CaCO_3$ content in TWN varied between 3% and 6.2%, which is within normal ranges for specimens not affected by diagenetic contamination. The $\delta^{13}C$ carbonate values from TWN range from −15.2‰ (rhinoceros) to +2.8‰ (bovid) (Table 1) with the mean −7.75‰, which translated into diet $\delta^{13}C$ values produce −29.2‰ to −11.2‰ with the mean value −19.2‰. This is consistent with a mixture of C3 to C4 habitats and C3 ecosystems ranging from forests to open environments. Percent C4 within diets ranged from 0% to 99%. Significant differences were observed in $\delta^{13}C$ values among species (carbonate Kruskal–Wallis H=23.9, df=6, p=0.001; ANOVA r^2=0.863, p<0.001; ecosystem Kruskal–Wallis H=19.18, df=6, p=0.003; ANOVA r^2=0.862, p< 0.001). All fossil bovids, which are chiefly the mainland serow and gaur, appear to have had a C4-dominated diet (−3‰ to +3‰) indicating 75–100% dietary C4. The majority of cervids followed this trend as well, while the two TWN cervids had a mixed C3–C4 diet (−3.7‰, −6.8‰, with around 70% and 50% of C4 in diet). In the two carnivores, most likely the hyenas, based on the abundance of this species in TWN, their prey C4 intake appeared to be around 80–100% similar to the $\delta^{13}C$ values of the bovids and cervids (both ANOVA, Kruskal–Wallis post hocs NS) and also close to the wild boar and porcupine $\delta^{13}C$ values (post hoc NS; Fig. 2). Rhinos are shown to have fed entirely

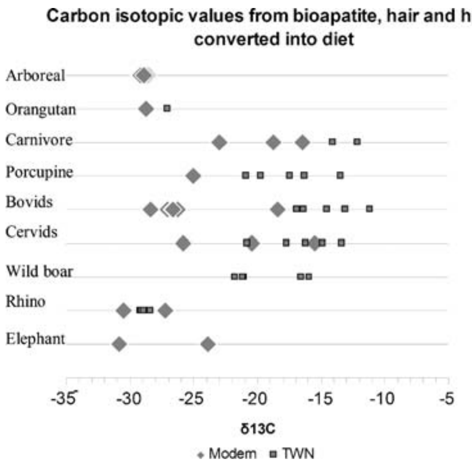

Fig. 2 Carbon isotopic values from bioapatite, hair and horn of fossil and modern species converted into the diet $\delta^{13}C$ values

on C3 vegetation (0–4% C4 in diet) and significantly different from bovids and carnivores (K-W post hocs $p=0.007$, $p=0.029$, respectively, in ANOVA significantly different from all ungulates and carnivores, all post hocs $p<0.001$). The orangutan appeared to be similar to pigs (ANOVA post hocs, $p=0.089$), but significantly different from porcupines ($p=0.023$) and the other analysed species ($p<0.01$). Its carbonate value is on the border (−13‰) of pure C3 and mixed C3–C4 for primates, likely corresponding to open C3 habitat. Using the fractionation value +9%, orangutan dietary C4 intake was about 30%. Wild boars and porcupines showed statistically similar values and a mixed diet inclusive of both C3 and C4 plants (dietary C4 25–70% for *Sus*; 32–89% for *Hystrix*).

In modern samples, $CaCO_3$ content in apatite varied between 3.6% and 7.8%. Carbon yield in hair/horn ranged from 45.9% to 49.9% yield and C/N between 3.6 and 4.0. The modern $\delta^{13}C$ values are significantly more negative than fossil TWN, which translated in the diet range from deep canopy forests (−30.9‰) to open habitats (−15.5‰) with the mean value −25.4‰ (ecosystem Wilcoxon Mann–Whitney $U=141.5$, $p<0.001$; ANOVA $r^2=0.269$, $p<0.001$), also when only carnivores, cervids, porcupines, rhinos and orangutans are analysed ($U=107.5$, $p=0.028$; ANOVA $p=0.016$). The $\delta^{13}C$ values are significantly affected by the interaction between the origin of the samples (TWN or modern) and among the species (ANOVA $r^2=0.841$, $p<0.001$). The fossil and modern bovid samples are significantly different ($r^2=0.796$, $p<0.001$, Wilcoxon MW $U=62$, $p=0.001$). In contrast, carnivores are not significantly different when comparing TWN to the modern samples. However, in carnivores, we did not compare the same species. Hyenas are long extirpated from Southeast Asia and nowadays remain only in Africa.

There are significant differences in $\delta^{13}C$ values among the modern species as well (ecosystem Kruskal–Wallis $H=15.48$, df=7, $p=0.03$; ANOVA $r^2=0.624$, $p=0.019$). Modern bioapatite and hair samples suggest C3 vegetation dominance in the habitats and diets of the majority of analysed species, such as the mainland serow, rhinoceros, orangutan, elephant, porcupine, several carnivores in this study (Indian civette, wild cat), deer and arboreal species (gibbon, macaques, langur). Among modern species, only Sambar deer appeared to feed in C4-dominated habitat (maximum C4%~84%), and the tiger to hunt prey that consumed C4 or mixed C3-C4 plants (65% C4 prey). Other modern species with mixed C3–C4 diet include gaur (66% C4), cervids (53% C4) and Indian civette (48% C4; Table 1). For modern orangutan, we obtained a dietary C4% around 17%, which a bit high considering their modern ecology (see 'Discussion' section).

Discussion

Environment

The spread of the C4 vegetation was suggested to have suddenly, simultaneously and globally occurred during the latest Late Miocene between 8 and 5 Ma at lower to middle latitudes (under 37°N) in North and South Americas, Pakistan and Africa, related to a decrease in atmospheric CO_2 concentrations (Quade et al. 1989; Quade and Cerling 1995; Cerling et al. 1997), which in turn was probably associated with a decrease in solar irradiance (Nahle 2007). The C4 vegetation spread could have been associated with other environmental and climatic factors (tectonic events, development of low-latitude seasonal aridity, global changes in growing conditions) rather than CO_2 decrease (Pagani et al. 1999; Keeley and Rundel 2005). However, there is also emerging evidence that the spread of C4 vegetation was not as simultaneous and global as it was previously thought. C4 plants were a minor component in many environments in Africa and Pakistan until the Late Pliocene and Early Pleistocene (Ségalen et al. 2007), although they became more prevalent during the latest Late Miocene and early Pliocene (Morgan et al. 1994).

The paleoenvironments of Eurasia as a whole should have had some variability due to its vast and different spatial and geographical setting, which several studies have demonstrated. For example, during the Late Miocene, C4 vegetation was completely absent or uncommon in Southeastern Europe and Southwestern Asia (Greece, Turkey), south of 37°N (Bocherens et al. 1994; Quade et al. 1994; Bocherens and Sen 1998; Deng 2006). In China too, C3 vegetation dominated during the Late Miocene (Deng 2006). In southern Tibet (28°N, Gyirong Basin, Southwestern China), which during the Late Miocene resided at lower elevation and had higher temperatures than modern, a significant amount of C4 plants was present based on data from rhinos (mean $\delta^{13}C=-7.9‰$ enamel, about 30% C4 in diet) and horses (mean $\delta^{13}C = -6‰$ from −2.4‰ to −8‰, about 30–70% C4) (Wang et al. 2006). In northern China (situated at 39°N, Baode), ecosystems in the Late Miocene were dominated by C3 vegetation with dietary C4 plant abundance up to 20% and 30% based on data from gazelles and horses, respectively (Passey et al. 2007).

Later on, during the Middle Pleistocene at the Zhoukoudian succession (39°N, Northeastern China), a significant amount of C4 appeared in mammalian diets, ranging from 0% to 75%. However, C4 flora apparently disappeared or decreased significantly by the early Middle Pleistocene (470,000 ya) likely due to the strengthening of winter monsoon (Gaboardi et al. 2005). The late Middle Pleistocene data from the Bubin basin caves in China (23°N) are again consistent with

100% C3 plant dominance of canopied woodland or forest (mean $\delta^{13}C=-13.6$‰ enamel, from −15.3‰ to −11.4‰) (Wang et al. 2007). And the data from the Linxia basin (35°N, China) also suggest C4 plants were either absent or insignificant (mean $\delta^{13}C=-10.$‰ enamel, from −8.4‰ to −12.4‰) prior to the Pleistocene (Wang and Deng 2005). In modern China, C4 plants represent about 25% of vegetation by species diversity (grasses, sedges and herbs) with the values averaging approximately −12‰, with the dominant subtropical forest with ferns, grasses, shrubs and trees averaging ~ −31‰, whereas in open habitats ferns, trees, shrubs, herbs and C3 grasses averaging ~ −27‰ (Ehleringer et al. 1987).

These C4 vegetation geographic distribution discrepancies in Eurasia were likely associated with the Tibetan Plateau uplift, which brought about strong monsoonal circulation (Passey et al. 2009) and initiated a forest development in Southeast Asia during the Late Neogene and Quaternary (Ruddiman and Kutzbach 1989, 1990). Recent data suggested that rainforests in Southeast Asia, including Thailand, started developing along with progressive reduction of grasslands and became widespread from the Late Miocene to Pleistocene (Ruddiman and Kutzbach 1989), suggesting a shift towards more C3 vegetation or at least decrease in mean $\delta^{13}C$. Climate in Southeast Asia during glaciations became more humid and less seasonal (including Indochinese province and Thailand) (Chaimanee 1998).

Based on the information presented above and its geographic location, Northern Thailand during the late Middle Pleistocene should have been in a region of C3 vegetation dominance similar to the Southeastern China or changing from C3 to C4 based on changing climate (usually becoming more seasonal during glaciations). Interestingly, our carbon isotope results from TWN cave have demonstrated that this rather mountainous area of Northern Thailand during the late Middle Pleistocene had a mosaic of C4 and C3 habitats, including open and semi-wooded savannah with forest patches and deep forest cover. TWN cave is suggested to have been wetter and cooler based on other paleoenvironmental indicators (Chaimanee 1998). And this locality probably represents the Saalian Glaciation, corresponding to the model of Cerling et al. (1997), which suggests C4 grass expansion at intermediate and low latitudes during the low CO_2 conditions of glaciations. Calculated from the representative samples of TWN and compared to the modern species, the C4 vegetation (as calculated by percentage of C4 plants in the diet) could represent over 70% of vegetation in TWN, whereas it is only around 10–20% in modern Thailand.

Interesting implications then emerge not only in the different timing of C4 vegetation spread in southern Eurasia but also in the different trends of its distribution in terms of the shifting proportions of C4 plants in ecosystems. While the spread of C4 ecosystems may have been global since it was probably associated with global trends in climate and environment, the C4 plant percentages discovered so far were not uniformly distributed in southern Eurasia. Supporting this conclusion are the original studies that proposed the spread of C4 plants based on the mammal dietary $\delta^{13}C$ and soil carbonate $\delta^{13}C$ (Morgan et al. 1994) and showed that after 8 Ma C4 plants represented only about 33% of the vegetation in Siwaliks (Pakistan), where in Kenya (Africa) the percentage was much higher (about 80%). Except for Pakistan and China where C4 plants represented about 30% based on mammalian diet, the C4 proportion during the latest Late Miocene is unknown in many other parts of Eurasia. Perhaps, high percentages of C4 plants have not yet been identified because it is difficult to infer the exact amount of C4 in ecosystem as this calculation depends on the dietary preferences of mammals. Where C4 plants are not representative or are insignificant on the landscape, the C4 signal could simply be missed in regions, where geographically limited and/or isolated mammals were sampled.

In summary, in southern Eurasia, C4 vegetation appears to represent about 30% of the vegetation at around 30°N, circling the Tibetan Plateau from north and south, but allegedly not reaching the area of Southeast China, which is protected by a maritime climate and the Himalayas Mountain range and Tibetan Plateau (similar to the Mediterranean region and Europe). During the late Middle Pleistocene, C4 plants were still present and abundant on the landscape in Northeastern Thailand (our data), and in China (Zhoukoudian, northeast of Tibet, see above), however, apparently significantly decreasing in abundance in Northeastern China by the late Middle Pleistocene. The Tibetan Plateau uplift appears to have triggered different vegetational responses in different regions of Eurasia and around the Plateau (Fortelius et al. 2002, 2006). Although the modern reversal from C4 to C3 in many parts of Eurasia (e.g., Central Asia, Pushkina 2006) appears global, data from the latest Late Miocene and the resolution of when C4 plants first appeared in Thailand are needed to help clarify the isotopic trends there.

Species

Equally interesting are the fossil species' diets and distribution in comparison to their modern activities. All surviving modern species, bovids, carnivores, rhinoceroses, orangutan, porcupine and cervids appear to have shifted their diets to include more C3 vegetation, implying foraging in deeper forest habitats. Most intriguingly, all TWN fossil bovids and the majority of cervids foraged in the open C4 habitats. We suspect the bovid remains unidentifiable to the species level to represent the mainland serow and gaur as these species are the most abundant at TWN (Tougard and Montuire 2006). It is reasonable to conclude then that the two sampled bovid species, especially the mainland serow, changed their feeding ecology since the late Middle Pleistocene. While the modern gaur remains predominantly in the mixed C3–C4 habitats, both horn and bioapatite samples of the modern serow uniformly demonstrate that this hypsodont caprine today inhabits and forages in deep canopy C3 forests. The serow is also known to be extensively hunted by humans in modern Southeast Asia (Thailand).

Porcupines' and wild pigs' mixed feeding habits appear to be similar to each other in TWN. Both species are known to eat bark, roots, bulbs, fallen fruits as well as cultivated crops, insects, small vertebrates and carrion and gnaw on bones for calcium and/or to sharpen incisors (Nowak 1999). Porcupines from TWN were also extensively feeding on remains of other recently deposited species, as evidenced by gnaw marks on the bones of other species (Chaimanee 1998) as well as indicated by their higher δ^{13}C values.

It is appealing to extrapolate foraging behaviour of the fossil carnivores from TWN (likely hyenas; Chaimanee 1998), as their diet appears to have been dominated by prey that consumed C4 plants, which are mainly bovids and to a decreasing extent, cervids, wild boars and porcupines. However, there are only two individuals and one of the carnivores also included C3 consumers in its diet. Further studies on discerning possible predator–prey interactions are needed. Remarkably, for modern carnivores in our study, the tiger (*Panthera tigris*) has shown high δ^{13}C values associated with a high C4 signal in prey, which corresponds to a fact that the tiger is known to hunt the gaur (Buchholtz 1989). For the modern samples, an anthropogenic factor can influence δ^{13}C values by incorporating human-related food from mixed or more open habitats, e.g., some elephants 'stealing' human food, tigers hunting humans or their commensals.

Our data suggest that TWN and modern rhinoceroses maintained their preferences for closed-canopy forests despite the presence of C4 habitats during the late Middle Pleistocene, although modern rhinos are shown to roam in more open C3 areas. The observed differences between ruminants and hindgut digesting rhinoceroses in δ^{13}C values are significant. This may indicate dietary changes related to habitat differences or the differences between the taxa may be associated with the different gut design and digestive 'strategies'. For instance, methane production greatly increases δ^{13}C values in large ruminants (Bocherens 2000). Palmqvist et al. (2008) obtained similar results, where δ^{13}C values in rhinos were significantly more negative than in bovids. And although Cerling and Harris (1999) found no difference between zebras and horses (hindgut digesters like rhinos) and antelopes (ruminants), the fractionation factor in rhinos may be lower than +14‰ for large ruminants (especially, for rhinos from deep canopy modern forest). We, however, suspect the lowest values in rhinos are genuinely explained by their habitat. Based on their known modern ecology, rhinoceroses are expected to occupy habitats that should be more negative than the average −26‰ (e.g., −29‰). TWN orangutan appears to have preferred and foraged in open C3 forests. Orangutan ancestors, having been arboreal and sometimes terrestrial woodland inhabitants during the Neogene, became larger bodied and fully terrestrial during the Middle Pleistocene, and by the Late Pleistocene, they finally became forest inhabitants (Smith and Pilbeam 1980; Ho et al. 1995). The approximate 30% of dietary C4 for TWN orangutan correspond better to the orangutan's ancestry from Southern China and Pakistan, which supposes they evolved in more temperate and seasonal climates with higher flexibility in feeding and preferences for open environments (Ho et al. 1995; Chaimanee et al. 2003). The Middle Pleistocene Chinese orangutan was larger in size than modern species and mostly terrestrial, having been unable to climb trees (Smith and Pilbeam 1980).

However, the δ^{13}C bioapatite values of the late Middle Pleistocene orangutan are still consistent with C3 vegetation being the dominant forage (probably fruits and leaves), similar to modern orangutans' diet, despite the availability of the whole range of environments and C4 plants that some suids and porcupine used. This result is consistent with the new evidence of orangutan's closer origin in Thailand, *Khoratpithecus*, which suggests its ancestor evolved under tropical similar to modern conditions (Chaimanee et al. 2004). These data are also similar to what is observed in modern chimpanzees (Sponheimer et al. 2006), while C4 resources are available to the primates only C3 resources are utilised.

It is possible that similar to rhinos, dietary percentage of C4 in orangutan depends on the differences in fractionation and more exact habitat δ^{13}C resolution. TWN orangutan's dietary percentage of C4 can be around 10% and decreasing to about 2% if the average for C3 and C4 habitats are higher (−24‰ and −8‰) or fractionation higher than +9‰, thus corresponding better to the orangutan's modern ecology. While it may be difficult to extrapolate the exact percentage of C4 plants consumed by TWN orangutans, it is clear that C4 consumption decreased into the Holocene.

The fact that the species are 'hiding' in remote places is probably related not only to the apparent increase in C3 vegetation but possibly also to direct or indirect anthropogenic pressures. While considerable interest has been brought to North American, Northern Eurasian and Australian Pleistocene and Holocene extinctions, South Eurasian extinctions have received the least amount of attention (Louys et al. 2007). Human influence already has been recognised in the fate of many species across the world (e.g., Nowak 1999; Hofreiter 2007) during the Holocene and especially, the last 500 years (Pushkina and Raia 2008). Many species trace their way of life to which they have become adapted through years of evolution to undisturbed and anthropologically inaccessible areas (Pushkina 2007, Pushkina and Raia 2008). For instance, behavioural changes occurred in a vast majority if not all large mostly diurnal Southeast Asian species (e.g., banteng, kouprey, etc.). While these species could be active at any time of the day, they became nocturnal in areas where they have been harassed by humans (Nowak 1999).

Currently, our results show great differences occurring in habitat and species diets when comparing modern and late Middle Pleistocene mammals in Southeastern Asia. Our data further implicate a human influence for modern species' ecology in Thailand. Future analyses on better dated and more numerous samples are needed to test our implications that humans affect the modern changes in remaining species foraging behaviour, distribution and survival.

The trend of shifting deeper into the forest is visible for all modern species analysed in this study although not always statistically significant.

Conclusions

Stable carbon isotope results from the enamel of terrestrial mammals from the late Middle Pleistocene TWN locality in Northeastern Thailand record the range of habitats in that area from closed-canopy forest to open C3 and C4 habitats. All analysed TWN bovids and the majority of cervids foraged in open C4 habitats likely including over 70% C4 plants in their diet. Data also show that carnivores likely preyed on the C4 consumers, yet incorporating some C3 consumers. Rhinoceroses and orangutan appear to have maintained their preferred forested C3 habitat through time (deep canopy forest for rhino and open C3 environment or high in the canopy for orangutan). Interesting is the separation of species diet and habitat preferences among the ungulates. TWN rhinos had the lowest δ^{13}C values indicating habitat and possibly physiological (hindgut fermenters) differences. Various species can have different δ^{13}C fractionation values depending on their habitat and rhinos could be a future study subject. There are implications of different timing and trends of the spread and distribution of the C4 plants in southern Eurasia associated with changing climate and vegetation cover in Thailand. Southeast Asia southward of Tibet could be part of the global C4 vegetation spread, although C4% in ecosystems varied among places. Despite an apparent modern reversal towards C3 vegetation due to increasing CO_2 or other climatic and environmental factors, anthropogenic pressure is currently known for many species original habitat and distribution and likely had an effect on them. It can well be responsible for a drastic habitat change deeper into the forest for the mainland serow as the most common bovid in TWN. To discern the above mentioned suppositions, future stable isotope studies are needed in Thailand.

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References

Bender MM (1968) Mass spectrometric studies of carbon 13 variations in corn and other grasses. Am J Sci Radiocarbon suppl 10:468–472

Bocherens H (2000) Preservation of isotopic signals (^{13}C, ^{15}N) in Pleistocene mammals. In: Katzenberg MA, Ambrose SH (eds) Biogeochemical approaches to paleodietary analyses. Kluwer Academic/Plenum Publishers, New York, pp 65–88

Bocherens H, Drucker DG (2007) Carbonate stable isotopes/terrestrial teeth and bones. In: Elias S (ed) Encyclopedia of Quaternary Sciences. Elsevier, pp 309–316

Bocherens H, Sen S (1998) Pliocene vertebrate locality of Çalta, Ankara, Turkey 11. Isotopic investigation. Geodiversitas 20:487–495

Bocherens H, Fizet M, Mariotti A, Bellon G, Borel JP (1994) Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie 10. Biogéochim isotop Bull Mus Hist Nat, 4 sér 16 C (1):211–223

Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger JJ (1996) Isotopic biogeochemistry (^{13}C, ^{18}O) of mammal enamel from African Pleistocene hominid sites: implications for the preservation of paleoclimatic isotopic signals. Palaios. doi:0883-1351/96/0011-0306

Bocherens H, Jacques L, Ogle N, Moussa I, Kalin R, Vignaud P, Brunet M (2009) Reply to the comment by A Zazzo, WP Patterson, TC Prokopiuk on Implications of diagenesis for the isotopic analysis of Upper Miocene large mammalian herbivore tooth enamel from Chad by Jacques et al (2008) Palaeogeogr Palaeoclimatol Palaeoecol 266:200-210. Palaeogeogr Palaeoclimatol Palaeoecol 277:269–271

Buchholtz C (1989) Cattle. In: Parker S (ed) Grzimek's Encyclopedia of Mammals, vol 5. McGraw-Hill, New York, pp 360–417

Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120:347–363

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) Global vegetation change through the Miocene–Pliocene boundary. Nature 389:153–15

Cerling TE, Harris JM, Leakey MG (1999) Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120:364–374

Chaimanee Y (1998) Plio–Pleistocene rodents of Thailand. Thai Studies Biodivers 3:1–303

Chaimanee Y (2007) Late Pleistocene vertebrate records from Southeast Asia. In: Elias S (ed) Encyclopedia of Quaternary Sciences. Elsevier, pp 3189–3197

Chaimanee Y, Jolly D, Benammi M, Tafforeau P, Duzer D, Moussa I, Jaeger JJ (2003) A Middle Miocene hominoid from Thailand and orangutan origin. Nature. doi:10.1038

Chaimanee Y, Suteethorn V, Jintasakul P, Vidthayanon C, Marandat B, Jaeger JJ (2004) A new orangutan relative from the Late Miocene of Thailand. Nature 427:439–441

Deng T (2006) Paleoecological comparison between late Miocene localities of China and Greece based on *Hipparion* faunas. Geodiversitas 28:499–516

Drucker DG, Bocherens H (2009) Carbon stable isotopes of mammal bones as tracers of canopy development and habitat use in temperate and boreal contexts. In: Creighton JD, Roney PJ (eds) Forest canopies: forest production, ecosystem health, and climate conditions. Nova Science Pulishers Inc

Drucker D, Bocherens H, Bridault A, Billiou D (2003) Carbon and nitrogen isotopic composition of red deer (*Cervus elaphus*) collagen as a tool for tracking palaeoenvironmental change during the Late-Glacial and Early Holocene in the northern Jura (France). Palaeogeogr Palaeoclimatol Palaeoecol 195:375–388

Drucker DG, Bridault A, Hobson KA, Szuma E, Bocherens H (2008) Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. Palaeogeogr Palaeoclimatol Palaeoecol 266:69–82

Ehleringer JR, Lin ZF, Field CR, Sun GC, Kuo CY (1987) Leaf carbon isotope ratios of plants from a subtropical monsoon forest. Oecologia 72:109–114

Esposito M, Reyss JL, Chaimanee Y, Jaeger JJ (2002) U-Series dating of fossil teeth and carbonates from Snake Cave, Thailand. J Archaeol Sci. doi:10.1006/jasc.2002.0718

Feranec RS (2007) Stable carbon isotope values reveal evidence of resource partitioning among ungulates from modern C3-dominated ecosystems in North America. Palaeogeogr Palaeoclimatol Palaeoecol 252:575–585

Feranec RS, MacFadden BJ (2006) Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. Paleobiology 32:191–205

Fortelius M, Eronen J, Jernvall J, Liu LP, Pushkina D, Rinne J, Teaskov A, Vislobokova I, Zhang ZQ, Zhou LP (2002) Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. Evol Ecol Res 4:1005–1016

Fortelius M, Eronen JT, Liu L, Pushkina D, Tesakov A, Vislobokova IA, Zhang Z (2006) Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. Palaeogeogr Palaeoclimatol Palaeoecol 238:219–227

Gaboardi M, Deng T, Wang Y (2005) Middle Pleistocene climate and habitat change at Zhoukoudian, China, from the carbon and oxygen isotopic record from herbivore tooth enamel. Quat Res 63:329–338

Gebauer G, Schulze E-D (1991) Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. Oecologia 87:198–207

Ho CK, Zhou GX, Swindler DR (1995) Dental evolution of the Orang-Utan in China. Hum Evol. doi:35400004426566.0010

Hofreiter M (2007) Pleistocene extinctions: haunting the survivors. Curr Biol 17:609–611

Keeley JE, Rundel PW (2005) Fire and the Miocene expansion of C4 grasslands. Ecol Lett. doi:10.1111/j.1461-0248.2005.00767.x

Koch PL (1998) Isotopic reconstruction of past continental environments. Ann Rev Earth Planetary Sci 26:573–613

Koch PL, Hoppe KA, Webb SD (1998) The isotopic ecology of late Pleistocene mammals in North America. I. Florida. Chem Geol. doi:10.1016/S0009-2541(98)00101-6

Kohn MJ, Cerling TE (2002) Stable isotope compositions of biological apatite. Rev Mineral Geochem. doi:10.2138/rmg.2002.48.12

Lee-Thorp JA, van der Merwe NJ (1987) Carbon isotope analysis of fossil bone apatite. S Afr J Sci 83:71–74

Lee-Thorp JA, Sealy JC, van der Merwe NJ (1989) Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. J Archaeol Sci 16:585–599

Lekagul B, McNeely JA (1977) Mammals of Thailand, Association for the Conservation of Wildlife. Kulusapa, Bangkok

Louys J, Curnoe D, Tong H (2007) Characteristics of Pleistocene megafauna extinctions in Southeast Asia. Palaeogeogr Palaeoclimatol Palaeoecol 243:152–173

MacFadden B, Solounias N, Cerling T (1999) Ancient diets, ecology, and extinction of 5 million-year-old horse from Florida. Science 283:824–827

Marino BD, McElroy MB (1991) Isotopic composition of atmospheric CO_2 inferred from carbon in C4 plant cellulose. Nature 249:127–131

Morgan M, Kingston J, Marino B (1994) Carbon isotopic evidence for the emergence of C4 plants in the Neogene from Pakistan and Kenya. Nature 367:162–165

Nahle N (2007) Total Solar Irradiance and Climate Change. Biology Cabinet Organization. http://www.biocab.org/SI_Anom_T_Anom.html. Last reading: 07 May 2008

Nowak R (1999) Walker's Mammals of the World. Vol II, 6th edn. Johns Hopkins University Press, Baltimore

Quade J, Cerling TE (1995) Expansion of C4 grasslands in the Late Miocene of Northern Pakistan-evidence from stable isotopes in paleosols. Palaeogeogr Palaeoclimatol Palaeoecol 115:91–116

Quade J, Cerling TE, Bowman JR (1989) Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature 342:163–166

Quade J, Solounias N, Cerling TE (1994) Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. Palaeogeogr Palaeoclimatol Palaeoecol 108:41–53

Pagani M, Freeman KH, Arthur MA (1999) Late Miocene atmospheric CO2 and the expansion of C4 grasses. Science 285:876–879

Palmqvist P, Perez-Claros JA, Janis CM, Figueirido B, Torregrosa V, Grocke DR (2008) Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. Palaios. doi:10.2110/palo.2007.p07-073r

Passey BH, Robinson TF, Ayliffe LK, Cerling TE, Sponheimer M, Dearing MD, Roeder BL, Ehleringer JR (2005) Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals. J Archaeol Sci 32:1459–1470

Passey BH, Eronen JT, Fortelius M, Zhang ZQ (2007) Paleodiets and paleoenvironments of late Miocene gazelles from North China: evidence from stable carbon isotopes. Vertebr Palasiat 45:118–127

Passey BH, Ayliffe LK, Kaakinen A, Eronen JT, Zhang ZQ, Cerling TE, Fortelius M (2009) Strengthened East Asian summer monsoons during a period of high-latitude warmth? Isotopic evidence from Mio-Pliocene fossil mammals and soil carbonates from northern China. Earth Planetary Sci Lett 277:443–452

Pushkina D (2006) Dynamics of the mammalian fauna in southern Siberia during the late Palaeolithic. Vertebr Palasiat 44:262–273

Pushkina D (2007) The Pleistocene easternmost Eurasian distribution of the species associated with the Eemian *Palaeoloxodon antiquus* assemblage. Mamm Rev 37:224–245

Pushkina D, Raia P (2008) Human influence on distribution and extinctions of the late Pleistocene Eurasian megafauna. J Hum Evol. doi:10.1016/j.jhevol. 2007.09.024

Ruddiman WF, Kutzbach JE (1989) Forcing the late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American West. J Geophys Res 94:409–427

Ruddiman WF, Kutzbach JE (1990) Late Cenozoic plateau uplift and climate change. Trans R Soc Edinb Earth Sci 81:301–314

Schleser GH, Jayasekera R (1985) δ^{13}C-variations of leaves in forests as an indication of reassimilated CO_2 from the soil. Oecologia 65:536–542

Ségalen L, Lee-Thorp JA, Cerling T (2007) Timing of C4 grass expansion across sub-Saharan Africa. J Hum Evol. doi:10.1016/j.jhevol. 2006.12.010

Smith BN, Epstein S (1971) Two categories of 13C/12C ratios for higher plants. Plant Physiol 47:380–384

Smith RJ, Pilbeam DR (1980) Evolution of the orangutan. Nature. doi:10.1038/284447a0

Sponheimer M, Loudon JE, Codron D, Howells ME, Pruetz JD, Codron J, de Ruiter DJ, Lee-Thorp JA (2006) Do savanna chimpanzees consume C4 resources? J Hum Evol 51:128–133

Tougard C (2001) Biogeography and migration routes of large mammal faunas in South-East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. Palaeogeogr Palaeoclimatol Palaeoecol 168:337–358

Tougard C, Montuire S (2006) Pleistocene paleoenvironmental reconstructions and mammalian evolution in South-East Asia: focus on fossil faunas from Thailand. Quat Sci Rev. doi:10.1016/j.quascirev.2005.04.010

Tütken T, Furrer H, Vennemann TW (2007) Stable isotope compositions of mammoth teeth from Niederweningen, Switzerland: Implications for the Late Pleistocene climate, environment, and diet. Quat Int doi:10.1016/j.quaint.2006.09.004

Urton EJM, Hobson KA (2005) Intrapopulation variation in gray wolf isotope (δ^{15}N and δ^{13}C) profiles: implications for the ecology of individuals. Oecologia 145:316–325

van der Merwe NJ, Medina E (1989) Photosynthesis and 13C/12C ratios in Amazonian rain forests. Geochim Cosmochim Acta 53:1091–1094

van der Merwe NJ, Medina E (1991) The canopy effect, carbon isotope ratios and foodwebs in Amazonia. J Archaeol Sci 18:249–259

Vogel JC, Fuls A, Ellis RP (1978) The geographic distribution of kranz grasses in southern Africa. S Afr J Sci 75:209–215

Wang Y, Deng T (2005) A 25 my isotopic record of paleodiet and environmental change from fossil mammals and paleosols from the NE margin of the Tibetan Plateau. Earth Planet Sci Lett. doi:10.1016/j.epsl.2005.05.006

Wang Y, Deng T, Biasatti D (2006) Ancient diets indicate significant uplift of southern Tibet after ca 7 Ma. Geol 34:309–312

Wang W, Potts R, Baoyin Y, Huang W, Cheng H, Edwards RL, Ditchfield P (2007) Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China. J Hum Evol. doi:10.1016/j.jhevol. 2006.10.003

Woodruff DS (2003) Neogene marine transgression, palaeogeography and biogeographic transitions on the Thai-Malay Peninsula. J Biogeogr 30:551–567