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Stable carbon and oxygen isotopic evidence for Late Cenozoic environmental change in Northern China

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ABSTRACT

Stable carbon and oxygen isotope ratios of 311 enamel samples from a diverse group of herbivorous mammals including Equidae, Rhinocerotidae, Bovidae, Rodentia and Ochotonidaewere were analyzed in order to reconstruct the Late Cenozoic history of vegetation and environmental change in the Yushe Basin in North China. The $\delta^{13}C$ values of bulk and serial enamel samples from large mammals show a wide range of variation from −13.3‰ to 1.4‰, with a mean of −7.4‰ ± 3.5‰ (n = 294). This indicates that large herbivorous mammals in the area had a variety of diets since 6.5 Ma, ranging from pure C_3 to mixed C_3–C_4 and pure C_4 diets. In contrast, the $\delta^{13}C$ values of small mammals vary from −11.9‰ to −7.6‰, with a mean of −9.7 ± 1.1‰ (n = 17), indicating that rodents and ochotonids were feeding mostly on C_3 plants. Variations in $\delta^{13}C$ values within and between species reflect the variations in the habitat and the vegetation consumed by the animals. In general, horses had higher amounts of C_4 grasses in their diets than other contemporary taxa such as bovids, rhinos, rodents and deer, suggesting that horses exploited more open habitats such as grasslands while deer, rhinos and rodents may have preferred more C_3 vegetation, which is more indicative of forested environments. The carbon isotope data show that C_4 grasses have been an important component of horses' diets and of local ecosystems since ~6.5 Ma, confirming that the "late Miocene C_4 expansion" occurred in North China as it did in Africa, Indian subcontinent and the Americas. This supports a global factor as a main driver of the late Miocene C_4 expansion. The combined carbon and oxygen isotope data reveal major shifts in climate to drier and/or warmer conditions after ~5.8, ~4.1, ~3.3, and ~2.5 Ma, and significant shifts to relatively wetter and/or cooler conditions after ~6.4, ~5, ~3.5 Ma. The shifts to drier and/or warmer climate after ~5.8 Ma and ~2.5 Ma coincide with two major fauna turnover events. Intra-tooth $\delta^{13}C$ and $\delta^{18}O$ values are negatively correlated within individual modern teeth and some fossil teeth, displaying the characteristic pattern of the summer monsoon regime and confirming a strong monsoon influence in the area since at least the early Pliocene. The data also suggest that the C_4 abundance in the area has fluctuated over the past 6.5 Ma in response to changes in climate, with more C_4 grasses during warmer and/or drier periods and a reduced C_4 component at cooler and/or wetter times.

1. Introduction

The Himalayan–Tibetan Plateau (HTP), one of the most significant topographic features on Earth, is thought to be important in driving the modern Asian monsoons and affecting global atmospheric circulation, climate and erosion (e.g., Kutzbach, 1987; Webster, 1987; Molnar and England, 1990; Prell and Kutzbach, 1992; Molnar et al., 1993; An et al., 2001; Wang et al., 2012). However, the timing of the Tibetan uplift is still a hotly debated issue. The uplift of the HTP would have affected the west-to-east airflow across the northern hemisphere, increased the precipitation along the Himalayas, and prevented the entry of warm humid monsoonal air from the East Pacific Ocean and Indian Ocean into the large area behind the high mountains, resulting in drying in central Asia and a strong southeast-to-northwest precipitation gradient in East Asia. In addition, the high mountains serve as geographic barriers to biological migration (Barry and Flynn, 1990; Qiu, 1990). These changes in climate and geography caused by the uplift of the HTP would have had a profound effect on ecosystems and mammalian evolution in the region. Therefore, long-term records of vegetation, fossil mammals, and climate changes in China are not only important in understanding paleoecology and paleoclimate in East Asia but also may shed some light on the growth history of the Himalayan–Tibetan Plateau. Furthermore, understanding the past climatic conditions and how and why they change is crucial for predicting future changes in climate.

Stable carbon and oxygen isotope analyses of fossil mammalian tooth enamel have been established as an important tool in

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paleoclimate research (e.g., Ericson et al., 1981; Lee-Thorp et al., 1989; Koch et al.,1992; Quade et al., 1992; Cerling et al., 1993; Wang et al., 1993; MacFadden et al., 1994; Quade et al., 1994; Wang and Cerling, 1994; Wang et al., 1994; Fricke et al., 1995; Lee-Thorp and Beaumont, 1995; Bochernens et al., 1996; Cerling et al., 1997a,b; MacFadden et al., 1999a,b; MacFadden, 2000a,b,c). Tooth enamel often preserves its original isotopic signatures that reflect the isotopic compositions of the diet and water ingested by an animal (Ayliffe et al., 1994; Bryant et al., 1994; Wang and Cerling, 1994; Fricke et al., 1995). Calcified tissues (i.e., bone, tooth enamel and dentine) are primarily made of hydroxyapatite ($Ca_{10}(PO_4)_6(OH)_2$), which contains a small amount of structural carbonate (Wang and Cerling, 1994). Studies have shown a consistent carbon isotope fractionation between structural carbonate in hydroxyapatite and the diet (Lee-Thorp and van der Merwe, 1987; Lee-Thorp et al., 1989; Wang et al., 1994; Cerling et al., 1997a). As a result, the stable carbon isotope ratios ($\delta^{13}C$ values) of structural carbonate in hydroxyapatite from herbivores can be used to determine the proportions of C_3 and C_4 plants in their diets and the types of vegetation available for consumption in local ecosystems (e.g., Lee-Thorp et al., 1989; MacFadden and Cerling, 1994; Wang et al., 1994; Cerling et al., 1997a,b; Koch, 1998; MacFadden et al., 1999a,b; Kohn and Cerling, 2002; Wang and Deng, 2005; Wang et al., 2006; Wang et al., 2006; Wang et al., 2008a,b). The oxygen isotope ratios ($\delta^{18}O$) of enamel from large mammals are strongly correlated with the $\delta^{18}O$ of local meteoric water (e.g., Bryant et al., 1994, 1996; Kohn and Cerling, 2002; Wang et al., 2008a,b). Because the $\delta^{18}O$ of meteoric water is sensitive to climatic variables such as temperature, seasonality of rain, and the amount of rain (Dansgaard, 1964; Rozanski et al., 1992), the $\delta^{18}O$ of tooth enamel has been used as a proxy for paleoclimatic conditions during tooth growth (e.g., Longinelli, 1984; Koch et al., 1989; D'Angela and Longinelli, 1993).

Furthermore, carbon and oxygen isotopic analyses of serial samples collected along the length of a tooth can provide a detailed record of seasonal variations in diet and climate during the time of mineralization of the tooth (up to 2–3 years for horses) (e.g., Koch et al., 1995; Fricke and O'Neil, 1996; Sharp and Cerling, 1998; Balassee et al., 2003; Nelson, 2005; Sponheimer et al., 2006). When the $\delta^{18}O$ values of serial enamel samples from an individual tooth are plotted, they often show troughs and peaks reflecting the seasonal changes in the $\delta^{18}O$ of local meteoric water, with peaks generally representing the summer months (Fricke and O'Neil, 1996; Sharp and Cerling, 1998). However, in Asian summer monsoon regions, the $\delta^{18}O$ peaks would correspond to winter months because summer precipitation has lower $\delta^{18}O$ values than the winter precipitation in the Asian monsoon region (Araguas-Araguas et al., 1998; Johnson and Ingram, 2004; Biasatti et al., 2010).

In this study, we determined the stable carbon and oxygen isotopic compositions of both fossil and modern herbivores including *Equus* (horse), *Hipparion* (horse), rhinos, bovids (goat, gazelle, cow), rodents and *Ochotonoides* from the Yushe Basin in North China. The data were used to examine long-term changes in diets and environments of mammals in the area over the past 6–7 million years. The results from this study were also compared with the data from other localities in the region to improve our understanding of the development of C_4 ecosystems in North China and the effects of Tibetan uplift on regional climate and ecosystems.

2. Study area

Yushe Basin (37.07°N, 112.98°E, elevation of 1045 m) is located at the eastern margin of the Loess Plateau (Fig. 1) and near the boundary between the temperate deciduous forest and steppe vegetation zones today (Liu, 1988). The basin covers 1875 km^2, but outcrops are patchy and the fossils are from a smaller portion of the basin, mostly the Yuncu sub-basin (Tedford et al., 2013). The present-day climate in the Yushe Basin is strongly controlled by East Asian monsoons that result in a strong seasonality in temperature and precipitation, with most of the precipitation falling during the summer. The thick late Cenozoic deposits in the basin – the Yushe Group – contain many fossil horizons with different species of mammalian fossils, providing a long and detailed record of biological and geological events (Tedford et al., 1991).

The late Cenozoic sedimentary sequence in the basin spans an age range from the late Miocene to the Holocene (Qiu et al., 1987; Tedford et al., 1991; Flynn et al., 1995; Flynn and Wang, 1997; Flynn and Wu, 2001). It consists primarily of fluvial, alluvial and lacustrine sediments, with a minimum total thickness of 800 m. The Yushe Group has been divided into four formations, the Mahui, Gaozhuang, Mazegou and Haiyan formations (Fig. 1., Tedford et al., 1991; Flynn, 1997; Flynn et al., 1997), which is overlain by the Pleistocene loess deposits containing paleosols and calcerous nodules (Liu et al., 1985; Tedford et al., 1991).

The Mahui Formation lies on Triassic bedrock and includes many Baodean elements (i.e., the "*Hipparion* Fauna"), murids and *Stegodon*. It also has the last records of the browsing horse *Sinohippus*, the hyaena *Adcrocuta*, and the bear *Indarctos*, the first North China elephant *Stegodon*, and diverse pigs, giraffes and deer. The overlying Gaozhuang Formation includes early camels and canids, advanced hipparionine horses, and high crowned gazelles. The Mazegou Formation contains similar fauna including several additional taxa such as *Felis*, *Lynx*,

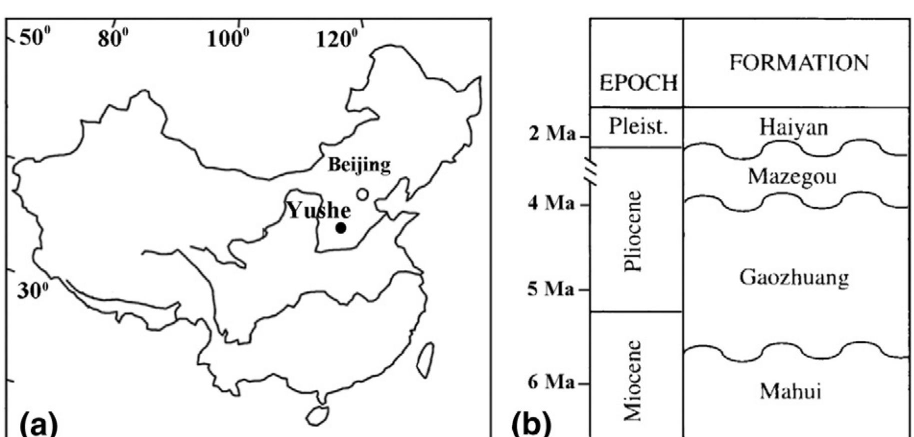

Fig. 1. (a) Location map and (b) chronostratigraphy of Yushe Basin, North China (modified from Flynn et al., 1997; Wang et al., 2006).

Homotherium, *Vulpes*, *Canis*, *Dama*, *Rusa*, several bovids and mammoth *Archidiskodon* (Flynn, 1997). The Haiyan Formation fauna greatly differs from the fauna of Mazegou Formation and contains advanced arvicolides and zokors (Flynn and Wu, 2001).

Ages of the fossils were estimated based primarily on the geological and paleomagnetic work of Tedford et al. (2013) and Opdyke et al. (2013). There are two important periods of turnover recorded in the Yushe Basin (Flynn et al., 1991; Tedford et al., 1991). The first turnover is across the Mahui–Gaozhang hiatus, in excess of 5 Ma, and 40% of the Mahui genera could not cross this interval, signaling the demise of late Miocene "*Hipparion* Fauna" (Kurten, 1952; Tedford et al., 1991). The second turnover is at the Mazegou–Haiyan boundary during a hiatus of at least 0.4 m.y., with the loss of about 25% of the Mazegou fauna. In addition, 27% of the Haiyan genera failed to continue in the Pleistocene. Small mammals also show major events of turnover near the Miocene/Pliocene boundary and in the late Pliocene (Flynn et al., 1991). The high faunal diversity and the presence of certain mammals (e.g., beavers, voles and bamboo rats) suggest that the Yushe Basin probably had an equable climate and probably wooded habitats until the Pleistocene and the faunal break at the Mazegou–Haiyan boundary may be related to changing climate and precipitation patterns (Flynn et al., 2011; Tedford et al., 2013).

3. Materials and methods

Stable carbon and oxygen isotope ratios of 311 enamel samples from 46 well preserved fossil and modern teeth collected from Yushe Basin (Suppl. Table 1) were analyzed to reconstruct the paleodiets and the paleoenvironment in the area. We selected M3, P4, P3 and P2, whenever possible, to avoid the potential "milk effect". Of all the teeth analyzed, only two fossil teeth – a M1 (ZL-3-t3) and a M2 (NZG-1-t1) – were formed before weaning. The milk effects are largely unstudied. But, available data suggest that they are small and insignificant relative to the natural isotopic variability of diet and water (Wang et al., 2008a; Kimura et al., 2013). Thus, data from these two early erupting teeth will unlikely affect the conclusions of the study. These samples represent a diverse group of herbivores including *Equus* (horse), *Hipparion* (horse), rhinos, deer, bovids and small mammals (i.e., rodents and ochotonoides), and range in age from 6.5 Ma to the present. For bulk enamel samples, the teeth or tooth fragments were cleaned by scraping off any dirt, dentine and other matter using a rotary tool, and then the cleaned enamel was ground into a fine powder using a mortar and pestle. Serial enamel samples were obtained from 18 selected teeth by drilling at different points along their growth axes with a rotary tool. All of the samples were prepared following the treatment procedure described in Wang and Deng (2005). The sample powder was treated with 5% sodium hypochlorite overnight to remove organic matter, followed by treatment with 1 M acetic acid over night to get rid of non-structural carbonate. The treated samples were then cleaned with distilled water at least three times, and finally freeze-dried. The enamel samples were then converted to CO_2 by reaction with 100% phosphoric acid for approximately 72 h at 25 °C; the carbon and oxygen isotope ratios of the resulting CO_2 were then analyzed using a Gas Bench II Autocarbonate device connected to a Finnigan MAT Delta Plus XP stable isotope ratio mass spectrometer at the Florida State University. The results are reported in the standard notation as $\delta^{13}C$ and $\delta^{18}O$ ($\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{18}O/{}^{16}O$), and the reference standard is the international carbonate standard V-PDB (Vienna Pee Dee Belemnite). The analytical precision (based on replicate analyses of lab standards processed with each batch of samples) is $\pm 0.1‰$ (1σ) or better for both $\delta^{13}C$ and $\delta^{18}O$. Sample ID prefixes ZL, HY, YSM, MZG,GZ, NGZ, and BMH are abbreviations for Zao-ling-gou, Haiyan, Yushe Museum, Mazegou, Gaozhuang, Nanzhuanggou, and Baimahui, respectively.

Table 1
Summary results of stable carbon and oxygen isotope analysis of herbivore teeth from Yushe Basin, N. China.

Age	Taxon	Average $\delta^{13}C$	1σ	Average $\delta^{18}O$	1σ	No. of teeth	No. of samples	Note
0	Bovid	−1.8	3.2	−6.3	2.0	1	19	This study
0	Goat	−10.2	2.3	−2.3	3.0	2	26	This study
2	Deer	−12.4		−9.4		1	1	Passey et al. (2009)
2	Horse	−2.8	0.2	−5.6	0.2	2	2	Passey et al. (2009)
2.2	Rodent	−11.3	0.9	−6.6	0.0	2	2	This study
2.5	Herbivore	−9.9	0.1	−5.2	0.6	1	7	This study
2.5	Horse	−8.6	1.7	−7.1	0.6	2	48	This study
3	Horse	−5.4	0.7	−6.6	0.0	2	2	This study
3.2	Bovid	−10.1	0.0	−6.4	0.3	2	2	Passey et al. (2009)
3.3	Horse	−9.4	0.8	−8.2	1.0	1	13	This study
3.3	Rhino	−10.9	0.7	−8.7	0.5	2	27	This study
3.35	Rodent	−9.6	0.8	−7.9	2.1	5	5	This study
3.5	Horse	−3.5	2.1	−4.8	1.5	6	6	Passey et al. (2009)
3.7	Bovid	−10.2	0.3	−2.8	0.4	2	2	Passey et al. (2009)
4.1	Horse	−5.2	1.7	−6.2	1.5	7	55	This study
4.2	Rhino	−9.3	2.0	−8.4	0.8	3	20	This study
4.35	Deer	−9.9		−5.8		1	1	Passey et al. (2009)
4.4	Bovid	−11.7	1.5	−7.0	1.6	2	2	Passey et al. (2009)
4.5	Rhino	−11.9	0.2	−6.6	0.7	1	11	This study
4.5	Rodent	−9.0	1.2	−7.4	0.9	6	6	This study
4.6	Bovid	−8.5		−2.9		1	1	Passey et al. (2009)
4.6	Horse	−4.9	1.6	−5.6	1.2	6	27	This study[a]
5	Horse	−0.5	1.1	−3.3	1.7	1	16	This study
5.6	Deer	−9.1		−9.4		1	1	This study
5.8	Horse	−6.9	2.3	−6.2	1.1	5	5	This study[a]
6	Rodent	−10.1	0.7	−6.4	0.4	4	4	This study
6.2	Bovid	−9.8	1.7	−5.3	0.7	4	4	This study
6.23	Deer	−10.9		−5.1		1	1	Passey et al. (2009)
6.3	Rhino	−10.1		−3.9		1	1	Passey et al. (2009)
6.4	Horse	−8.3	1.9	−5.2	0.8	6	24	This study[a]
6.5	Herbivore	−10.2		−6.9		1	1	This study

[a] Included a few samples from Passey et al., 2009.

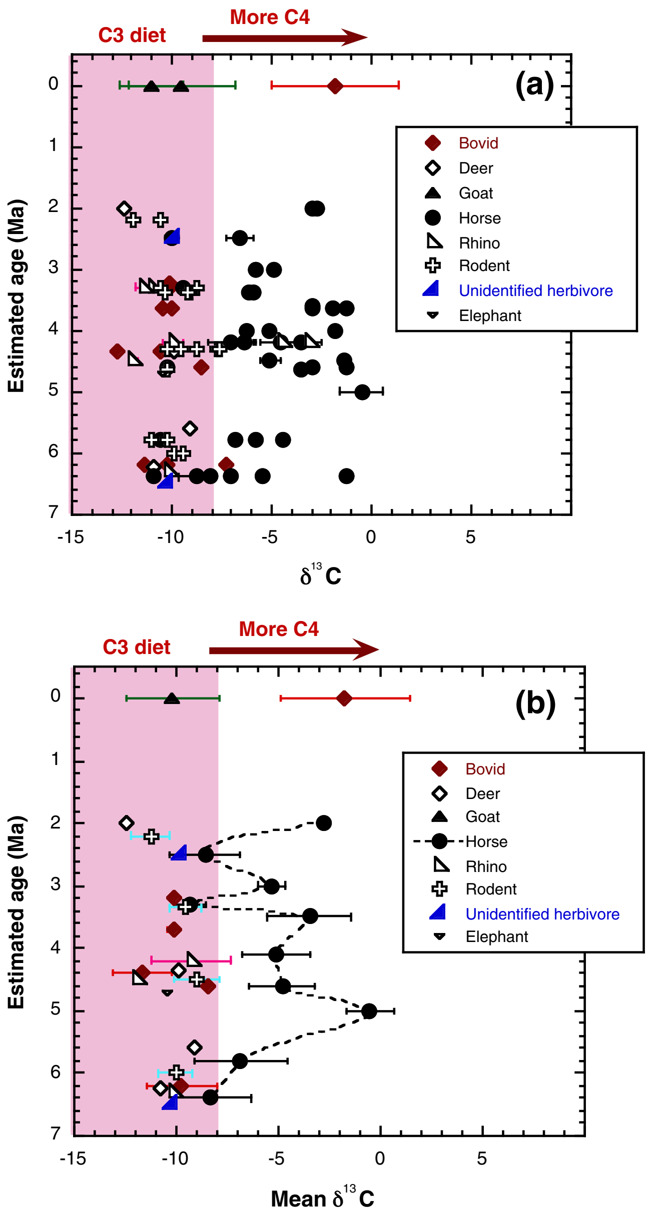

Fig. 2. (a) $\delta^{13}C$ values of bulk enamel samples and (b) mean $\delta^{13}C$ values of various herbivores from Yushe, North China (including data from Passey et al., 2009). For any tooth that was serial-sampled, the bulk $\delta^{13}C$ value for that tooth in (a) was calculated by averaging all its serial data. Error bars indicate 1 standard deviation (1σ) from the mean.

4. Results and discussion

4.1. Carbon isotopic composition of tooth enamel, diets and ecosystem change

The tooth enamel $\delta^{13}C$ values reflect the $\delta^{13}C$ composition of the diet that is primarily determined by the relative amounts of C_3 and C_4 plants digested by an animal. C_3 plants (trees, most shrubs, forbs and cool season grasses) have a $\delta^{13}C$ range of −34‰ to −22‰; C_4 plants (mostly warm season grasses) have $\delta^{13}C$ of −9‰ to −17‰ (Deines, 1980; O'Leary, 1988; Farquhar et al., 1989). There is a consistent carbon isotope offset ($\varepsilon_{en\text{-}diet}$) of ~14‰ between structural carbonate in hydroxyapatite and the diet due to biochemical fractionation for large herbivores (Lee-Thorp and van der Merwe, 1987; Lee-Thorp et al., 1989; Wang et al., 1994; Cerling et al., 1997a). For small mammals, the $\varepsilon_{en\text{-}diet}$ value is estimated to be about 11‰ (Passey et al., 2005). As a result, for modern herbivores, an enamel-$\delta^{13}C$ value of −9‰ or less in general indicates a pure C_3 diet, while enamel $\delta^{13}C$ values of −2‰ or higher indicate a pure C_4 diet. In water-stressed environments, the conservative "cut-off" value for a pure C_3 diet is −8‰ for modern samples and may be even −7‰ or higher for samples that were formed prior to the industrial resolution due to changes in the $\delta^{13}C$ of atmospheric CO_2 (Cerling et al., 1997a; Wang et al., 2008a; Passey et al., 2009).

The $\delta^{13}C$ values of bulk and serial enamel samples from large mammals from the Yushe Basin (Table 1; Suppl. Table 1) show a wide range of variation from −13.3‰ to 1.4‰, with a mean of −7.4 ± 3.5‰ (n = 294). This indicates that large herbivorous mammals in the area had a variety of diets over the last 6.5 million years, ranging from pure C_3 to mixed C_3–C_4 and pure C_4 diets (Fig. 2). In contrast, the enamel-$\delta^{13}C$ values of small mammals (rodents and *Ochotonoides* sp.) vary from −11.9‰ to −7.6‰, with a mean of −9.7 ± 1.1‰ (n = 17) (Fig. 2). Using the $\varepsilon_{en\text{-}diet}$ value of 11‰ for small mammals (Passey et al., 2005), these enamel-$\delta^{13}C$ values correspond to diet-$\delta^{13}C$ values of −21 ± 1‰, indicating that the diets of the small mammals consisted mostly of C_3 plants, with C_4 grasses accounting for less than 35% of their dietary intake. The enamel carbon isotope data suggest more diverse habitats than inferred from fossil assemblages (Flynn et al., 2011; Tedford et al., 2013). In addition to forests, the enamel-$\delta^{13}C$ data reveal that the Yushe Basin also had more open habitats (such as wooded grasslands or grasslands) containing some C_4 grasses.

The $\delta^{13}C$ data also show significant changes in diets over the past 6.5 Ma (Fig. 2). In the latest Miocene, while most of the mammals had C_3-based diets, about a third of the individuals (7 out of 23 individuals) had mixed C_3–C_4 diets as indicated by higher $\delta^{13}C$ values (>−8‰) (Fig. 2a; Supplementary Table). This suggests that the local ecosystems in the Yushe Basin were dominated by C_3 plants (i.e., trees, shrubs, cool season grasses) but contained some C_4 grasses as an important component at ~6.5–6 Ma (Fig. 2). Enamel $\delta^{13}C$ values increased significantly after ~5.8 Ma, indicating that C_4 grasses became a significant part of herbivores' diets and of local ecosystems since then (Fig. 2). Some of the $\delta^{13}C$ values fall on or near the boundary between C_3 and C_3–C_4 mixed diet (Fig. 2a), which indicate either intake of C_3 plants experiencing water-stressed conditions or ingestion of small amounts of C_4 plants. Variations in $\delta^{13}C$ values within and between species likely reflect variations in the habitat preference and the vegetation consumed by the animals. In general, horses had higher amounts of C_4 grasses in their diets than other contemporary taxa such as bovids, rhinos, rodents and deer, suggesting that horses lived in more open habitats such as grasslands while deer, rhinos and rodents may have preferred to live in or near more forested environments (Fig. 2). The mean enamel-$\delta^{13}C$ values from horses, however, show four prominent positive shifts after ~5.8, ~4.1, ~3.3, and ~2.5 Ma (Fig. 2b; Table 2), indicating significant changes in diet. These positive $\delta^{13}C$ shifts coincided with significant shifts in $\delta^{18}O$ values (Fig. 3b; Table 2), likely reflecting an increased proportion of C_4 biomass in local ecosystems in the Yushe Basin in response to changes in climate to drier and/or warmer conditions (Fig. 3b).

The carbon isotope data show that C_4 grasses had spread into the Yushe Basin by 6.5 Ma although the local ecosystems at that time were dominated by C_3 plants (Fig. 2). Because of the lack of samples older than 6.5 Ma, the exact timing of the expansion of C_4 plants into the area cannot be determined. Nonetheless, the results confirm that C_4 expansion occurred in North China in the late Miocene (Passey et al., 2009; Zhang et al., 2009) as it did in Africa, Indian subcontinent and the Americas, supporting a global factor as a driver of the late Miocene C_4 expansion (e.g., Cerling et al., 1997a).

4.2. Oxygen isotopes in tooth enamel and long-term climate change

The $\delta^{18}O$ of enamel is controlled by a number of factors including the $\delta^{18}O$ of ingested water (in drinks and food), physiological processes, and dietary and drinking behavior (e.g., Kohn, 1996). For large mammals,

Table 2
Two-tailed *t*-test results for significant isotopic differences between mean isotopic compositions of horses and bovids at different ages. MD (mean difference), df (degree of freedom), t (t value), p (t probability).

	Sample	MD (‰)	df	t	p	Significant difference at 95% CI?
Horse $\delta^{13}C$	6.4 Ma vs 5.8 Ma	1.4	27	−1.48	0.15	No
	5.8 MA vs 5 Ma	6.3	19	−8.51	<0.0001	Yes
	5 MA vs 4.6 Ma	4.3	41	9.51	<0.0001	Yes
	4.6 MA vs 4.1 Ma	0.3	80	0.83	0.4053	No
	4.1 MA vs 3.5 Ma	1.6	59	−2.27	0.02717	Yes
	3.5 MA vs 3.3 Ma	5.8	17	9.04	<0.0001	Yes
	3.3 MA vs 3.0 Ma	4.0	13	−6.37	<0.0001	Yes
	3.0 MA vs 2.5 Ma	3.2	48	2.65	0.01088	Yes
	2.5 MA vs 2 Ma	5.8	48	−4.71	<0.0001	Yes
Horse $\delta^{18}O$	6.4 Ma vs 5.8 Ma	0.9	27	2.26	0.03177	Yes
	5.8 MA vs 5 Ma	2.8	19	−3.41	0.00289	Yes
	5 MA vs 4.6 Ma	2.2	41	4.96	<0.0001	Yes
	4.6 MA vs 4.1 Ma	0.6	80	1.88	0.0632	No
	4.1 MA vs 3.5 Ma	1.4	59	−2.27	0.0271	Yes
	3.5 MA vs 3.3 Ma	3.5	17	6.04	<0.0001	Yes
	3.3 MA vs 3.0 Ma	1.6	13	−2.24	0.04284	Yes
	3.0 MA vs 2.5 Ma	0.5	48	1.04	0.3033	No
	2.5 MA vs 2 Ma	1.4	48	−3.13	0.00299	Yes
Bovid $\delta^{13}C$	6.2 Ma vs 4.6 Ma	1.2	4	−0.97	0.3849	No
	4.6 Ma vs 4.4 Ma	1.9	4	1.29	0.2677	No
	4.4 Ma vs 3.7 Ma	1.5	2	−1.36	0.3078	No
	3.7 Ma vs 3.2 Ma	0.1	2	−0.5	0.6667	No
	3.2 Ma vs < 3.2 Ma	2.5	61	−0.76	0.4484	No
Bovid $\delta^{18}O$	6.2 Ma vs 4.6 Ma	2.4	4	−4.51	0.0108	Yes
	4.6 Ma vs 4.4 Ma	4.1	2	3.72	0.06504	No
	4.4 Ma vs 3.7 Ma	4.3	2	−3.68	0.0665	No
	3.7 Ma vs 3.2 Ma	3.7	2	8.6	8.6023	No
	3.2 Ma vs < 3.2 Ma	2	61	−0.91	0.3665	No

their enamel $\delta^{18}O$ values are strongly correlated with the $\delta^{18}O$ of local meteoric water which provides drinking water and water in plants consumed by the animal although the relationship varies among animals (e.g., Longinelli, 1984; Luz et al., 1984; Kohn and Cerling, 2002; Wang et al., 2008a). Since the $\delta^{18}O$ of meteoric water is controlled by climate (Dansgaard, 1964), a significant $\delta^{18}O$ shift over time in enamel from the same taxon in a given region would indicate a change in regional climate (e.g., Longinelli, 1984; Koch et al., 1989; Wang and Deng, 2005; Wang et al., 2008a,b, 2013). In addition, the oxygen isotopic differences between different animals may be utilized as an aridity index (Levin et al., 2006; Yann et al., 2013). Because evaporation enriches leaf water in the heavy oxygen isotope ^{18}O relative to local meteoric water and the magnitude of this ^{18}O enrichment increases with increasing aridity (e.g., Yakir, 1992), animals that obtain a larger fraction of water from leaves tend to have higher enamel $\delta^{18}O$ values compared to co-existing obligate drinkers (e.g., Sponheimer and Lee-Thorp, 1999; Levin et al., 2006; Wang et al., 2008a). Thus, the difference between enamel-$\delta^{18}O$ values of "Evaporation Sensitive" (ES) animal (such as giraffids, dikdik, oryx and Camelidae) and "Evaporation Insensitive" (EI) animal (such as hippopotamus, elephant, rhino, and warthog) has been suggested as a viable indicator of the degree of aridity (Levin et al., 2006; Yann et al., 2013).

As shown in Fig. 3, co-existing horses and rhinos at 3.3 Ma had similar enamel-$\delta^{18}O$ values ($\Delta^{18}O_{horse-rhino} = 0.5‰$), suggesting the area was not under water-stress at that time. The 6.2-Ma deer and bovids also yielded very similar enamel-$\delta^{18}O$ values ($\Delta^{18}O_{deer-bovid} = 0.1‰$), but no contemporary EI species were available for analysis. One 2-Ma deer had a lower enamel-$\delta^{18}O$ value than contemporary horses ($\Delta^{18}O_{deer-horse} = -3.8‰$) while the enamel-$\delta^{18}O$ values of bovids living at 4.6 Ma were higher than those of co-existing horses by ~2.6‰ ($\Delta^{18}O_{bovid-horse} = 2.6‰$; Fig. 3b). Because of a lack of sufficient samples from co-coexisting EI animals, it is currently impossible to apply the enamel $\Delta^{18}O_{ES-EI}$ index to the available data from the Yushe Basin (Fig. 3b). Nonetheless, the enamel-$\delta^{18}O$ data from horses, which span a longer period of time than the data from other animals in the Yushe Basin, show several significant shifts over the last 6.5 million years, reflecting changes in climate (Fig. 3b). The mean enamel-$\delta^{18}O$ values of horses shifted to higher values after ~5.8 Ma, ~4.1 Ma, ~3.3 Ma, and ~2.5 Ma (Fig. 3b; Table 2). These positive $\delta^{18}O$ shifts correspond to positive shifts in the $\delta^{13}C$ record (Fig. 2b), indicating shifts to drier and/or warmer conditions (Fig. 3b). Similarly, the mean enamel-$\delta^{18}O$ values shifted to more negative values after ~6.4 Ma, ~5 Ma, and ~3.5 Ma, indicating shifts to wetter or cooler climates (Fig. 3b). With one exception (~6.4 to ~5.8 Ma), the negative shifts in the $\delta^{18}O$ record (Fig. 3b) generally parallel the negative shifts in the $\delta^{13}C$ record (Fig. 2b), suggesting relatively wetter or cooler conditions at ~4.6–4.1 Ma, ~3.3 Ma and ~2.5 Ma. Since the negative $\delta^{18}O$ shift after ~6.4 Ma is accompanied by a positive $\delta^{13}C$ shift, it most likely indicates a shift to a wetter and warmer climate at ~5.8 Ma.

Most notably, the positive $\delta^{18}O$ shift after ~5.8 Ma coincides with a major fauna turnover event across the Mahui–Gaozhuang hiatus when 40% of the Mahui genera failed to cross this interval (Flynn et al., 1991), signaling the demise of late Miocene "*Hipparion*Fauna" (Kurten, 1952; Tedford et al., 1991). The positive $\delta^{18}O$ shift after ~2.5 Ma is also coincident in timing with another major fauna turnover at the Mazegou–Haiyan boundary around 2–2.5 Ma, when about 25% of the Mazegou fauna failed to continue into the Pleistocene (Flynn et al., 1991). The coincidence of major fauna turnover events in the fossil record with significant changes in climatic and ecological conditions in the Yushe Basin underscores the important role of climate in the evolution of mammalian and plant communities.

4.3. Intra-tooth isotopic profiles and seasonal variations in diet and climate

Analysis of serial enamel samples from modern teeth show large intra-tooth isotopic variations within individual teeth (i.e., $\Delta^{13}C$ of 5.0‰–9.4‰ and $\Delta^{18}O$ of 5.9‰–9.2‰) (Fig. 4). The $\delta^{13}C$ values of serial samples from a modern cow tooth range from −8.6‰ to 0.8‰, indicating a seasonal variation in its diet from pure C_3 in the winter to pure C_4 vegetation in the summer (Fig. 4a). Serial samples from two modern goats show a smaller intra-tooth $\delta^{13}C$ variation (from −12.0‰ to −4.6‰ for sample ZL-4-t1 and from −13.3 to −8.3‰ for ZL-4-t2) and indicate a seasonal dietary change from pure C_3 to mixed C_3–C_4 diets (Fig. 4b,c). Serial oxygen isotope data from the modern cow and

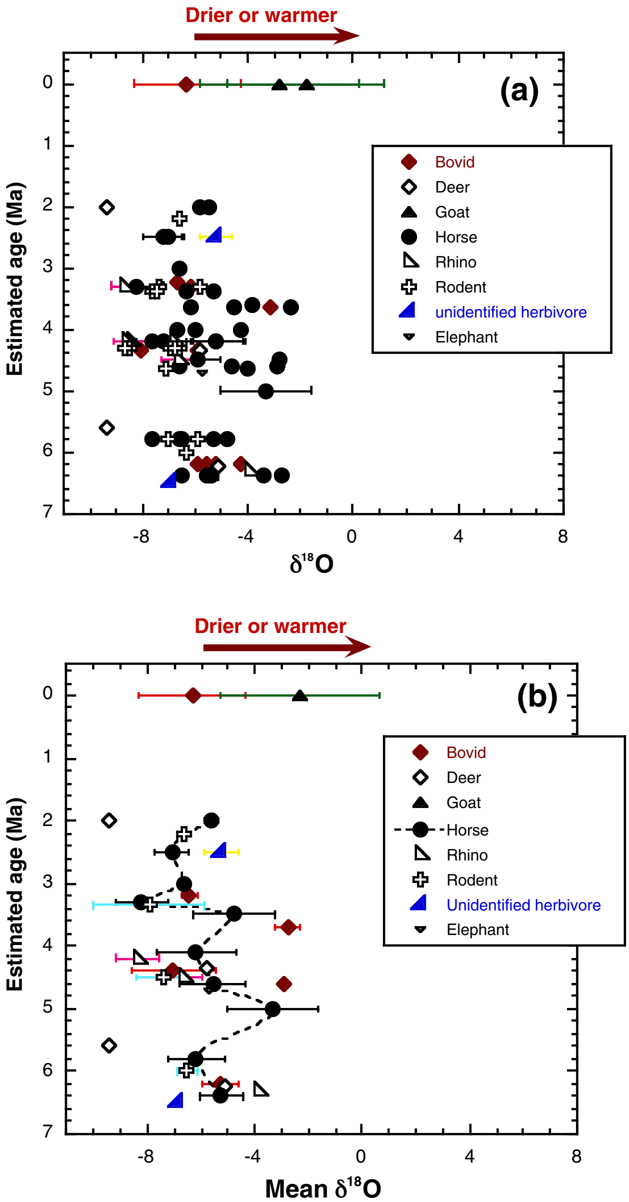

Fig. 3. (a) $\delta^{18}O$ values of bulk enamel samples and (b) mean $\delta^{18}O$ values of various herbivores from Yushe, North China (including data from Passey et al., 2009). For any tooth that was serial-sampled, the bulk $\delta^{18}O$ value for that tooth in (a) was calculated by averaging all its serial data. Error bars indicate 1 standard deviation (1σ) from the mean.

goats also display large intra-tooth variations ($\Delta^{18}O$ = 5.9‰–9.2‰) indicating that these individuals drank from ephemeral streams and/or puddles and their $\delta^{18}O$ values primarily reflect seasonal variations in the oxygen isotopic composition of precipitation (Fig. 4). Precipitation is known to display much larger seasonal $\delta^{18}O$ variability than groundwater (Clark and Fritz, 1997) because the oxygen isotopic composition of groundwater reflects a weighted mean annual $\delta^{18}O$ of precipitation in the catchment. Therefore, ephemeral streams and puddles that consist mainly of local rainwater and have short water residence times have $\delta^{18}O$ values that more accurately reflect the oxygen isotope composition of seasonal precipitation; whereas the $\delta^{18}O$ values of lakes and rivers that consist predominantly of groundwater reflect average annual isotope compositions of precipitation in the catchment modified by evaporation (Koch et al., 1989; Clark and Fritz, 1997). Thus, tooth enamel from animals that drank from large bodies of water (such as lakes or rivers) would be expected to show dampened seasonal signals compared to that from animals that drank from smaller and more temporary water sources such as puddles or ephemeral streams.

All modern samples from the region show strong negative correlations ($R = -0.80$ to -0.99) between $\delta^{13}C$ and $\delta^{18}O$ values within individual teeth (Fig. 4a,b,c), a pattern observed only in summer monsoon regions that contain C_4 grasses (Wang et al., 2008a; Biasatti et al., 2010). In the Asian summer monsoon region, precipitation has lower $\delta^{18}O$ values in the summer (than in the winter) while the growth of C_4 grasses (i.e., warm season grasses) in the summer months provide a ^{13}C-enriched food resource for herbivores, leading to a negative correlation between $\delta^{13}C$ and $\delta^{18}O$ values within an individual tooth (Biasatti et al., 2010).

Most of the fossil teeth from Yushe show significant intra-tooth isotopic variations reflecting seasonal variations in diets (from C_3 to mixed C_3–C_4 or C_4 diets) and climate (Fig. 4d–s). Although the fossil teeth (all from horses and rhinos) display smaller intra-tooth carbon and oxygen isotopic variations (i.e., $\Delta^{13}C$ of 0.2–3.3‰ and $\Delta^{18}O$ of 1.0–6.2‰) compared to modern bovid teeth (Fig. 4a–c), this difference may be due to differences in physiology and diet/drinking behavior of different animals as no fossil bovid serial data were available for comparison with the modern serial data. The serial data confirm the conclusion from bulk data that horses had mostly mixed C_3–C_4 diets and C_4 grasses have been a significant component of local ecosystems since ~6.5 Ma. Negative correlations between $\delta^{13}C$ and $\delta^{18}O$ values seen in modern teeth are also observed in a 5-Ma horse tooth (GZ-2, $R = -0.719$), a 4.5-Ma horse tooth (NZG-1-t1, $R = -0.647$), and three 4.2-Ma horse teeth (ZL-3-t3, $R = -0.780$; ZL-3-t2, $R = -0.234$; ZL-3-t1, $R = -0.162$) (Fig. 4), indicating that the summer monsoon had a strong influence in the Yushe Basin in the early Pliocene. This is in general agreement with the physical and geochemical evidence from the Red Clay deposits on the Chinese Loess Plateau (Ding et al., 1999, 2001; An et al., 2001) that suggests a strengthened summer monsoon at about 5–4 Ma. In addition to large amplitudes of intra-tooth $\delta^{13}C$ variations, these individuals also show large intra-tooth $\delta^{18}O$ variations ($\Delta^{18}O$ = 3.0–6.2‰) suggesting that they drank from water sources with a short residence time (such as small streams or puddles) that more closely track the seasonal changes in the $\delta^{18}O$ of precipitation.

The $\delta^{13}C$ values of serial samples from a 4.2-Ma rhino tooth (ZL-1-t1, Fig. 4j) range from −9.0‰ to −11‰ ($\Delta^{13}C$ = 1.6‰), indicating a C_3-based diet, and do not show any correlation ($R = 0.095$) with the $\delta^{18}O$ values that show a relatively small intra-tooth variation ($\Delta^{18}O$ = 2.5‰). Serial samples from a 4.5-Ma rhino tooth fragment also yielded $\delta^{13}C$ values indicating a pure C_3 diet and display small intra-tooth isotopic variations ($\Delta^{13}C$ = 0.6‰, $\Delta^{18}O$ = 2.1‰) (Fig. 4p). This suggests that these rhinos probably lived in a forested habitat and drank from isotopically buffered water sources such as a river or a lake. As shown in Fig. 2, rhinos generally have more negative $\delta^{13}C$ values than contemporary horses, suggesting that rhinos may have a dietary preference for C_3 plants. The small intra-tooth $\delta^{13}C$ variations (<2‰) observed in rhino teeth also suggests that these animals were probably very selective in their diet and preferred C_3 plants over C_4 grasses.

4.4. Comparison with other proxy climate records in the region

Various proxies have been used to reconstruct the paleoenvironments in China and the Asian Monsoons, including physical and chemical properties (such as magnetic susceptibility, elemental concentrations, grain size and sedimentation rates) of loess-paleosol-red clay deposits (e.g., Ding et al., 1999; An et al., 2001; Ding et al., 2001; Vanderberghe et al., 2004; Wen et al., 2005; Zhu, 2008; He et al., 2013), $\delta^{13}C$ and $\delta^{18}O$ of terrestrial carbonates (e.g., Wang and Deng, 2005; Passey et al., 2009; Zhang et al., 2009; Biasatti et al., 2010; Wang et al., 2012), fossils and pollen records (e.g., Fortelius et al., 2006; Wu et al., 2006; Wang et al., 2006; Jiang and Ding, 2008; Li et al., 2008; Liu et al., 2011; Li et al., 2014). However, interpretations

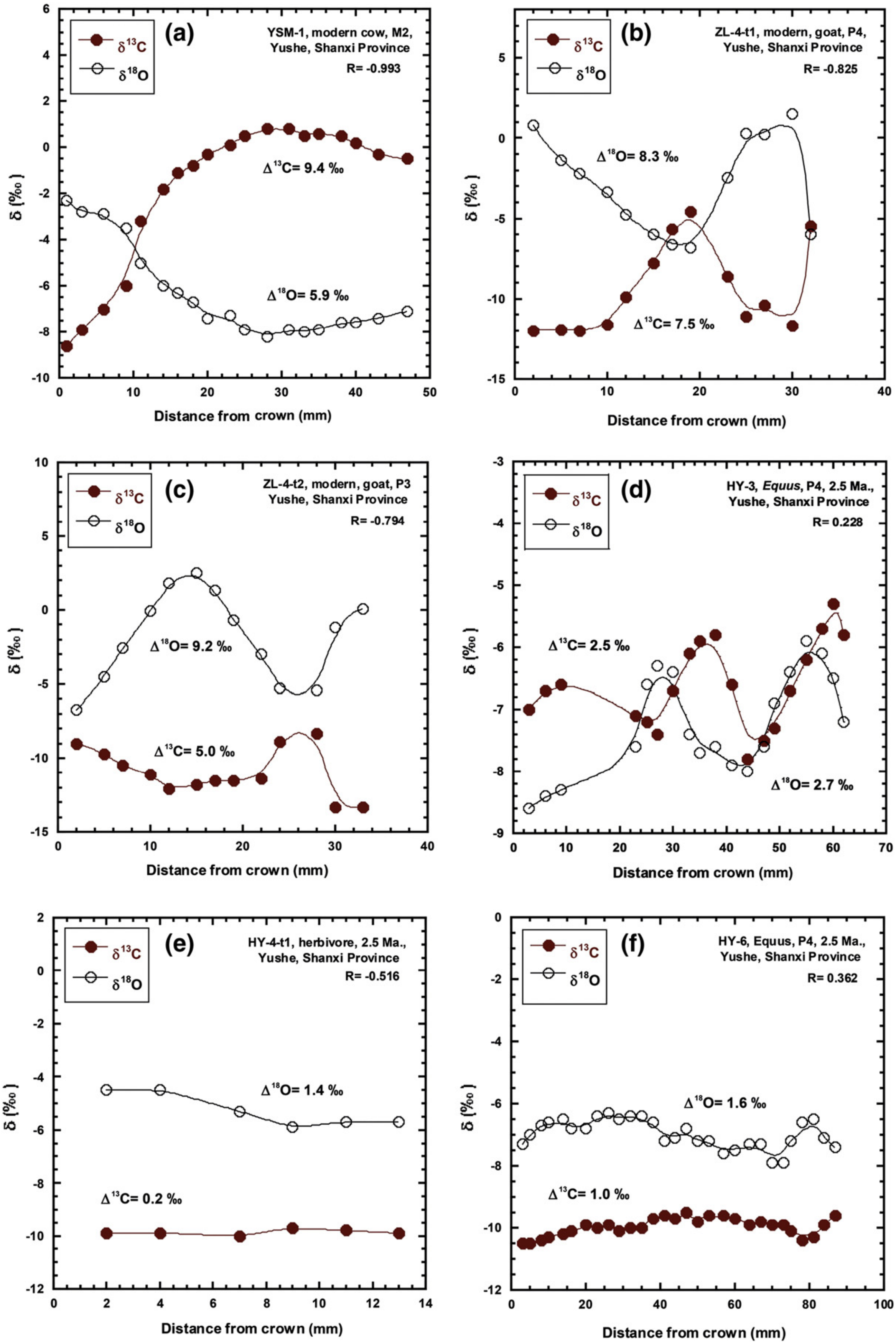

Fig. 4. Intra-tooth carbon and oxygen isotopic variations of modern and fossil mammals from Yushe, North China.

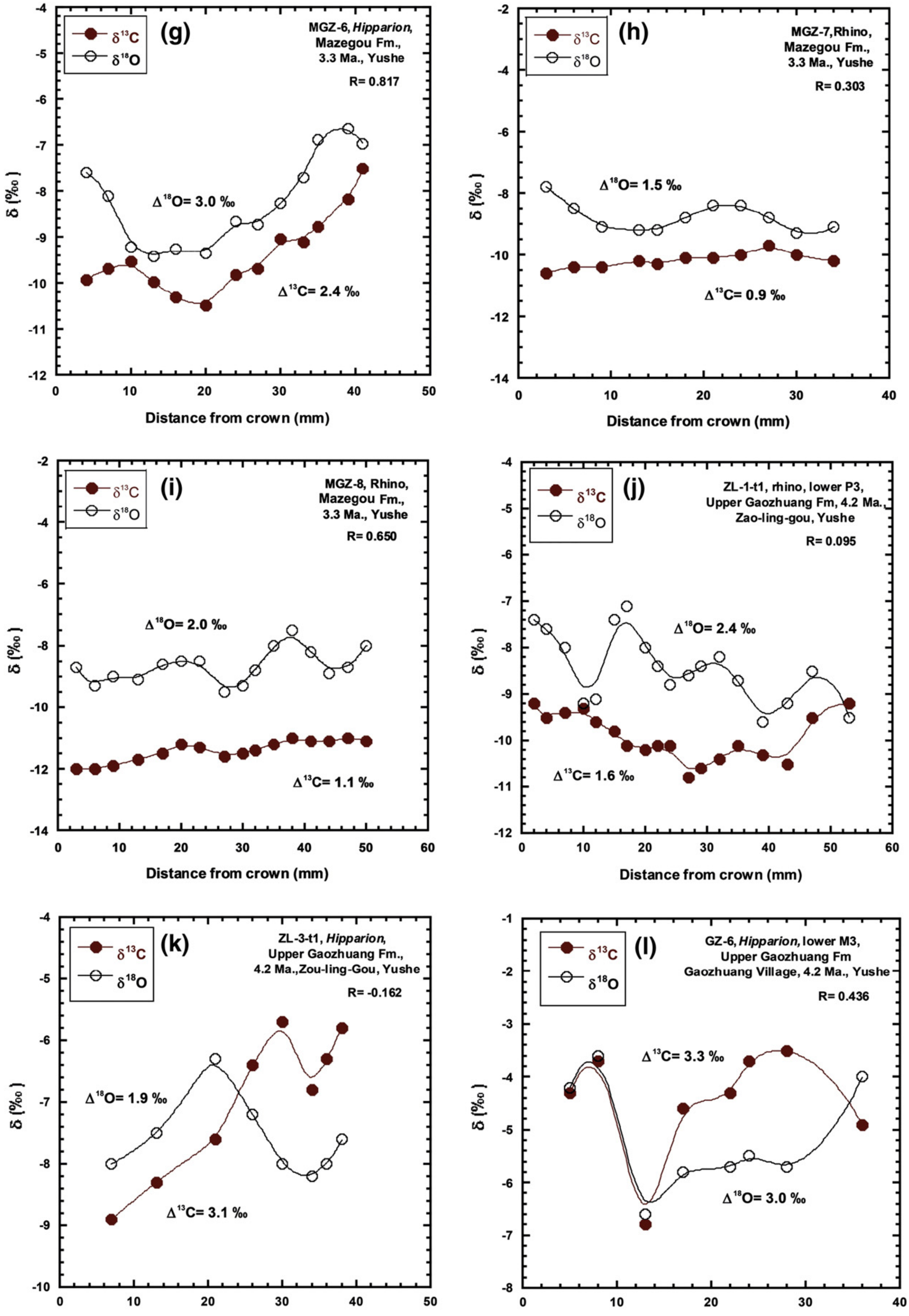

Fig. 4 (*continued*).

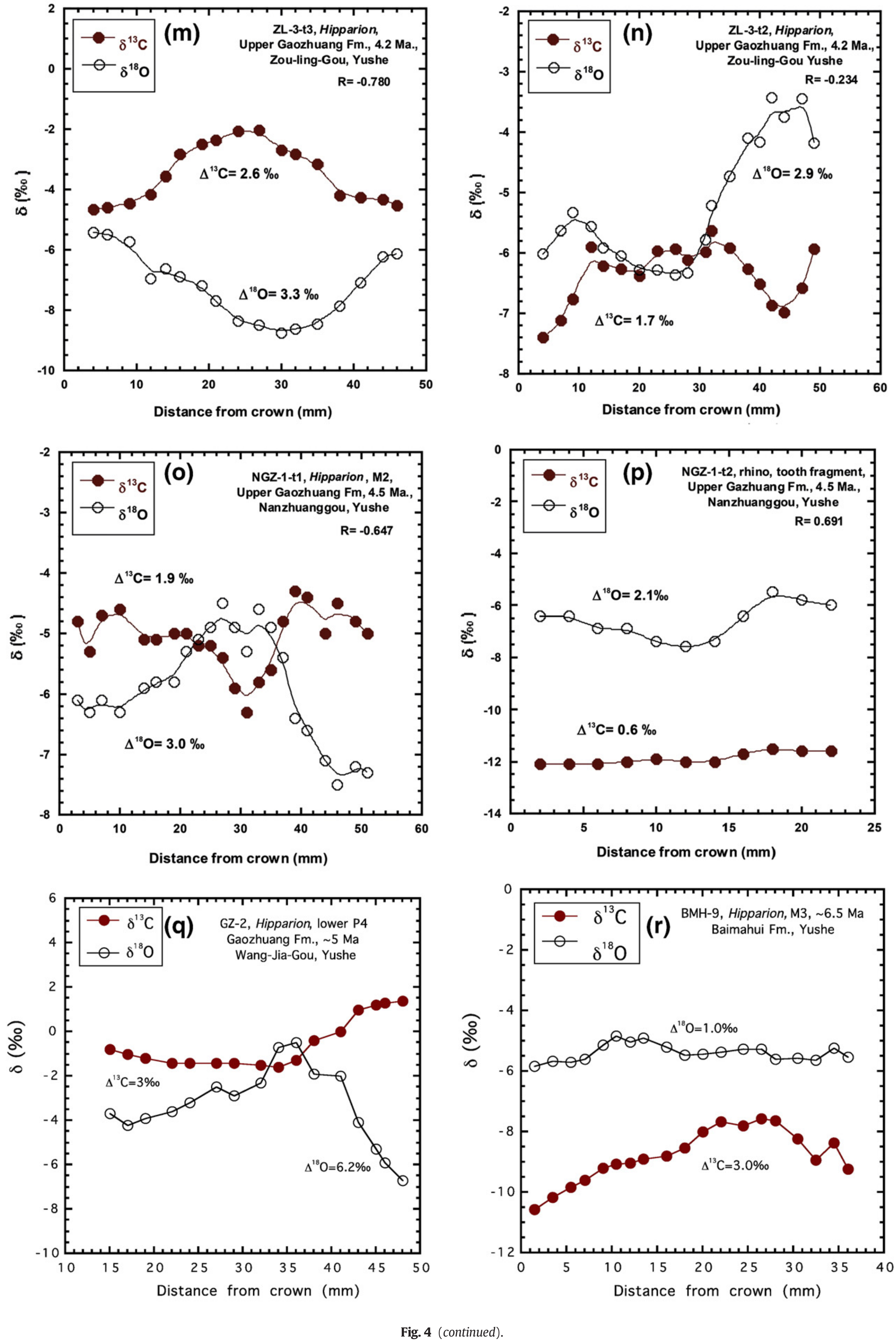

Fig. 4 (*continued*).

of different proxies often yielded inconsistent and sometime conflicting results. For example, the terrestrial mollusk records from the Chinese Loess Plateau suggests cold and dry conditions (weak summer monsoon) in the latest Miocene (~6.2–5.4 Ma) and a warm and humid climate (stronger summer monsoon) in the early Pliocene (Wu et al., 2006; Li et al., 2014). The pollen records from northern China also suggest humid conditions in the early Pliocene, at ~5.4 to 4.4 Ma (Wang et al., 2006; Jiang and Ding, 2008). In contrast, hysodonty analysis of mammalian fossils suggests a stronger summer monsoon or wetter conditions during the late Miocene (~8–5 Ma) and a drier climate in the Pliocene in northern China (Fortelius et al., 2006). These discrepancies are due to inherent limitations of each proxy, uncertainties in chronology, and differences in time resolution of different proxy records.

As discussed in the previous sections, our enamel $\delta^{13}C$ and $\delta^{18}O$ records from the Yushe Basin reveal significant changes in diet and climate over the past 6.5 million years. The large positive shift in the $\delta^{13}C$ and $\delta^{18}O$ records after ~5.8 Ma also corresponds to a large increase in the amplitude of intra-tooth $\delta^{18}O$ variation (Fig. 5). This suggests that a shift to drier and warmer climate may have been accompanied by an increased seasonality in precipitation or intensified monsoonal circulation. However, more data are needed to verify the relationship. Our data show that fossil teeth from the early Pliocene (~5–4.2 Ma) generally show negative correlations between $\delta^{13}C$ and $\delta^{18}O$ values and strong seasonality, which is characteristic of summer monsoon regions that contain C_4 plants (Biasatti et al., 2010). Because Yushe is in the monsoon region where summer precipitation has lower $\delta^{18}O$ values than winter precipitation, relatively lower $\delta^{18}O$ values associated with higher $\delta^{13}C$ values within individual teeth indicate not only the presence of warm season C_4 grasses in local ecosystems in summer months but also the strong influence of the summer monsoon in the area at ~5–4.2 Ma (Figs. 2 and 4). This is consistent with the terrestrial mollusk and pollen records and also the pedogenic/geochemical evidence from the Loess Plateau suggesting strengthened summer monsoon between ~5.5 and ~4 Ma (Ding et al., 1999, 2001; Wang et al., 2006; Wang et al., 2006; Jiang and Ding, 2008; Li et al., 2008, 2014). The positive shift after ~2.5 Ma in the enamel isotopic record is consistent with the enamel isotope record from the Linxia Basin on the western margin of the Loess Plateau (Wang and Deng, 2005; Biasatti et al., 2010), most likely indicating a shift in regional climate to drier conditions. This isotopic shift is also roughly synchronous with a major phase of intensification of the monsoon circulation that was characterized by strengthened winter monsoon, possible weakening of summer monsoon and increased variability around ~2.6 Ma as inferred from the onset of widespread loess deposition in central China (Liu, 1985; Ramstein et al., 1997; An et al., 2000, 2001).

Climate model simulations suggest that the growth of the Himalaya–Tibetan plateau have played a significant role in controlling the evolution of the Asian monsoons and climate (Kutzbach et al., 1993; An et al., 2001), which would have had a profound influence on ecosystems and mammalian evolution in the region (e.g., Deng et al., 2011, 2012). High-resolution proxy records from the Loess Plateau and southern Tibet have revealed wet–dry cycles during the late Miocene and Pliocene, which have been linked to orbitally induced climatic changes (e.g., Li et al., 2008; Wang et al., 2012). The wet–dry shifts observed in the Yushe record could have been caused by orbitally-induced changes in global climate and/or tectonic changes in the Tibetan region. However, the poor resolution of the fossil record does not allow establishment of firm links between environmental changes in the Yushe Basin and orbitally induced global climate changes or tectonic events in the Tibetan region. More long-term paleoclimate data with good age control and time resolution from Asia are needed in order to test the models and to elucidate the linkage between tectonics and climate and ecosystem changes.

5. Conclusion

Stable carbon and oxygen isotopic analyses of herbivorous mammalian tooth enamel from Yushe Basin indicate significant changes in vegetation and climate over the past 6.5 million years. The combined carbon and oxygen isotope data show four significant shifts to drier and/or warmer climate after ~5.8, ~4.1, ~3.3, and ~2.5 Ma, and three significant shifts to relatively wetter and/or cooler conditions after ~6.4, ~5, and ~3.5 Ma. The shifts to drier and/or warmer climate after ~5.8 Ma and ~2.5 Ma coincide with two major fauna turnover events observed in the fossil record in Yushe, suggesting a linkage of

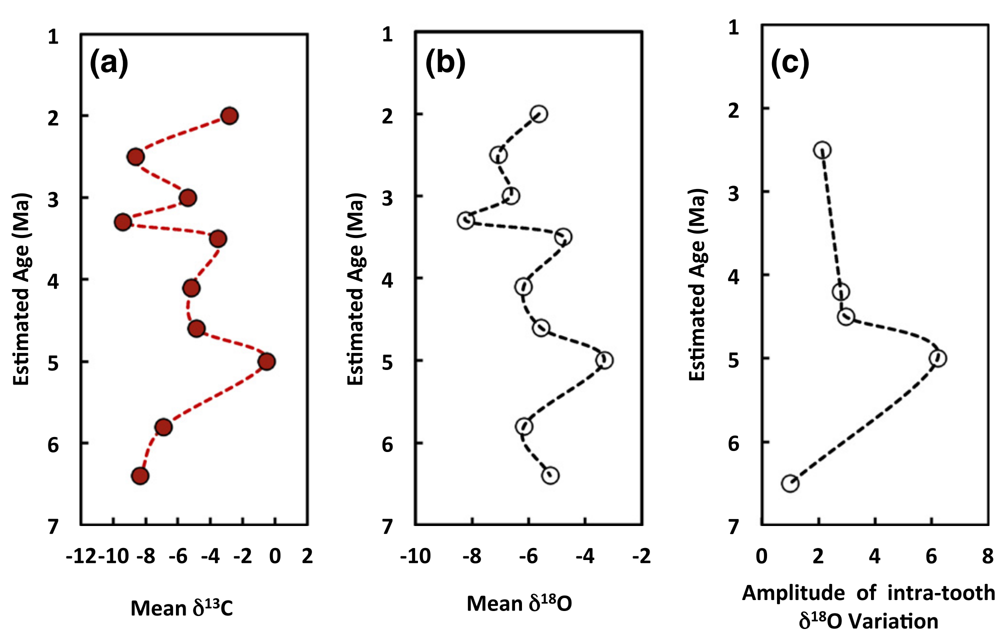

Fig. 5. Comparison of (a) mean $\delta^{13}C$ values, (b) mean $\delta^{18}O$ values, and (c) range of intra-tooth $\delta^{18}O$ variations of horses of various ages in Yushe Basin, showing that the positive shift in mean enamel $\delta^{13}C$ and $\delta^{18}O$ values at ~5 Ma corresponds to the largest range of intra-tooth $\delta^{18}O$ variations.

mammalian evolution to climate change. The $\delta^{13}C$ values indicate that herbivores were feeding predominantly on C_3 plants around 6.5 Ma although some individuals had consumed small amounts (no more than 30%) of C_4 grasses. This suggests that the local ecosystems were likely dominated by C_3 plants and C_4 grasses were not a significant component of local ecosystems in Yushe at ~6.5–6.4 Ma. After ~6.4 Ma, the $\delta^{13}C$ values of mammalian tooth enamel indicate that their diets consisted of significant amounts of C_4 plants, reflecting an increased C_4 biomass in the basin. At ~5 Ma, the region experienced one of the warmest or driest periods in the last 6.5 million years.

Serial enamel samples collected along the growth axes of individual teeth from various fossil and modern herbivores generally display significant intra-tooth isotopic variations that indicate significant seasonal variations in diet and climate. All modern enamel samples show strong negative correlations between the $\delta^{13}C$ and $\delta^{18}O$ values within individual teeth, which is consistent with what is expected in the summer monsoon region and reflects the strong influence of the summer monsoon in the basin today. Samples from the 2.5 Ma fossil mammals display smaller intra-tooth carbon and oxygen isotopic variations compared to modern samples. The negative correlation observed in modern teeth is also weaker or non-existent in the 2.5 Ma fossil teeth. This suggests a weaker summer monsoon around 2.5 Ma. Most of the Pliocene mammals from Yushe show significant intra-tooth isotopic variations reflecting seasonal variations in diets (from C_3 to mixed C_3–C_4 or C_4 diets) and climate. Negative correlations between $\delta^{13}C$ and $\delta^{18}O$ values are also observed in fossil teeth from ~5–4.2 Ma, indicating that the summer monsoon had a strong influence in the Yushe Basin in the early to middle Pliocene. Taken together, the isotope data show that C_4 grasses have been an important component of herbivores' diets and of local ecosystems since ~6.5 Ma, confirming that the “late Miocene C_4 expansion” occurred in North China as it did in Africa, the Indian subcontinent and the Americas. This supports a global factor as a main driver of the late Miocene C_4 expansion. The data also show that the Yushe Basin has been under the influence of the monsoon system since at least 6.5 Ma. The significant shifts observed in the enamel-$\delta^{18}O$ record, which indicate shifts in climate, are accompanied by parallel shifts in the enamel-$\delta^{13}C$ record. This indicates that the C_4 abundance in the area has fluctuated in response to changes in climate with more C_4 grasses during warmer and/or drier periods and a reduced C_4 component to the vegetation during cooler and/or wetter climatic conditions.

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