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Carbon and oxygen isotopic evidence for diets, environments and niche differentiation of early Pleistocene pandas and associated mammals in South China

Shannon Stacklyn [a], Yang Wang [a,b,c,*], Chang-zhu Jin [c], Yuan Wang [c], Fajun Sun [a], Chunfu Zhang [d], Shijun Jiang [b], Tao Deng [c,e]

[a] Department of Earth, Ocean & Atmospheric Science, Florida State University and National High Magnetic Field Laboratory, Tallahassee, FL 32306-4100, USA
[b] Institute of Hydrobiology, The Jinan University, Guangzhou, Guangdong Province, PR China
[c] Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
[d] Department of Geosciences, Fort Hays State University, Hays, KS 67601, USA
[e] CAS Center for Excellence in Tibetan Plateau Earth Sciences, Beijing, China

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ABSTRACT

To better understand the dietary evolution and habitat change of pandas, this study analyzed the stable carbon and oxygen isotope compositions of tooth enamel samples from the early Pleistocene pandas *Ailuropoda microta* and *Ailuropoda wulingshanensis* and their associated mammals recovered from Yanliang Cave and Longgu Cave in South China. The enamel $\delta^{13}C$ values indicate that mammals living in these cave areas during the early Pleistocene had C_3–based diets but some individuals consumed small amounts of C_4 grasses. This suggests that C_4 grasses were present in the region during the early Pleistocene, likely in patches of open areas (or savanna-woodlands) in a predominantly forested landscape. The $\delta^{13}C$ and $\delta^{18}O$ data clearly show niche partitioning among panda, pig, and other animals. The pandas had the lowest enamel-$\delta^{13}C$ values among all mammals examined, indicating that these early Pleistocene pandas had pure C_3 diets composed of plants growing in the understories of closed-canopy forests. A pure C_3 diet for these ancient pandas is consistent with an already established dietary niche of bamboo (a C_3 plant) in the early Pleistocene. These ancient pandas also had higher $\delta^{18}O$ values than all other contemporaneous mammals (except the deer at Longgu Cave), suggesting that they did not drink as much as other large mammals did. The available isotope data suggest that pygmy panda (*A. microta*) was less ecologically flexible compared to other mammals such as pig, rhino, deer and bovid. The limited ecological flexibility of pygmy panda may have contributed to its demise during climatic fluctuations in the Pleistocene. The reconstructed $\delta^{18}O$ values of meteoric water in the study areas during the early Pleistocene are lower than the present-day mean annual precipitation $\delta^{18}O$ values in the region, suggesting a wetter climate or stronger summer monsoon in the early Pleistocene than today.

1. Introduction

Reconstruction of ancient diets and environments is important as it provides valuable information about how animals lived and how they responded to past climate changes. Stable carbon and oxygen isotope analysis of tooth enamel has long been established as a useful tool for reconstructing diets, ecologies, and environments of ancient mammals (e.g., Cerling et al., 1993; Ciner et al., 2015; Ciner et al., 2016; MacFadden et al., 1994; Wang and Cerling, 1994; Wang et al., 1994; Wang et al., 1993; Wynn et al., 2013).

Terrestrial plants have a wide range of carbon isotopic compositions ($\delta^{13}C$ values), reflecting differences in their photosynthetic pathways as well as variations in environmental conditions which vary with habitats such as closed canopy forest vs. savanna (e.g., Cerling and Harris, 1999; Codron et al., 2005; Farquhar et al., 1989). Modern C_4 plants (mostly warm-season grasses) use the C_4 photosynthetic pathway for carbon fixation and have $\delta^{13}C$ values of −9‰ to −17‰, averaging −13‰; while the $\delta^{13}C$ values of C_3 plants (trees, most shrubs, forbs, and cool-season grasses), which utilize the C_3 photosynthetic pathway, are −27‰, ranging from −22 to −36‰ (Cerling and Harris, 1999; Cerling et al., 2004; O'Leary, 1988; Smith and Epstein, 1971). C_3 plants growing under closed canopies have the most negative $\delta^{13}C$ values

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* Corresponding author at: Department of Earth, Ocean and Atmospheric Science, Florida State University and National High Magnetic Field Laboratory, Tallahassee, FL 32306-4100, USA.
E-mail address: ywang@magnet.fsu.edu (Y. Wang).

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due to the influence of soil respired CO_2 and light limitation, while C_3 plants in water stressed environments tend to have higher $\delta^{13}C$ values (>-27‰) (e.g., Williams and Ehleringer, 1996; Zhang et al., 2012). When an animal consumes carbon through its diet, the amount of ^{13}C incorporated into the tooth enamel is enriched by about 13–14‰ relative to its food source (Cerling et al., 1997; Cerling and Harris, 1999; Lee-Thorp and van der Merwe, 1987). The higher end member of this enrichment factor ($\varepsilon^*_{\text{diet-enamel}} = 14.1 \pm 0.5$‰) is associated with large ruminant mammals (Cerling and Harris, 1999). Non-ruminant mammals have measured smaller enrichment factors of ~13‰, which is likely due to lower methane production (Passey et al., 2005). Thus, the diets of mammals can be reconstructed from their enamel $\delta^{13}C$ values, using the $\varepsilon^*_{\text{diet-enamel}}$ value of 13‰ for non-ruminants or 14‰ for ruminants. Carnivores are slightly enriched in the heavy C isotope ^{13}C (by ~1‰) relative to their prey due to the trophic level effect (Lee-Thorp et al., 1989). The oxygen isotopic composition ($\delta^{18}O$) of tooth enamel, on the other hand, contains valuable information about climatic conditions as well as the diet and drinking behavior of an animal (Cerling et al., 2004; Kohn and Cerling, 2002; Tseng et al., 2013; Wang et al., 2008a; Wang et al., 2008b; Wang et al., 2013). For large obligate drinkers, their $\delta^{18}O$ values serve as a proxy for the oxygen isotopic composition of local meteoric water (and its derivatives such as streams and ponds) and thus the climate (e.g., Kohn and Cerling, 2002; Longinelli, 1984; Sponheimer and Lee-Thorp, 1999) because the $\delta^{18}O$ of meteoric water is controlled by climatic conditions (Dansgaard, 1964). Furthermore, obligate drinkers tend to have lower $\delta^{18}O$ values than animals that obtain most of their water from plants because leaf water is generally enriched in ^{18}O relative to local meteoric water due to evaporation (Dongmann et al., 1974; Epstein et al., 1977). Thus, carbon and oxygen isotope data allow insights into not only the feeding behaviors and habitat preferences of particular fossil taxa (e.g., Bocherens, 2015; Wynn et al., 2013) but also paleoclimate (Biasatti et al., 2010; Ciner et al., 2015; Zhang et al., 2012).

In this study, we analyzed the stable carbon and oxygen isotope compositions of tooth enamel samples from early Pleistocene pandas and their associated mammals uncovered from two fossiliferous caves in South China. The new data, in conjunction with data from the literature, were used to reconstruct the diets and environments of these ancient animals and to address the following questions: What kind of environments and habitats did these early Pleistocene mammals live in? Did various mammals share the same food resources or differentiate their niches to reduce competition? Were there C_4 grasses in the local habitats? Did the early Pleistocene pandas eat plants or did they still consume some meat? What are the climatic implications of the isotope data?

2. Study sites

Fossils analyzed in the study were recovered from two early Pleistocene fossil caves in South China - Yanliang Cave and Longgu Cave (Fig. 1).

Yanliang Cave (22°13′54″N, 107°36′35″E) is on the Gaoyan Mountain of Chongzuo City in Guangxi Province (Fig. 1). The Chongzuo area is within the humid subtropical climate zone characterized by a long and warm summer and a short and mild winter. Most of the annual precipitation falls in the summer during the summer monsoon season (http://www.climate-charts.com). The mean annual temperature is 20.8–22.4 °C (69.4–72.3 °F) and annual precipitation is between 1088 and 1799 mm (www.en.wikipedia.org/wiki/Chongzuo). The abundance of limestone and high rainfall in the area has allowed for the dissolution of carbonate rocks underground forming numerous caves. Most of the caves in the area contain fossiliferous deposits. The ages of the caves generally increase with increasing elevation due to continued uplift of the area since the early Quaternary (Jin et al., 2009a; Jin et al., 2009b; Jin et al., 2014). The Yanliang Cave is part of the Chongzuo karst cave system and currently ~200 m above sea level. The cave is ~18 m long and ~10 m wide, and has preserved a 6.8-m-thick sedimentary deposit that has yielded numerous fossils (Jin et al., 2009a; Jin et al., 2009b). The sediments consist of yellow sands, yellowish brown silts with numerous tiny breccias and red clays (Yan et al., 2014). The sedimentary sequence inside the cave has been divided into 4 levels from top to bottom and our fossils were collected from the third level (Yan et al., 2014). More than 40 mammalian species have been recovered from the cave, including *Gigantopithecus blacki, Ailuropoda microta, Pachycrocuta licenti, Rhinoceros fusuiensis, Tapirus sanyuanensis, Leptobos* sp., *Hesperotherium sinensis, Typhlomys intermedius, Chiropodomys primitivus, Niviventer*

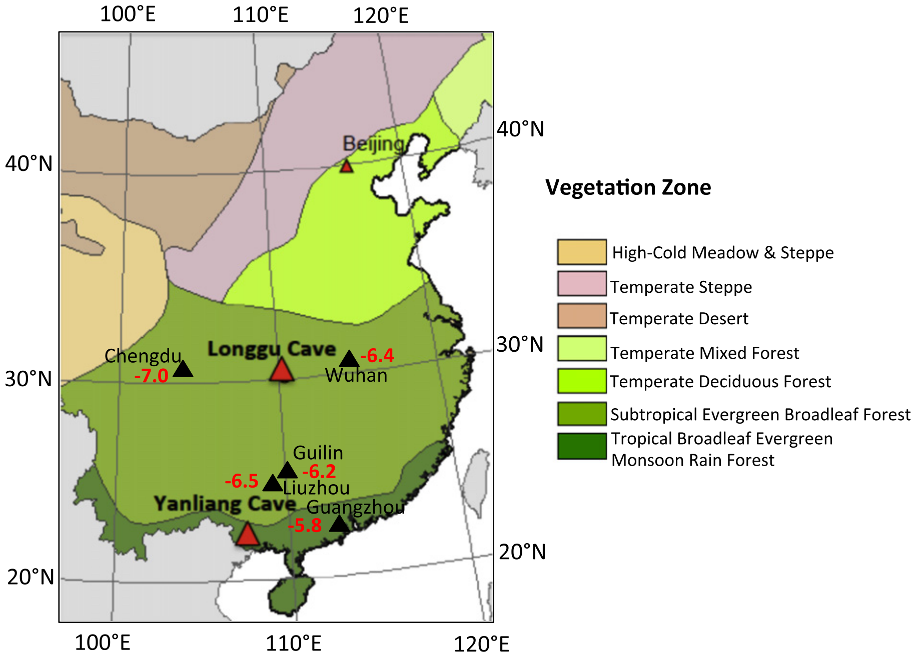

Fig. 1. Map showing locations of study sites (marked by red triangles) and modern vegetation zones in east China (modified from Liu, 1988). Dark triangles are the IAEA-GNIP (International Atomic Energy Agency Global Network for Isotopes in Precipitation) stations near the fossil caves. The numbers are the average annual precipitation $\delta^{18}O$ values measured at the IAEA-GNIP stations (IAEA, 2001).

preconfucianus, and *Leopoldamys edwardsioides* (Yan et al., 2014). These species are the typical elements of the Early Pleistocene "*Gigantopithecus* fauna" or "*Gigantopithecus-Sinomastodon* fauna" in southern China (Wang et al., 2014). Based on the fossil assemblage, the age of the Yanliang fauna was estimated to be early Pleistocene, more or less contemporaneous with the Mahui cave fauna in the same area (Wang et al., 2005; Yan et al., 2014; Zhao and Zhang, 2013).

Longgu Cave (30°39′14.9″N, 110°04′29.1″E) is located in Jianshi County in southwestern Hubei Province (Fig. 1). The area is in the subtropical monsoonal climate zone. The mean annual temperature is ~14.9 °C and annual precipitation is ~1480 mm. Spring and summer precipitation accounts for 64–76% of the annual precipitation (Zheng, 2004). Longgu Cave is about 738 m above sea level and was developed in Triassic limestone, extending from east to west nearly 110 m. It has preserved a thick sequence of Quaternary sediments that almost completely filled the cave. The cave has produced abundant fossils including *Gigantopithecus blacki, Ailuropoda wulingshanesis, Pachycrocuta licenti, Sivapanthera pleistocaenicus, Equus* sp., *Tapirus peii, Nestortherium praesinensis, Rhinoceros sinensis, Stegodon preorientalis, Sinomastodon* sp., *Sus xiaozhu, Sus peii, Cervus fenqii, Cervus yunnanensis, Capricornis jianshiensis*, and *Cuon dubius* (Zheng, 2004). Based on the fossil assemblage and paleomagnetic studies, the age of the Longgu fauna was estimated to be about 1.95–2.15 Ma (Zheng, 2004), roughly synchronous or slightly younger than the Yanling fauna in Guangxi Province (Yan et al., 2014; Zhao and Zhang, 2013; Zheng, 2004).

3. Materials and methods

Fossil teeth from twenty individuals representing six taxa were obtained from Yanliang Cave and three individual pandas were sampled from Longgu Cave for this study. Our samples include two pygmy pandas (*Ailuropoda microta*), five pigs (*Sus* sp.), two hyaenas (*Pachycrocuta licenti*), four rhinos (*Rhinoceros fusuiensis*), three bovids (*Leptobos* sp.), and four deer (*Cervus* sp.) from Yanliang Cave, and three endemic pandas (*Ailuropoda wulingshanesis*) from Longgu Cave. In order to obtain information about seasonal variations in diets and water isotopic compositions, serial enamel samples were drilled with a hand-held diamond tip drill in lateral bands (of 1 mm wide) perpendicular to the growth axis of each tooth at ~1–3 mm intervals (e.g., Biasatti et al., 2010). A total of 183 enamel samples were obtained from these teeth for stable isotope analyses. The Longgu Cave fauna has been the subject of two previous isotopic studies (Nelson, 2014; Zhao et al., 2011); these previously published data were compiled and compared with our data to provide new insights into the paleodiets and paleoclimatic conditions in the region.

The enamel samples were then treated with 5% sodium hypochlorite overnight to remove organic material, followed by an overnight treatment with 1 M acetic acid to remove non-structural carbonate (Wang and Deng, 2005). After being cleaned with deionized water and freeze-dried, the samples (now containing only hydroxyapatite) were converted to CO_2 by reaction with 100% phosphoric acid for approximately 72 h at 25 °C. The C and O isotopic compositions of the CO_2 were then analyzed using a Finnegan MAT Delta Plus XP Stable Isotope Ratio Mass Spectrometer (IRMS) at the Florida State University. The results are reported in the standard notation as $\delta^{13}C$ and $\delta^{18}O$ values in reference to the international standard VPDB. The analytical precision (based on repeated analyses of lab standards processed with each batch of samples) is ±0.1‰ (1σ) or better for both $\delta^{13}C$ and $\delta^{18}O$.

4. Results

We analyzed 172 enamel samples from a diverse group of animals from Yanliang Cave and 11 enamel samples from three pandas from Longgu Cave (Suppl. Table 1). The results are summarized in Table 1 and Figs. 2–4.

4.1. $\delta^{13}C$ and $\delta^{18}O$ of tooth enamel and diets of mammals from Yanliang Cave

Enamel $\delta^{13}C$ values of herbivores from Yanliang Cave range from −11.7 to −19.7‰, with a mean of −15.3 ± 1.5‰ (n = 172), whereas the $\delta^{18}O$ values vary from −2.9 to −8.9‰, with a mean of −5.8 ± 0.9‰ (n = 172) (Suppl. Table 1). The large isotopic variations among different species reflect differences in their diets and habitats (Fig. 2). Using an enrichment factor $\varepsilon^*_{\text{diet-enamel}}$ value of 14‰ for rhinos, bovids and deer (ruminants) and 13‰ for other animals (i.e. pigs, hyaenas, horses, giant apes, tapirs and pandas), respectively, we reconstructed the diet-$\delta^{13}C$ values of these ancient animals (Suppl. Table 1).

For pygmy pandas (*Ailuropoda microta*), the $\delta^{13}C$ values of enamel samples range from −17.8 to −19.7‰, with an average of −19.1 ± 0.5‰. This gives a reconstructed diet-$\delta^{13}C$ of −32.1 ± 0.5‰, ranging from −30.8 to −32.7‰. The $\delta^{18}O$ values of these samples vary from −2.9 to −4.9‰, averaging to −4.0 ± 0.7‰.

For pigs (*Sus* sp.), the enamel $\delta^{13}C$ values vary from −12.1 to −15.0‰, with an average of −13.5 ± 0.8‰. The reconstructed diet-$\delta^{13}C$ values are −25.1 to −28.0‰, averaging −26.5 ± 0.8‰. The $\delta^{18}O$ values range from −5.9 to −8.9‰, with an average of −6.9 ± 0.7‰.

Tooth enamel samples from hyaenas (*Pachycrocuta licenti*) yielded $\delta^{13}C$ values of −14.9 ± 1.8‰, ranging from −13.0 to −17.3‰. This gives an average diet-$\delta^{13}C$ value of −27.9 ± 1.8‰, with a range from −26.0 to −30.3‰. The $\delta^{18}O$ values vary from −5.0 to −6.4‰, with a mean of −5.6 ± 0.5‰.

The enamel $\delta^{13}C$ values of rhinos (*Rhinoceros fusuiensis*) range from −11.7 to −16.4‰ averaging −15.1 ± 0.7‰. The reconstructed diet-$\delta^{13}C$ is −29.1 ± 0.7‰, ranging from −25.7 to −30.4‰. The $\delta^{18}O$ values range from −5.2 and −6.7‰, with an average of −5.7 ± 0.4‰.

Bovids (*Leptobos* sp.) had enamel $\delta^{13}C$ values ranging from −13.3 to −16.7‰ with an average of −15.7 ± 0.6‰. The reconstructed diet-$\delta^{13}C$ values are −29.7 ± 0.6‰, ranging from −27.3 to −30.7‰. The enamel $\delta^{18}O$ values of bovids vary from −4.1 to −7.0‰, with an average of −5.5 ± 0.8‰.

For deer (*Cervus* sp.), the enamel $\delta^{13}C$ values range from −13.4 to −18.0‰, averaging −15.7 ± 1.1‰. This gives an average diet-$\delta^{13}C$ value of −29.7 ± 1.1‰ and a range from −27.4 to −32.0‰. The $\delta^{18}O$ values are −5.9 ± 0.7‰, varying from −4.2 to −7.1‰.

4.2. $\delta^{13}C$ and $\delta^{18}O$ of tooth enamel and diets of mammals from Longgu Cave

The $\delta^{13}C$ values of enamel samples from pandas (*Ailuropoda wulingshanesis*) from Longgu Cave range from −17.2‰ to −18.6‰, with a mean of −17.9 ± 0.4‰ (n = 11) (Suppl. Table 1). These enamel $\delta^{13}C$ values are slightly higher than those of pygmy pandas found at Yanliang Cave (Table 1; Fig. 3). The estimated diet-$\delta^{13}C$ values are −30.9 ± 0.4‰, with a range of −30.2 to −31.6‰. The enamel $\delta^{18}O$ values vary from −5.6 to −10.0‰, averaging −7.4 ± 1.8‰ (n = 11). Zhao et al. (2011) analyzed 1 panda tooth enamel sample from Longgu Cave, yielding a $\delta^{13}C$ value of −18.3‰, similar to our results. They also reported enamel $\delta^{13}C$ data for other large mammals found in this cave that ranged from −14.1 to −18.0‰, corresponding to diet-$\delta^{13}C$ values of −27.1 to −31.0‰ (Table 1). Unfortunately, they did not report the $\delta^{18}O$ data. Similarly, Nelson (2014) analyzed various large mammals from the same site, and reported enamel $\delta^{13}C$ values ranging from −13.4 to −16.7‰ (Table 1), slightly but consistently higher than the $\delta^{13}C$ values of the same species reported in Zhao et al. (2011). The $\delta^{13}C$ value of the sole panda enamel sample analyzed by Nelson (2014) was −16.7‰, also higher than our results (Fig. 2B; Table 1). The difference between the $\delta^{13}C$ data in Nelson (2014) and Zhao et al. (2011) and data produced in this study may be due to differences in pretreatment methods. Nelson (2014) pretreated enamel samples with 3% hydrogen peroxide for 15 min to remove organic matter in the samples, followed by treatment with 0.1 M acetic acid for another 15 min to remove non-structural carbonate in the samples, different

Table 1
Summary of results of carbon and oxygen isotope analyses of early Pleistocene mammalian tooth enamel samples from Yanliang Cave and Longgu Cave in South China.

Species	Common Name	Estimated Age (Ma)	Mean δ^{13}C ± 1σ (‰ vs. VPDB)	Mean δ^{18}0 ± 1σ (‰ vs. VPDB)	Estimated Mean Diet δ^{13}C (‰ vs. VPDB)	Range of diet-δ^{13}C (‰ vs. VPDB)	Estimated water δ^{18}O (‰ vs. VSMOW)	No. of samples	No. of individuals	Notes
Yanliang Cave, Chongzuo, Guangxi Province:										
Ailuropoda microta	Pygmy panda	2.3-2.6	−19.1 ± 0.5	−4.0 ± 0.7	−32.1	−30.8 to −32.7		10	2	This study
Sus sp.	Pig	2.3-2.6	−13.5 ± 0.8	−6.9 ± 0.7	−26.5	−25.1 to −28.0	−9.2	24	5	This study
Pachycrocuta licenti	Hyaena	2.3-2.6	−14.9 ± 1.8	−5.6 ± 0.5	−27.9	−26.0 to −30.3	−7.7	11	2	This study
Rhinoceros fusuiensis nov.	Rhino	2.3-2.6	−15.1 ± 0.7	−5.7 ± 0.4	−29.1	−25.7 to −30.4	−7.8	56	4	This study
Leptobos sp.	Bovid	2.3-2.6	−15.7 ± 0.6	−5.5 ± 0.8	−29.7	−27.3 to −30.7	−7.5	44	3	This study
Cervus sp.	Deer	2.3-2.6	−15.7 ± 1.1	−5.9 ± 0.7	−29.7	−27.4 to −32.0		27	4	This study
Longgu Cave, Jiangshi, Hubei:										
Ailuropoda wulingshanensis	Panda	1.95-2.42	−17.9 ± 0.3	−7.4 ± 1.8	−30.9	−30.2 to −31.6		11	3	This study
Ailuropoda wulingshanensis	Panda	1.95-2.42	−18.3		−31.3			1	1	Zhao et al., 2011
Ailuropoda wulingshanensis	Panda	1.95-2.42	−16.7	−7.7	−29.7			1	1	Nelson 2014
Sus sp.	Pig	1.95-2.42	−16.0		−29.0			1	1	Zhao et al, 2011
Pachycrocuta licenti	Hyaena	1.95-2.42	−14.1		−27.1			1	1	Zhao et al, 2011
Rhinoceros sinensis	Rhino	1.95-2.42	−15.3 ± 0.6		−29.3	−28.4 to −29.8		5	5	Zhao et al, 2011
Leptobos sp.	Bovid	1.95-2.42	−15.9 ± 0.8		−29.9	−29.3 to −31.1		4	4	Zhao et al, 2011
Cervus sp.	Deer	1.95-2.42	−16.7 ± 1.2		−30.7	−29.5 to −31.8		3	3	Zhao et al, 2011
Ursus sp.	Bear	1.95-2.42	−15.9		−28.9			1	1	Zhao et al, 2011
Tapirus sinensis	Tapir	1.95-2.42	−16.7 ± 0.7		−29.7	−30.1 to −31.7		4	4	Zhao et al, 2011
Equus sp.	Horse	1.95-2.42	−18.0 ± 0.7		−31.0	−29.1 to −30.7		4	4	Zhao et al, 2011
Gigantopithecus blacki	Giant ape	1.95-2.42	−16.4 ± 1.7		−29.4	−27.2 to −31.2		4	4	Zhao et al, 2011
Sus sp.	Pig	1.95-2.42	−13.4	−11.2	−26.4			1	1	Nelson, 2014
Pachycrocuta licenti	Hyena	1.95-2.42	−13.7	−9.8	−26.7		−12.4	1	1	Nelson, 2014
Rhinoceros sinensis	Rhino	1.95-2.42	−14.4 ± 0.8	−8.8 ± 1.4	−28.4		−11.3	5	5	Nelson, 2014
Leptobos sp.	Wild cattle	1.95-2.42	−14.7 ± 0.7	−8.9 ± 1.1	−28.7		−11.4	4	4	Nelson, 2014
Cervus sp.	Deer	1.95-2.42	−15.3 ± 1.2	−6.5 ± 1.0	−29.4			3	3	Nelson, 2014
Tapirus sinensis	Tapir	1.95-2.42	−15.5 ± 0.5	−10.7 ± 1.3	−28.5			4	4	Nelson, 2014
Equus sp.	Horse	1.95-2.42	−15.0 ± 0.6	−9.1 ± 0.4	−28.0		−11.6	4	4	Nelson, 2014
Gigantopithecus blacki	Giant ape	1.95-2.42	14.9 ± 1.9	−8.6 ± 1.2	−27.9		−11.0	7	7	Nelson, 2014

from the methods used in this study and in Zhao et al. (2011). Assuming that the small differences between different datasets reflect the natural isotopic variability in these animals, the average enamel-δ^{13}C value for all mammals analyzed from Longgu Cave is −16.1 ± 1.4‰ (n = 39).

5. Discussion

Enamel samples from various mammals found in Yanliang Cave and Longgu Cave exhibit significant carbon and oxygen isotopic variations (Fig. 2). The reconstructed diet-δ^{13}C values range from −25.1‰ to −32.7‰ for the Yanliang Cave fauna and from −26.4‰ to −31.3‰ for Longgu Cave fauna, with the highest δ^{13}C values found in pigs and lowest in pandas (Fig. 3; Suppl. Table 1). All of the reconstructed diet-δ^{13}C values fall within the range for C_3 plants, indicating that these early Pleistocene mammals ate predominantly C_3 vegetation and lived in an environment dominated by C_3 plants (Figs. 2 and 3). However, the δ^{13}C values of serial samples for some of the large ruminant and grazing species including a bovid (YLC-11), a deer (YLC-13) and two rhinos (YLC-8 and YLC-17) display a relatively high intra-tooth (or seasonal) variability (Fig. 4), suggesting that these individuals may have consumed a small amount of C_4 grasses seasonally (averaging about 4 ± 4% C_4, assuming end-member δ^{13}C values for pure C_3 and C_4 diets were −29‰ and −13‰, respectively) (Suppl. Table 1). The magnitude of seasonal variations in diets and water composition may be larger than indicated by our serial isotope data due to the time-averaging effect likely induced by our sampling method (Passey and Cerling, 2002; Zazzo et al., 2010). This, combined with the low reconstructed diet-δ^{13}C values (as low as −33‰) and the large range of δ^{13}C variations among species, suggest that the area had diverse wooded habitats ranging from closed canopy forests to woodlands and/or savanna-woodlands (Figs. 3 and 4).

Today, Yanliang Cave and Longgu Cave are located within tropical broadleaf evergreen monsoon rain forest and subtropical broadleaf evergreen forest zone, respectively (Fig. 1). Both vegetation zones contain small amounts of C_4 grasses but only in open areas not in dense forests (Ehleringer et al., 1987; Yin and Li, 1997). Similar to the present-day forests of the region (Ehleringer et al., 1987; Yin and Li, 1997), our δ^{13}C data suggest that small amounts of C_4 grasses were present in local habitats, most likely in patches of open areas where forest or woodland canopies were broken. An isotopic study of plants in a monsoon evergreen

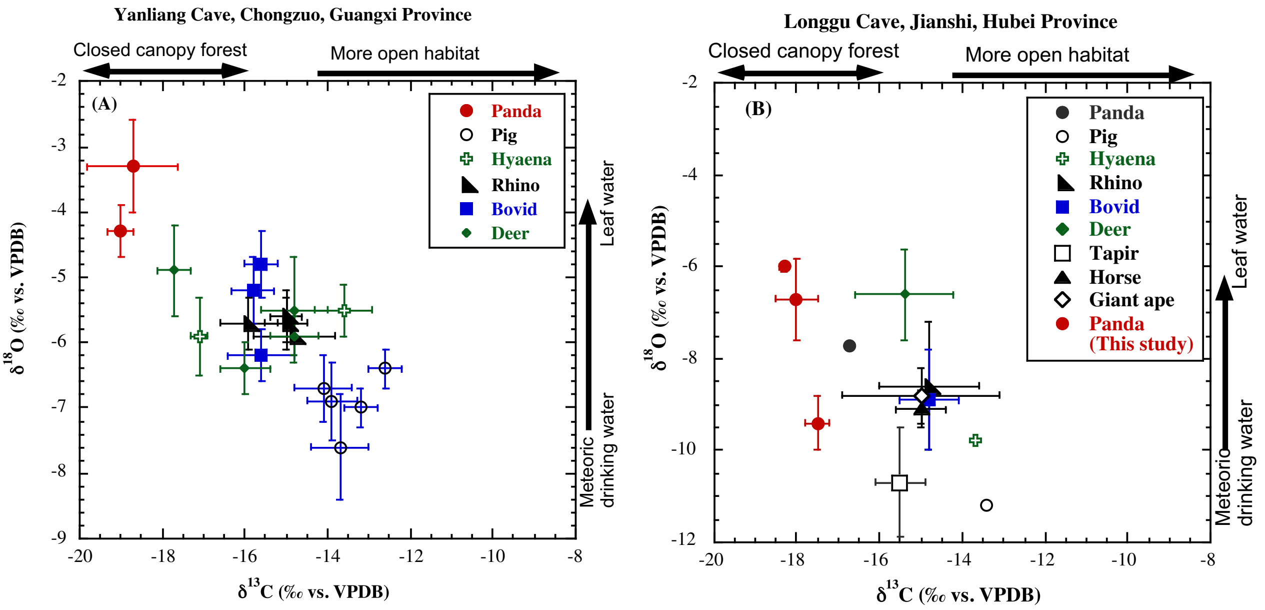

Fig. 2. Enamel-$\delta^{13}C$ and $\delta^{18}O$ values of various mammals found in (A) Yanliang Cave, Chongzuo, Guangxi Province, and (B) Longgu Cave, Jianshi, Hubei Province. Each point in (A) represents a bulk enamel isotope value calculated by averaging the $\delta^{13}C$ ($\delta^{18}O$) values of all serial enamel samples from an individual tooth; error bar indicates 1σ from the mean. With the exception of panda, data for all other mammals from Longgu Cave in (B) are from Nelson (2014). Data for Longgu Cave in Zhao et al. (2011) are not included in (B) as they did not report their $\delta^{18}O$ data.

broadleaf forest in south China shows that subcanopy plants in the dense forest typically have $\delta^{13}C$ values of < −30‰ to as low as −34.9‰ (Ehleringer et al., 1987). The lowest diet-$\delta^{13}C$ value reconstructed from enamel-$\delta^{13}C$ values is −32.7‰ (Table 1). Considering that the present-day $\delta^{13}C$ value of atmospheric CO_2 is about 1–2‰ lower than that of the early Pleistocene (Tipple et al., 2010), this low end-member diet-$\delta^{13}C$ value is equivalent to a modern value of ~−34 to −35‰, essentially the same as the lowest plant-$\delta^{13}C$ value observed under closed canopy deep inside a modern monsoon evergreen broadleaf forest (23°08′N, 112°35′E) (Ehleringer et al., 1987) near Guangzhou in Guangdong Province (Fig. 1).

The variation in diet among species reflects the type of habitats and eating behaviors of the animals (Fig. 3). Comparisons of enamel $\delta^{13}C$ and $\delta^{18}O$ values of contemporary animals from each cave site clearly show niche partitioning among panda, pig, giant ape and other animals (Figs. 2 and 3). The primal panda (*Ailurarctos lufengensis*) dates to the late Miocene and are thought to be carnivores or omnivores (Qiu and Qi, 1989). It has been hypothesized that the dietary switch to bamboo in panda occurred ~3 million years ago when pygmy pandas emerged (Pei, 1974; Zhao et al., 2010). Our carbon isotope data show that the early Pleistocene pandas in South China had the lowest $\delta^{13}C$ values among all mammals at each cave site, suggesting that they had a very specialized, pure C_3 diet and lived in closed-canopy forest habitats (Fig. 3). This also rules out the incorporation of animal foodstuff in the diets of these early Pleistocene pandas because consumption of animal matter would have led to higher $\delta^{13}C$ values (Lee-Thorp et al., 1989)

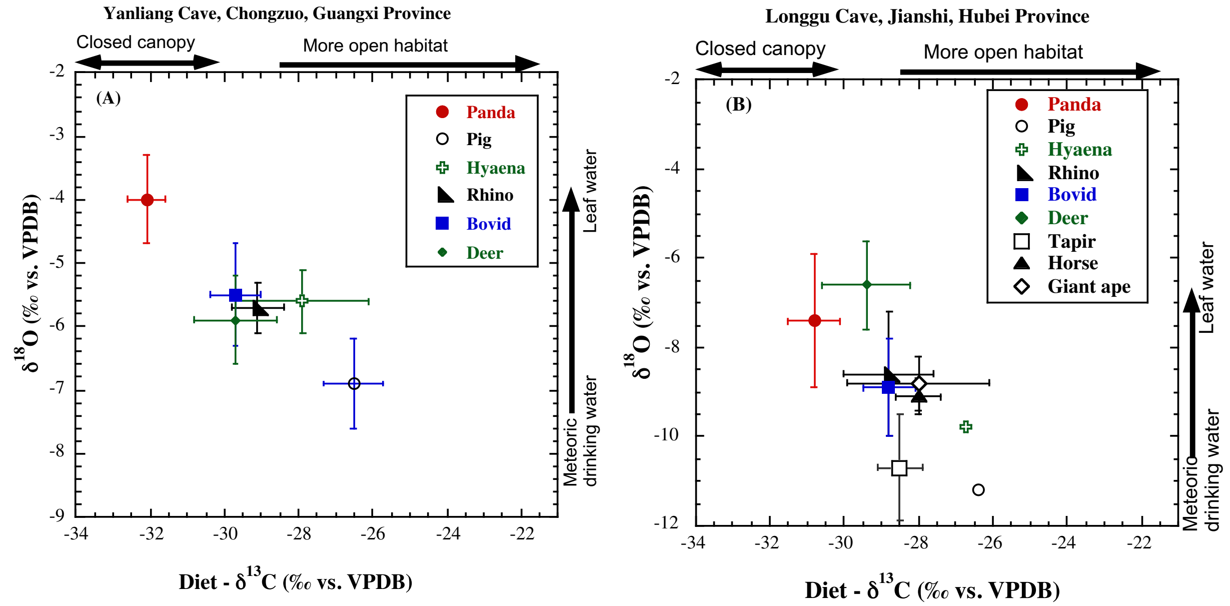

Fig. 3. Plot of enamel-$\delta^{18}O$ vs. reconstructed mean diet-$\delta^{13}C$ values of various mammals found in (A) Yanliang Cave, Chongzuo, Guangxi Province, and (B) Longgu Cave, Jianshi, Hubei Province. Error bar indicates 1σ from the mean. Data for Longgu Cave in (B) are mostly from Nelson (2014), except for pandas.

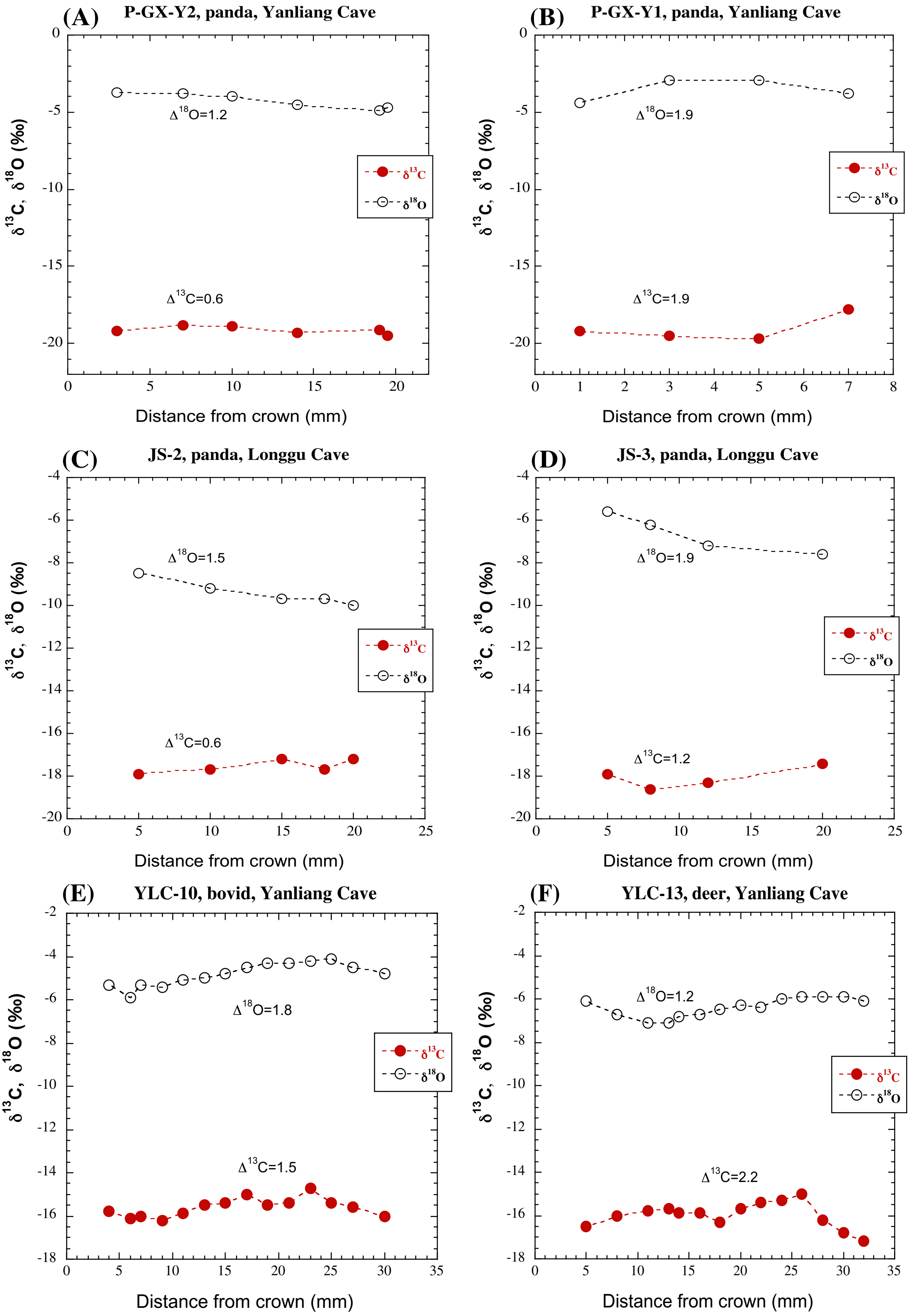

Fig. 4. Intra-tooth isotopic variations in selected fossil teeth from the Yanliang Cave, Chongzuo, Guangxi Province. $\Delta^{13}C$ and $\Delta^{18}O$ values indicate the range of carbon and oxygen isotopic variations, respectively, within each tooth.

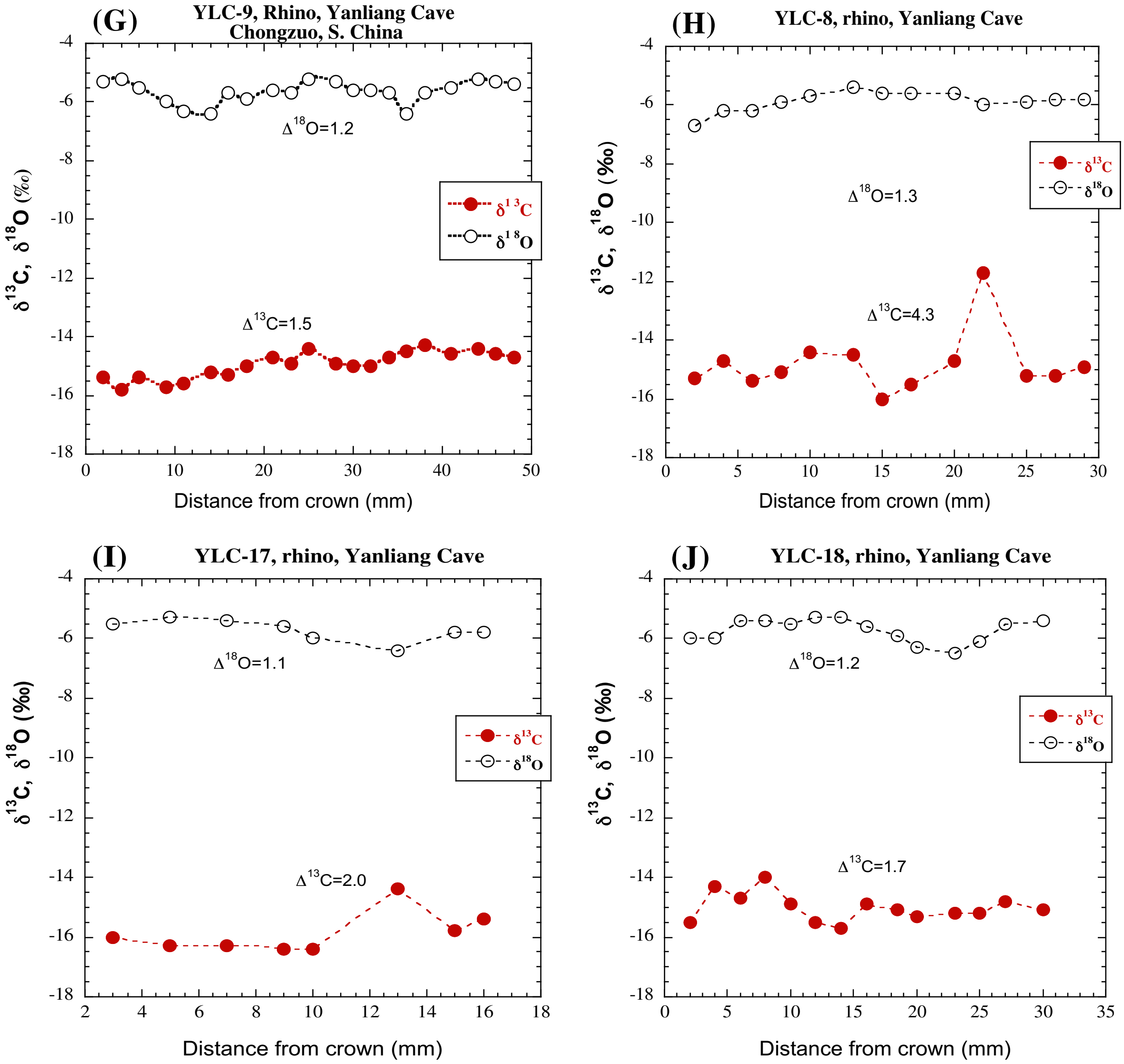

Fig. 4 (*continued*).

and increased $\delta^{13}C$ variability as seen in pigs and hyaenas (Fig. 3). Omnivorous pigs and carnivorous hyaenas exhibited higher $\delta^{13}C$ values, indicating consumption of some C_4 plants or food resources derived from C_4-plants. Thus, our $\delta^{13}C$ data from fossils suggest that the dietary shift in panda from carnivorous or omnivorous to vegetarian was completed before the early Pleistocene, and both *Ailuropoda microta* and *Ailuropoda wulingshanesis* were eating C_3 plants, probably bamboos, like their modern counterparts. This is consistent with an already established dietary niche of bamboo (a C_3 plant) in the early Pleistocene (Jin et al., 2007). However, without the extended molar of more recent pandas and a weaker jaw (Jin et al., 2007), the pygmy panda (*A. microta*) may not have been able to eat bamboo as effectively, which perhaps is related to its smaller size. The two pygmy pandas from Yanliang Cave had not only the lowest $\delta^{13}C$ values but also the highest $\delta^{18}O$ values, among all the animals analyzed in this study (Figs. 2A and 3A). This suggests that pygmy pandas (*A. microta*) obtained a larger proportion of their body water from plant water compared to the other animals studied. The highly specialized diet and restricted habitat as suggested by the $\delta^{13}C$ and $\delta^{18}O$ data may have given pandas an advantage during times when other resources were limited or over exploited by other species, but may also make them vulnerable to climate changes impacting their habitat. The carbon isotopic difference (~1‰) between *A. microta* and *A. wulingshanesis* suggests a denser forest habitat for the pygmy panda than that for the *A. wulingshanesis*. The $\delta^{18}O$ difference between the two, on the other hand, most likely reflects the “latitude effect” on the $\delta^{18}O$ of precipitation (Dansgaard, 1964) that provided both water for plants (ingested by animals) and drinking water for the animals.

In stark contrast to the pandas, pigs had the highest $\delta^{13}C$ and lowest $\delta^{18}O$ values among all species analyzed in this study (Figs. 2 and 3). This indicates that these early Pleistocene pigs (*Sus* sp.) preferred more open habitats and consumed a small amount of C_4 plants or animal matter, and that a larger proportion of their body water came from drinking water compared to other animals analyzed.

Giant apes (*Gigantopithecus blacki*) from Longgu Cave had a pure C_3 diet (Nelson, 2014; Zhao and Zhang, 2013). Their reconstructed diet-$\delta^{13}C$ value ($-29.1 \pm 1.6‰$) is ~2‰ higher than that of panda (Fig. 3B). Some studies have suggested that giant apes, like pandas, fed on bamboo or other tough foods, based on dental and mandibular morphologies (Kupczik and Dean, 2008; White, 1975). The carbon and oxygen isotopic differences between the two, however, suggest that giant ape and panda did not have the same diet and drinking habits (Fig. 3B).

Bovids and Rhinos had similar $\delta^{13}C$ values indicating that they had C_3-based diets (Figs. 2 and 3). This $\delta^{13}C$ similarity, coupled with an overlap in $\delta^{18}O$ values, implies that they both utilized the same resources.

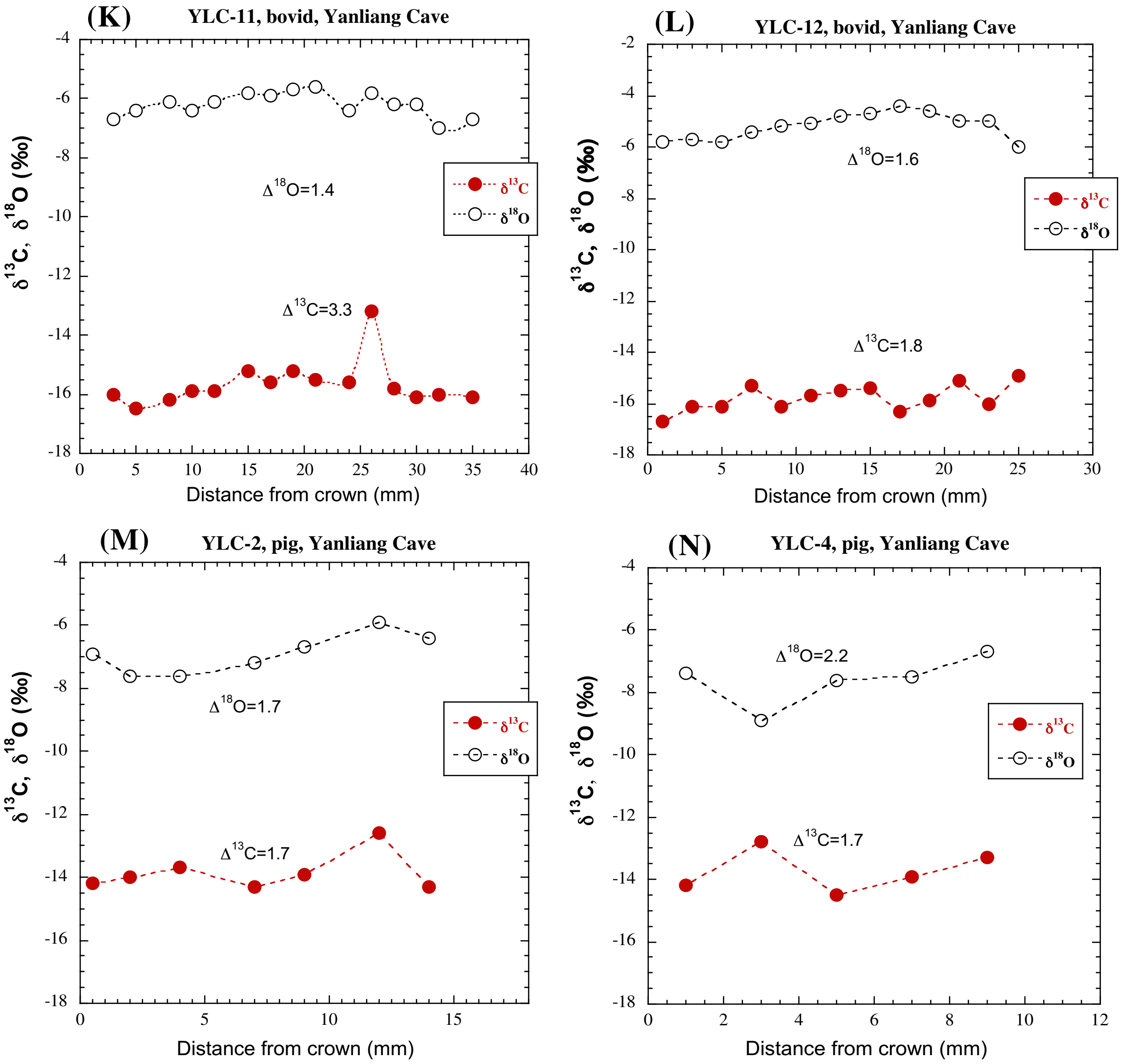

Fig. 4 (*continued*).

Some of the rhinos and bovids show significant intra-tooth $\delta^{13}C$ variations, suggesting that they may have consumed a small amount of C_4 grasses (Fig. 4). For example, the positive excursion at 22 mm from the crown in the $\delta^{13}C$ profile of sample YLC-8 (Fig. 4H) is significant enough to suggest that this rhino had occasionally ingested some C_4 grasses (up to ~21% C_4 assuming end-member $\delta^{13}C$ values for pure C_3 and C_4 diets were −29‰ and −13‰, respectively). This species, *Rhinoceros fusuiensis*, is believed to be the ancestor of the now critically endangered *R. sondaicus* (Yan et al., 2014). The modern lineage, also known as the Javan rhino, is predominantly a browser that prefers more open habitats without large trees (such as shrub lands, forest clearings). They eat a diverse range of plants including leaves, shoots, twigs and fruit, and graze occasionally on grasses (Waters, 2000). Our isotope data suggest that its ancestor *R. fusuiensis* had a similar dietary behavior and habitat preference (Figs. 3 and 4).

The largest intra-species $\delta^{13}C$ variations are observed in deer (4.6‰) and hyaena (4.3‰) from the Yanliang Cave (Table 1). Despite differences in their feeding behaviors, the data show that both deer (herbivore) and hyaenas (carnivore) inhabited a wide range of habitats and ate a variety of foods. They did not show as much dietary specialization as other species and may not have had to drink as much as pigs (Figs. 2 and 3). This suggests that both animals were more ecologically flexible than other co-existing animals.

Studies have shown that enamel-$\delta^{18}O$ values of obligate drinkers are strongly correlated with the $\delta^{18}O$ of meteoric water (e.g., Kohn and Cerling, 2002; Wang et al., 2008a). Precipitation is known to display large seasonal variations in response to seasonal variations in climate (Dansgaard, 1964; Rozanski et al., 1993). It is also well known that rivers and lakes have a much smaller isotopic variability than precipitation as their water is mostly derived from groundwater that integrates precipitation spatially and temporally over the watershed (Clark and Fritz, 1997). The $\delta^{18}O$ values of precipitation recorded at the IAEA-GNIP (International Atomic Energy Agency Global Network for Isotopes in Precipitation) stations in our study areas show that summer precipitation is more depleted in ^{18}O than winter precipitation (Fig. 5), which is characteristic of the Asian summer monsoon regime (Johnson and Ingram, 2004). In the Asian summer monsoon region, most of the annual precipitation falls during the summer monsoon season (May through August). The available data (IAEA, 2001) show that the annual average $\delta^{18}O$ values of

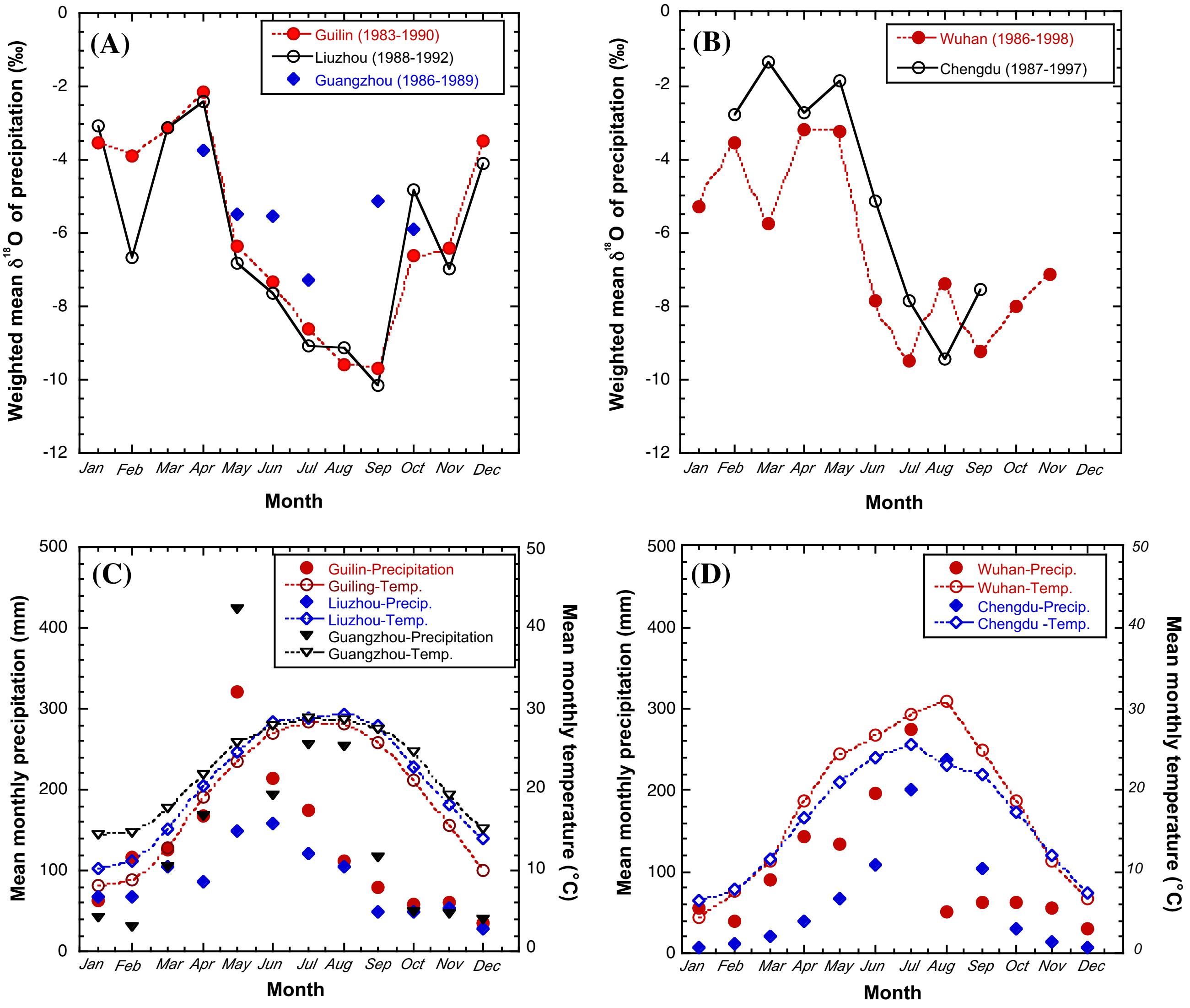

Fig. 5. Weighted mean $\delta^{18}O$ of monthly precipitation at IAEA-GINP stations (A) near Yanliang Cave and (B) near Longgu Cave. Mean monthly precipitation (solid symbols) and air temperatures (open symbols) measured at the same stations are shown in (C) and (D).

precipitation in this region display a general decreasing trend with increasing distance from the ocean (the moisture source) from -5.8 ± 1.1‰ (for the period of 1986–1989) in Guangzhou, -6.2 ± 0.9‰ (1983–1990) in Guilin, -6.5 ± 0.7‰ (1988–1991) in Liuzhou, to -6.4 ± 2.1‰ (1986–1998) in Wuhan and -7.0 ± 1.1‰ (1987–1997) in Chengdu (Fig. 1), reflecting the "continental effect" and the "latitude effect" (Dansgaard, 1964). During the summer, summer monsoons carry moisture from the ocean inland, resulting in increased precipitation over the continent. Because condensation preferentially removes heavy isotopes from vapor, the remaining vapor in an air mass and the precipitation formed subsequently from it become more depleted in ^{18}O as the air mass moves away from its source area and more vapor condenses to form precipitation. In any given area within the summer monsoon region, the heavier the rain, the lower the $\delta^{18}O$, owing to the "amount effect" (Dansgaard, 1964).

We reconstructed the $\delta^{18}O$ of local meteoric waters from the average enamel-$\delta^{18}O$ values of rhinos, pigs, bovids, horses, giant apes and hyaenas (all presumably obligate drinkers), using the following equation (Wang et al., 2013; Zhang et al., 2012) derived from the enamel/bone phosphate-water $\delta^{18}O$ relationship for obligate drinkers (Kohn and Cerling, 2002) and the relationship between $\delta^{18}O$ of phosphate and structural carbonate components of hydroxyapatite for modern mammals (Iacumin et al., 1996):

$$\delta^{18}O_w\ (VSMOW) = \left[\delta^{18}O_c\ (VPDB) - 1.244\right]/0.891 \qquad (1)$$

where $\delta^{18}O_w$ is the oxygen isotope composition of water in reference to the international standard VSMOW and $\delta^{18}O_c$ the oxygen isotope composition of structural carbonate in tooth enamel hydroxyapatite in reference to VPDB.

The estimated paleo-water $\delta^{18}O$ values were about −7.5‰ to −9.2‰ for Yanliang Cave area and −11.0‰ to −12.4‰ for the Longgu Cave area (Table 1). These reconstructed paleo-water $\delta^{18}O$ values are ~2–4‰ lower than the average precipitation-$\delta^{18}O$ values in the region today, likely indicating a wetter condition or stronger summer monsoon in the early Pleistocene than today. The change in regional climate as inferred from the $\delta^{18}O$ data could be caused by a change in the mean state of global climate or tectonic change in the Tibetan region. However, without precise age data for our fossils and for the growth of the Tibetan Plateau, it is impossible at present to determine the exact cause of the observed change in regional climate. The small intra-tooth $\delta^{18}O$ variations observed in the fossil teeth (Fig. 4) likely indicate that these animals drank from isotopically buffered water sources such as rivers or lakes (Clark and Fritz, 1997), implying abundant fresh water sources in the area.

6. Conclusions

Stable isotope analyses of tooth enamel samples from a diverse group of fossil mammals from Yanliang Cave and Longgu Cave in South China show that these early Pleistocene mammals had C_3-based diets but some individuals including rhinos, pigs, deer and bovids may have consumed small amounts of C_4 grasses. Although the study areas were dominated by C_3 habitats including closed canopy forests and woodlands in the early Pleistocene, small amounts of C_4 grasses were present likely in patches of open areas where the forest (or woodland) canopies were broken. The data also reveal clear niche partitioning among various mammals in the study areas in the early Pleistocene. In particular, the $\delta^{13}C$ and $\delta^{18}O$ values of the pygmy pandas are highly differentiated from other co-existing mammals, indicating a specialized diet and a restricted habitat. These ancient pandas all had lower $\delta^{13}C$ and higher $\delta^{18}O$ values than contemporaneous mammals. If confirmed with more data, this would indicate that pygmy pandas were vegetarians, ate only C_3 plants growing in the understory of a closed-canopy forest, and obtained a larger proportion of their body water from plants compared to other mammals analyzed in this study. A pure C_3 diet for the pygmy panda is consistent with the morphological evidence suggesting that the dietary shift in panda from carnivorous or omnivorous to vegetarian was completed by the early Pleistocene. Both *Ailuropoda microta* and *Ailuropoda wulingshanesis* were feeding exclusively on C_3 plants, presumably bamboos, like the modern giant panda. The isotope data also suggest that *A. microta* was less ecologically flexible than other contemporaneous mammals such as pig, *Rhinoceros fusuiensis*, deer, and bovid. The limited ecological flexibility of *A. microta* may have contributed to its demise. Reconstructed $\delta^{18}O$ values of paleo-waters were significantly lower than the annual average $\delta^{18}O$ values of modern precipitation in the region, suggesting a wetter climate or stronger summer monsoon in the early Pleistocene than today.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2016.12.015.

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