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# Paleoecology of Pleistocene mammals and paleoclimatic change in South China: Evidence from stable carbon and oxygen isotopes

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## ABSTRACT

The role of climate change in the evolution and diversification of hominoids remains a hotly debated issue. Stable isotope analyses of fossil mammals that coexisted with the hominoids can provide insights into hominoid palaeoenvironments and shed light on this debate. Here, we report results of stable carbon and oxygen isotope analyses of tooth enamel samples from a variety of Pleistocene mammals including pandas, deer, elephants, pigs, rhinos, and bovids from two hominoid fossil localities (Yugong Cave and Baxian Cave) in South China. Enamel $\delta^{13}C$ values indicate that most of the mammals living in the study area during the late Middle Pleistocene had $C_3$-based diets but a small number of individuals consumed some $C_4$ grasses. This indicates the presence of $C_4$ plants in the region during the late Middle Pleistocene, most likely in patches of open areas in a predominantly forested environment. However, during the early Late Pleistocene, all of the mammals examined had $C_3$-based diets, except one bovid and one panda that may have ingested small amounts of $C_4$ plants. This indicates a dense forested environment with little $C_4$ grasses during the early Late Pleistocene. Like the Early Pleistocene pygmy panda (*Ailuropoda microta*) from Yanliang Cave, the late Middle Pleistocene *Ailuropoda baconi* from Yugong Cave and the early Late Pleistocene *Ailuropoda melanoleuca* from Baxian Cave had higher mean diet-$\delta^{13}C$ values than other co-occurring herbivores, indicating they preferred relatively open forest habitats and had more restricted diets compared to other mammals. The reconstructed mean paleo-meteoric water $\delta^{18}O_w$ values are lower than the annual average $\delta^{18}O_w$ value of modern precipitation in the region, suggesting that the climatic conditions during the times when these Pleistocene mammals were alive were colder and/or wetter than today. In addition, $\delta^{18}O$ values of the obligate drinkers (pigs, rhinos, bovids) display an overall decreasing trend, accompanied by increased range of $\delta^{18}O$ variations, from the Early Pleistocene to the early Late Pleistocene. This suggests that the regional climate became colder and/or wetter, with increased seasonality, from the Early Pleistocene to the early Late Pleistocene, likely related to intensified glaciation. The change in climate to colder conditions may be responsible for the extinction of the *Gigantopithecus* in this region.

## 1. Introduction

Fossils are important archives of ancient diets and environments and have been widely utilized to address a variety of ecological and environmental questions (e.g., Cerling et al., 1997; Koch, 1998; Kohn, 1999), and to test hypotheses regarding the role of climate change in human evolution (e.g., Ungar and Sponheimer, 2011; Cerling, 2013). Stable carbon and oxygen isotopic analyses of fossil mammalian tooth enamel is an important tool in the study of paleoclimate and paleoecology. Such analyses may allow insights into the biology and ecology of ancient taxa and increase our understanding of the effects of a changing environment on the evolution of these and related mammals (e.g., Cerling et al., 1993; Ciner et al., 2015; Ciner et al., 2016).

Carbon isotopes are valuable for distinguishing diets based directly or indirectly on plants using different photosynthetic pathways (Cerling et al., 1989; Koch, 1998; Kohn and Cerling, 2002). Plants can be divided into three groups based on their photosynthetic pathways: $C_3$ plants (trees, most shrubs, forbs, and cool season grasses), $C_4$ plants (warm season grasses), and CAM plants (succulents). In the modern world, $C_3$ plants have $\delta^{13}C$ ($\delta = [R_{sample}/R_{standard} - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ for carbon isotopes or $R = {}^{18}O/{}^{16}O$ for oxygen isotopes, and the standard is the international carbonate standard VPDB) values ranging from $-36‰$ to $-22‰$, with an average of $-27‰$ (O'Leary, 1988; Farquhar et al., 1989; Cerling et al., 1997; Kohn, 2010). $C_3$ plants

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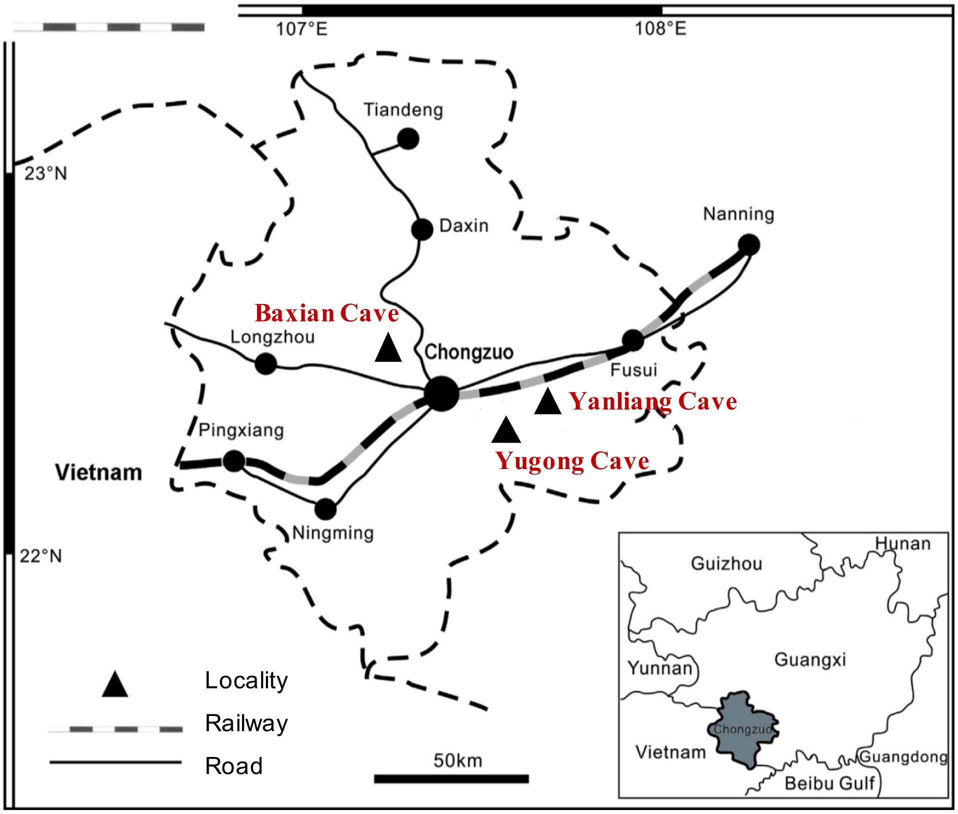

**Fig. 1.** Map showing the locations of Yugong Cave, Baxian Cave, and Yanliang Cave in Guangxi Province in China, modified from Wang et al. (2017b).

that grow under closed canopies have the most negative $\delta^{13}C$ values due to the influence of soil respired $CO_2$ and light limitation, while $C_3$ plants in water stressed conditions tend to have higher $\delta^{13}C$ values ($> -27‰$) that can be as high as $-22‰$ in deserts (e.g., Williams and Ehleringer, 1996; Cerling and Harris, 1999; Zhang et al., 2012). $C_4$ plants, mostly consisting of warm growth season grasses, are commonly found in low elevation grasslands at low to mid latitudes. The $\delta^{13}C$ values of $C_4$ plants vary from $-17‰$ to $-9‰$, with an average of $-13‰$, much higher than those of $C_3$ plants (Farquhar et al., 1989; Cerling and Harris, 1999). The distinct isotopic difference between $C_3$ and $C_4$ plants is passed along the food chain to animal tissues with further isotopic fractionation. Compared to bones and dentine or other tissues, fossil tooth enamel often preserves original isotopic signatures because of large crystal size, low organic content and low porosity, reducing influx of diagenetic fluids (Ayliffe et al., 1994; Wang and Cerling, 1994). The isotopic signatures can provide information about the diet and water ingested by an animal around the time of the tooth formation. For medium to large mammalian herbivores, their tooth enamel carbonate is enriched in heavy carbon isotope $^{13}C$ by 13 to 14‰ relative to diet due to biochemical isotope fractionation (Cerling and Harris, 1999). Thus, a tooth enamel $\delta^{13}C$ value $< -10‰$ is generally indicative of a pure $C_3$ diet and a $\delta^{13}C$ value $> -2‰$ would reflect a pure $C_4$ diet (e.g., Lee-Thorp et al., 1989; Cerling et al., 1997; Biasatti et al., 2012; Stacklyn et al., 2017). In a dense forested environment, the end-member enamel $\delta^{13}C$ value for a pure $C_3$ diet could be as low as $-17‰$ (Cerling et al., 1997). In general, temporal shifts in enamel-$\delta^{13}C$ values of mammals from a given locality would indicate shifts in diet, habitat, or regional climatic conditions. In terms of habitat, enamel-$\delta^{13}C$ values $< -13‰$ typically represent closed habitats, while those $> -10‰$ suggest affinities for more open habitats. As a result, carbon isotope analyses allow us to understand the feeding behavior and habitat preference of particular fossil taxa.

Oxygen isotopes in fossil mammals can provide information on paleoclimates (Bryant et al., 1996; Kohn, 1996; Chritz et al., 2009; Blumenthal et al., 2017). The $\delta^{18}O$ values of herbivore tooth enamel can be influenced by different variables, including drinking water, water in food, physiological processes, and mammals' dietary/drinking behavior (Bryant et al., 1996; Kohn, 1996; Blumenthal et al., 2017). Studies have shown that $\delta^{18}O$ values of body water for obligate drinkers mainly carry information about meteoric water because most of their ingested water comes from meteoric water (e.g., Kohn and Cerling, 2002; Levin et al., 2006; Wang et al., 2008; Blumenthal et al., 2017). $\delta^{18}O$ values of meteoric water are sensitive to climatic variables such as temperature, seasonality of rain, and amount of rain (Dansgaard, 1964). Thus, $\delta^{18}O$ values of tooth enamel have been used as a proxy for paleoclimatic conditions during the growth of teeth (Wang and Deng, 2005). Obligate drinkers tend to have lower body water $\delta^{18}O$ values than non-obligate drinkers that obtain most of their water from plants because leaf water is usually enriched in heavy oxygen isotope $^{18}O$ relative to local meteoric water due to evapotranspiration (Dongmann et al., 1974; Epstein et al., 1977; Levin et al., 2006; Faith, 2018).

Southeast Asia has been home for a diverse assemblage of large mammal species (Jablonski et al., 2000; Wang et al., 2007). Over the last decades, hominoid fossils such as the orangutan *Pongo*, the giant ape *Gigantopithecus*, and *Homo sapiens*, along with abundant coexisting mammalian fossils have been discovered from a series of cave sites and fissure deposits in South China (Jin et al., 2009, 2014; Dong et al., 2014; Liu et al., 2015; Wang et al., 2017a, 2017b; Zhang et al., 2018). Although previous studies have utilized carbon and oxygen isotopic compositions of tooth enamel samples from a few fossil localities (Biasatti et al., 2010, 2012; Stacklyn et al., 2017; Ma et al., 2017) in South China to reconstruct the diets, ecology and habitats of mammals that lived along with hominids, the method has not been applied to majority of the fossil sites in the region.

In this study, we analyzed the carbon and oxygen isotopic compositions of tooth enamel samples from a diverse group of mammalian fossils uncovered from two Pleistocene hominoid fossil sites in South China to reconstruct the paleodiets and paleoenvironment of these

**Table 1**

Summary of results of carbon and oxygen isotope analyses of mammalian tooth enamel samples from Yugong Cave and Baxian Cave in South China.

| Species | Common name | Mean $\delta^{13}C$ (‰, VPDB) | Mean $\delta^{18}O$ (‰, VPDB) | Estimated mean diet $\delta^{13}C$ | Range of diet-$\delta^{13}C$ | Estimated water $\delta^{18}O$ | No. of samples | No. of individuals |
|---|---|---|---|---|---|---|---|---|
| Yugong Cave, Chongzuo, Guangxi Province | | | | | | | | |
| *Ailuropoda baconi* | Panda | −17.2 ± 0.9 | −5.6 ± 0.9 | −26.9 | −28.2 to −25.2 | | 14 | 6 |
| *Rhinoceros sondaicus* | Rhino | −15.8 ± 0.7 | −7.2 ± 0.8 | −28.8 | −29.8 to −27.8 | −9.5 ± 0.8 | 11 | 4 |
| *Stegodon* | Elephant | −16.0 ± 0.6 | −8.1 ± 0.6 | −29.0 | −25.5 to −22.0 | −10.5 ± 0.6 | 12 | 3 |
| *Cervus* sp. | Deer | −14.9 ± 3.3 | −6.8 ± 1.1 | −28.9 | −35.1 to −24.5 | | 44 | 4 |
| *Leptobos* sp. | Bovid | −14.3 ± 5.1 | −6.1 ± 0.6 | −28.3 | −34.0 to −18.4 | −8.2 ± 5.1 | 85 | 4 |
| *Suidae* | Pig | −14.7 ± 0.9 | −7.1 ± 0.9 | −27.7 | −29.7 to −25.4 | −9.4 ± 0.9 | 23 | 6 |
| *Ursus thibetanus* | Bear | −13.5 ± 0.2 | −5.7 ± 0.1 | −26.5 | −26.6 to −26.2 | | 3 | 2 |
| Baxian Cave, Chongzuo, Guangxi Province | | | | | | | | |
| *Ailuropoda melanoleuca* | Panda | −17.1 ± 1.1 | −4.2 ± 1.4 | −26.8 | −28.4 to −23.9 | | 46 | 11 |
| *Rhinoceros sondaicus* | Rhino | −17 ± 1.0 | −7.6 ± 1.1 | −30.0 | −31.5 to −28.9 | −9.9 ± 1.0 | 31 | 2 |
| *Cervus* sp. | Deer | −16.6 ± 4.9 | −5.3 ± 0.8 | −30.6 | −34.0 to −27.1 | | 2 | 2 |
| *Leptobos* sp. | Bovid | −14.6 ± 3.9 | −8.1 ± 0.7 | −28.6 | −32.7 to −24.0 | −10.5 ± 3.9 | 34 | 2 |
| *Suidae* | Pig | −14.9 ± 0.7 | −8.6 ± 3.3 | −27.9 | −29.3 to −26.6 | −11.0 ± 0.7 | 18 | 4 |
| *Ursus thibetanus* | Bear | −15.8 ± 0.7 | −7.9 ± 1.1 | −28.8 | −29.7 to −28.1 | | 5 | 5 |

mammals. Reconstruction of paleodiets and paleoenvironments for the mammalian faunas contemporaneous with *Homo sapiens* and other hominoids (i.e., orangutan *Pongo*; *Gigantopithecus*) can provide valuable insights into the environments in which these primates lived. Results from this study were also compared with previously published data from the region to better understand long-term environmental change and its impact on habitats and mammalian communities during the Pleistocene epoch. The objective of this study is to obtain a more detailed and clearer view of the environments and habitats in which these Pleistocene mammals lived.

## 2. Study sites

Fossils analyzed in this study were collected from two Pleistocene fossil localities, Yugong and Baxian Caves, in Chongzuo City of Guangxi Province, South China (Fig. 1). Chongzuo City is located within humid subtropical climate zone. Climate in this area is influenced by East Asian summer monsoon and characterized by a long warm summer and a short mild winter. The area lies in southern edge of southern subtropical zone with strong solar radiation. The average lowest temperature is above 13 °C and the highest day time temperature can reach about 40 °C. The annual precipitation is 1150 mm to 1550 mm (Jin et al., 2009). The area is primarily underlain by carbonate rocks and characterized by karst topography. Because of high rainfall and abundant limestone, this region has many Early to Late Pleistocene caves formed due to dissolution of limestone underground. *Gigantopithecus*, *Pongo* and some *Homo sapiens* fossils, along with coexisting mammalian fossils, have been uncovered in several caves in Chongzuo area after many years of detailed archaeological excavations (Dong et al., 2014). The discovery of early *Homo sapiens* and hominoid fossils in Chongzuo of Guangxi Province in South China has a significant role in the study of origin and evolution of modern humans in East Asia. Reconstructing the environments and habitats of the coexisting fossil mammals can provide environmental context to help understand evolution of the primate genera.

Yugong Cave is located in the Gongjishan area (~22°14′N, 107°23′E) of Banli County, in Chongzuo City, Guangxi Province (Fig. 1). A variety of mammals have been uncovered from this cave, including *Sus xiaozhu wenzhongi* subsp., *Sus* cf. *s. peii* Linnaeus, *Muntiacus* sp., *Cervus* (*Rusa*) cf. *unicolor*, Capinae gen. et sp. indet., *Bos* (*Bibos*) sp., and *Ailuropoda baconi*. Analysis of the fossil assemblage suggests that Yugong fauna was younger than Sanhe Cave, Boyueshan, Juyuan Cave and Mohui Cave from the Early Pleistocene, but older than Zhiren Cave and Xiapubu Cave from the Late Pleistocene (Dong et al., 2014). Thus, the age of Yugong fauna was estimated to be the late Middle Pleistocene (Dong et al., 2014).

Baxian Cave (22°34′31.6″N, 107°21′0.2″E) was discovered in the town of Zuozhou in Chongzuo City, Guangxi Province (Fig. 1). The sediments inside the Baxian Cave are approximately 5 m thick and are divided into five layers from top to bottom (Ma et al., 2017). A variety of mammal species were uncovered after systematic excavations, including primates (*Pongo* sp., *Macaca* sp., *Nomascus* sp., and *Rhinopithecus* sp.), *Ailuropoda baconi*, *Ursus thibetanus*, *Arctonyx collaris*, *Panthera tigris*, stegodonts (*Stegodon orientalis*), perissodactyls (*Rhinoceros sondaicus* and *Megatapirus augustus*), *Elephas maximus*, and artiodactyls (*Sus scrofa*, *Muntiacus* sp., *Cervus* [*Rusa*] sp., and *Bos* [*Bibos*] sp.). The primate fauna mainly consists of *Pongo* sp., and *Nomascus* sp., and > 1600 isolated teeth have been discovered in Baxina Cave (Takai et al., 2014). The Baxian faunal assemblage is currently estimated to be the early Late Pleistocene (Ma et al., 2017) based on the similarity to faunas from Zhiren Cave, dated to 100 to 113 ka (Jin et al., 2009; Liu et al., 2010; Cai et al., 2016) and Fuyuan Cave, dated to 80 to 120 ka (Liu et al., 2015).

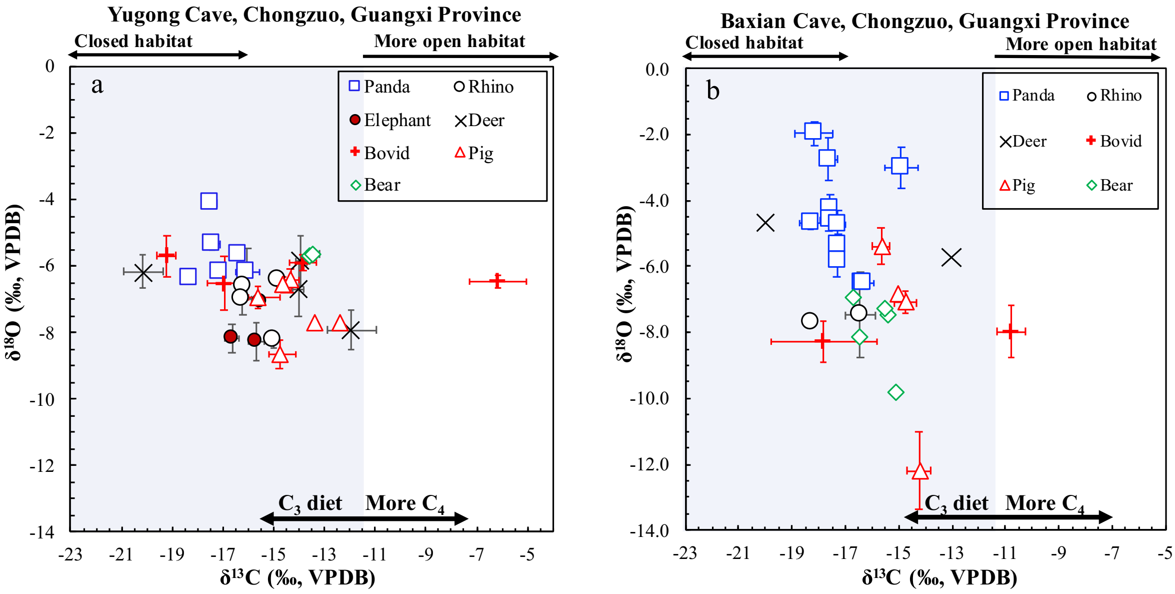

**Fig. 2.** Enamel-$\delta^{13}$C and $\delta^{18}$O values of various mammals from Yugong Cave (a) and Baxian Cave (b) in Chongzuo, Guangxi Province (South China). Each point represents the average value for an individual animal based on either analysis of a bulk enamel sample or by averaging all serial $\delta^{13}$C (or $\delta^{18}$O) values from a tooth. Error bar indicates 1$\sigma$ from the mean.

## 3. Materials and methods

In this study, 192 enamel samples were collected from 29 mammalian teeth or dental fragments from Yugong Cave for stable carbon and oxygen isotope analyses (Table 1). These samples represent a diverse group of animals, including six pandas (*Ailuropoda baconi*), four rhinos (*Rhinoceros sondaicus*), three elephants (*Stegodon*), four deer (*Cervidae*), four bovids (*Leptobos* sp.), six pigs (*Suidae*), and two bears (*Ursus thibetanus*). In addition, 136 fossil tooth enamel samples were obtained from 26 teeth representing six taxa from Baxian Cave for this study. Samples from Baxian Cave include eleven pandas (*Ailuropoda melanoleuca*), two rhinos (*Rhinoceros sondaicus*), two deer (*Cervidae*), two bovids (*Leptobos* sp.), four pig (*Suidae*), and five bears (*Ursus thibetanus*). The fossil teeth selected for this study are well preserved, showing no visible signs of alternation. An earlier XRD and FTIR analyses on enamel samples from the same fossil collection from Baxian Cave detected no signs of alteration or recrystallization (Ma et al., 2017). In addition, significant inter- and intra-tooth isotopic variations are observed in the samples (as discussed in the next sections), also suggesting little or no alteration, as diagenesis would have obliterated such variations.

Both bulk and serial tooth enamel samples were analyzed in this study. Isotope analysis of a bulk tooth enamel sample yields the average isotopic composition for the growth period of a tooth while serial enamel samples obtained along the growth axis of an individual tooth provide a record of seasonal variations in diet and climate during growth of the tooth (e.g., Sharp and Cerling, 1998). Bulk enamel samples were obtained either by drilling along the entire length of a tooth using a slow-speed rotary drill or by cutting off section of each tooth from crown to root, and manually separating enamel from dentine using a rotary tool. Samples were primarily collected from late erupting teeth (mainly the third molar if available) in order to avoid the sampling teeth mineralized while nursing or weaning. The samples were then grounded into powder using a mortar and pestle. Serial samples were drilled using a slow-speed rotary tool at intervals 1 to 3 mm perpendicular to the growth axis of the tooth from near the occlusal surface to root, with the youngest samples being near the root and oldest samples being near the occlusal surface at the top of crown. The powered tooth enamel samples (2 to 3 mg) were pretreated in 5% sodium hypochlorite (NaOCl) overnight to remove any possible organic contaminants, then cleaned with distilled water. Next, the samples were treated with 1 M acetic acid overnight to remove non-structural carbonates and cleaned with distilled water and freeze-dried (Wang and Deng, 2005). The treated enamel samples were finally reacted with 100% phosphoric acid for about 72 h at 25 °C to produce $CO_2$.

The carbon and oxygen isotopic ratios of the $CO_2$ produced were measured using a Gas Bench II Auto carbonate device connected to a Finnigan MAT Delta Plus XP stable isotope ratio mass spectrometer (IRMS) at Florida State University. Two standards were run for every twelve samples. Results are reported in standard delta ($\delta$) notation as $\delta^{13}$C and $\delta^{18}$O values in reference to the international carbonate standard VPDB (Gonfiantini et al., 1995). The analytical precision (based on replicate analyses of standards including NBS-19 and other lab-standards processed with each batch of samples) is ± 0.1‰ or better for both $\delta^{13}$C and $\delta^{18}$O.

When plants are consumed by herbivores, there is an enrichment in the heavy carbon isotope as plant carbon is incorporated into enamel due to biochemical fractionation of carbon isotopes. The enrichment factor $\varepsilon_{\text{enamel-diet}}$ is related to the fractionation factor $\alpha_{\text{enamel-diet}}$ by the following equation (Cerling and Harris, 1999; Passey et al., 2005):

$$\varepsilon_{\text{enamel-diet}} = [\alpha_{\text{enamel-diet}} - 1] * 1000$$

In this study, we used 14‰ as enrichment factor ($\varepsilon_{\text{enamel-diet}}$) for bovid and deer (ruminants), and 13‰ for other animals (non-ruminants) except panda (Cerling and Harris, 1999; Passey et al., 2005) to reconstruct the diet-$\delta^{13}$C values. For pandas, the $\varepsilon_{\text{enamel-diet}}$ value of 9.7‰ given in Han et al. (2016) was used to reconstruct their diet-$\delta^{13}$C values.

## 4. Results

We analyzed the stable carbon and oxygen isotope compositions of 328 enamel samples from a diverse group of animals from Yugong Cave and Baxian Cave in Chongzuo City, Guangxi Province (Supplementary Table). The results are summarized in Table 1 and Figs. 2 to 4.

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

Enamel-$\delta^{13}$C values of herbivores from Yugong Cave range from

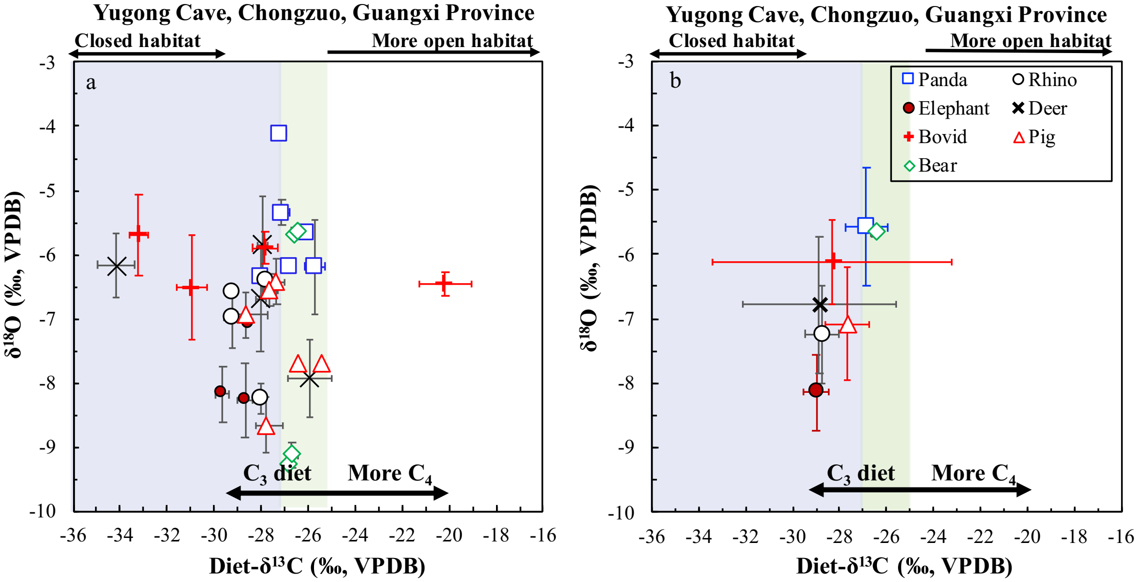

**Fig. 3.** Plot of enamel-δ$^{18}$O values vs. reconstructed mean diet-δ$^{13}$C values of various mammals found from Yugong Cave area. Each point in (a) represents an average of the reconstructed diet-δ$^{13}$C values based on serial samples from one individual tooth; each point in (b) represents the reconstructed mean diet-δ$^{13}$C (δ$^{18}$O) value for one species. Error bar indicates 1σ from the mean. Note that diet-δ$^{13}$C values of −27 to −25‰ (shaded in light green) could indicate dietary intake of some C$_4$ grasses in areas dominated by dense forests as sub-canopy C$_3$ plants have more negative δ$^{13}$C values (< −30‰). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

−21.1 to −4.4‰, with a mean of −14.9 ± 3.8‰ (all means reported ± 1 standard deviation), whereas the δ$^{18}$O values vary from −9.1 to −3.6‰, averaging −6.5 ± 1.0‰ ($n = 192$) (Table 1, Fig. 2A). The reconstructed diet-δ$^{13}$C (after fractionation adjustment of 14‰ for ruminants, 13‰ for nonruminants, 9.7‰ for pandas) yield values ranging from −35.1 to −18.4‰ (Fig. 3).

For pandas (*Ailuropoda baconi*), the δ$^{13}$C values of enamel samples vary from −18.5 to −15.5‰, averaging −17.2 ± 0.9‰ ($n = 14$). The reconstructed diet δ$^{13}$C values range from −28.2 to −25.2‰, averaging −26.9 ± 0.9‰. The average δ$^{18}$O value is −5.6 ± 0.9‰.

Tooth enamel samples from rhino (*Rhinoceros sondaicus*) yield δ$^{13}$C values of −15.8 ± 0.7‰, ranging from −16.8 to −14.8‰ ($n = 11$). This corresponds to reconstructed diet δ$^{13}$C values of −29.8 to −27.8‰, averaging −28.8 ± 0.7‰. The δ$^{18}$O values vary from −8.4 to −6.4‰, with an average of −7.2 ± 0.8‰.

Tooth enamel samples from pigs (*Suidae*) have average δ$^{13}$C values of −14.7 ± 0.9‰ ($n = 23$), ranging from −16.7 to −12.4‰ ($n = 23$). The reconstructed diet δ$^{13}$C values vary significantly from −29.7 to −25.4‰, averaging −27.7 ± 0.9‰. The δ$^{18}$O values for these samples vary from −9.1 to −5.9‰ with an average of −7.1 ± 0.9‰.

Enamel δ$^{13}$C values of bovids (*Leptobos* sp.) vary from −20.0 to

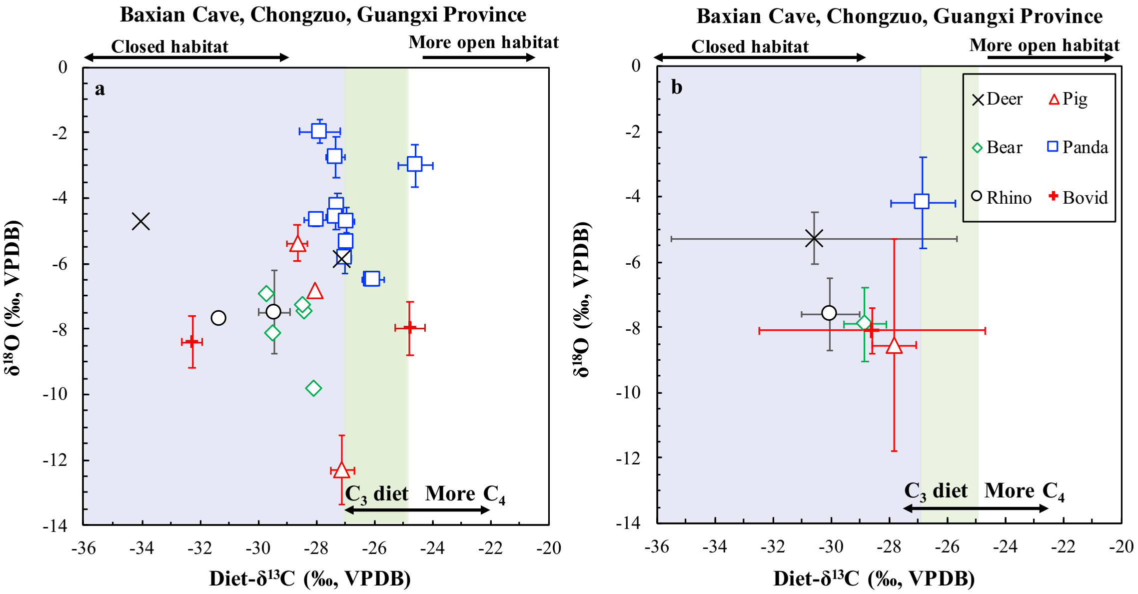

**Fig. 4.** Plot of enamel-δ$^{18}$O values vs. reconstructed mean diet-δ$^{13}$C values of various mammals found from Baxian Cave. Each point in (a) represents an average of the reconstructed diet-δ$^{13}$C values from one individual tooth; each point in (b) represents the reconstructed mean diet-δ$^{13}$C (δ$^{18}$O) values from one species; error bar indicates 1σ from the mean. Note that diet-δ$^{13}$C values of −27 to −25‰ (shaded in light green) could indicate dietary intake of some C$_4$ grasses in areas dominated by dense forests as sub-canopy C$_3$ plants have more negative δ$^{13}$C values (< −30‰). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

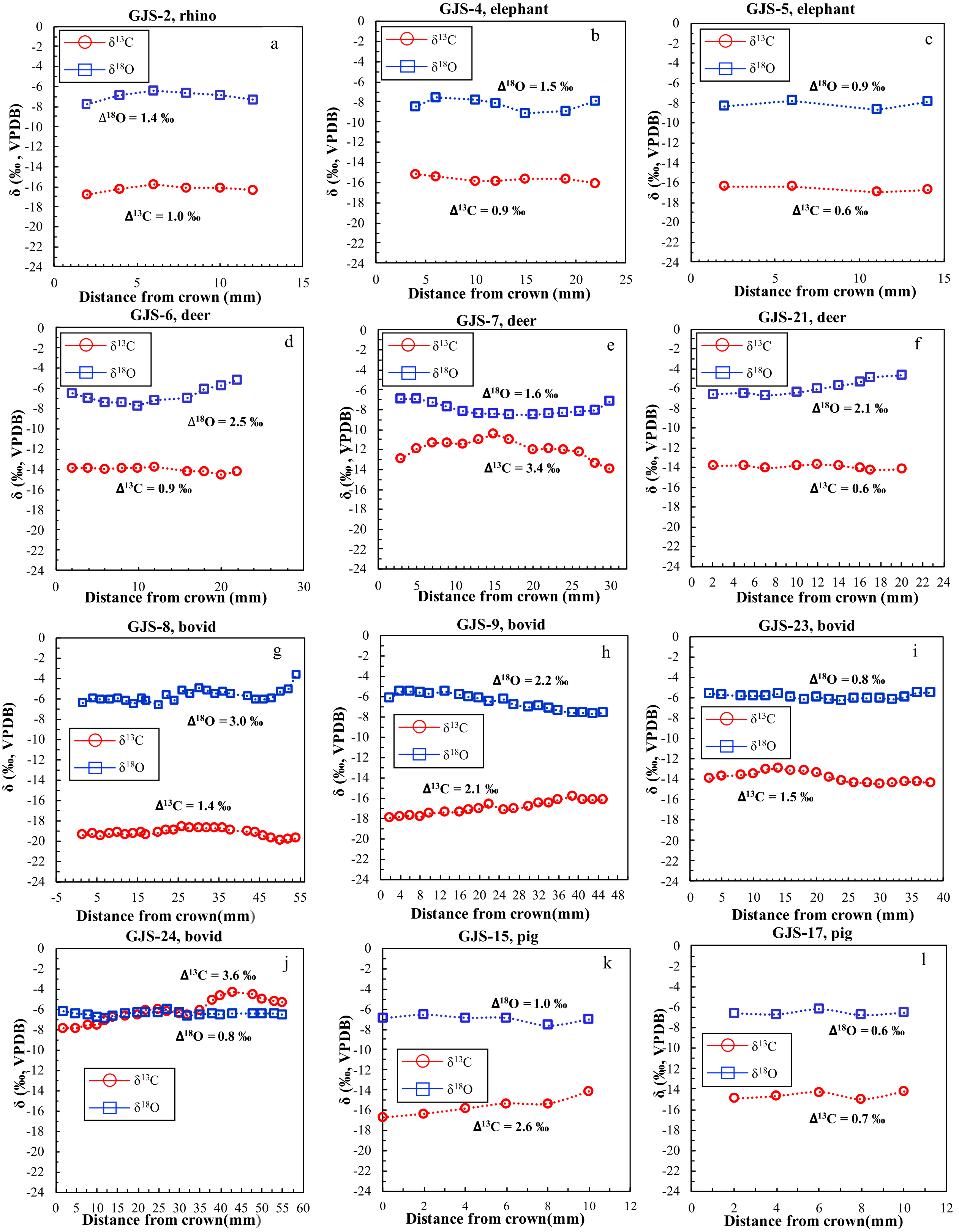

**Fig. 5.** Intra-tooth isotopic variations in selected fossil teeth from Yugong Cave, Chongzuo, Guangxi Province. $\Delta^{13}C$ and $\Delta^{18}O$ values indicate the range of carbon and oxygen isotopic variations respectively, within each tooth.

−4.4‰, with an average of −14.3 ± 5.1‰ ($n = 85$). The reconstructed diet $\delta^{13}C$ values vary widely from −34.0 to −18.4‰, averaging to −28.3 ± 5.1‰. The $\delta^{18}O$ values also vary significantly from −7.7 to −3.6‰ with an average of −6.1 ± 0.6‰. Bovids also displayed large intra-tooth $\delta^{13}C$ and $\delta^{18}O$ variations (Fig. 5g, $\Delta^{18}O$ = 3.0‰; Fig. 5j, $\Delta^{13}C$ = 3.6‰).

For deer (*Cervus* sp.), the enamel $\delta^{13}C$ values range from −21.1 to −10.5‰, with an average of −14.9 ± 3.3‰ ($n = 44$). The reconstructed diet $\delta^{13}C$ values vary from −35.1 to −24.5‰, averaging to −28.9 ± 3.3‰. The $\delta^{18}O$ values of these samples are −6.8 ± 1.1‰, ranging from −8.5 to −4.6‰.

The enamel $\delta^{13}C$ values of elephants (*Stegodon*) vary from −17.0 to −15.2‰, with an average of −16.0 ± 0.6‰ ($n = 12$). The reconstructed diet $\delta^{13}C$ values range from −30.0 to −28.2‰ with an average of −29.0 ± 0.6‰. The $\delta^{18}O$ values vary from −9.1 to −7.1‰, with an average of −8.1 ± 0.6‰.

As for bear (*Ursus thibetanus*), the enamel $\delta^{13}C$ values range from −13.6 to −13.2‰, with an average of −13.5 ± 0.2‰ ($n = 3$). The reconstructed diet $\delta^{13}C$ values vary from −26.6 to −26.2‰, averaging to −26.5 ± 0.2‰. The $\delta^{18}O$ values for these samples vary from −5.7 to −5.6‰ with an average of −5.7 ± 0.1‰.

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

The enamel-$\delta^{13}C$ values of all fossil taxa sampled from Baxian Cave are −16.2 ± 2.4‰ ($n = 136$), ranging from −20.0 to −10.0‰, whereas the $\delta^{18}O$ values vary from −14.0 to −1.6‰, averaging to −6.7 ± 2.4‰ (Table 1; Fig. 2b). The reconstructed diet-$\delta^{13}C$ values of these animals vary from −34‰ to −23.9‰ (Fig. 4; Table 1).

For pandas (*Ailuropoda melanoleuca*), the $\delta^{13}C$ values of enamel samples vary from −18.5 to −5.5‰, with an average value of −17.1 ± 1.1‰ ($n = 46$). The reconstructed diet $\delta^{13}C$ values range from −28.4 to −23.9‰, averaging −26.8 ± 1.1‰. The average $\delta^{18}O$ value is −4.2 ± 1.4‰.

Tooth enamel samples from rhino (*Rhinoceros sondaicus*) yield $\delta^{13}C$ values of −17.0 ± 1.0‰, ranging from −18.5 to −15.9‰ ($n = 31$). This gives reconstructed diet $\delta^{13}C$ values of −31.5 to −28.9‰, averaging −30.0 ± 1.0‰. The $\delta^{18}O$ values vary significantly from −10.3 to −6.0‰, with an average of −7.6 ± 1.1‰. Large intra-tooth $\delta^{18}O$ variations are also observed in rhinos (e.g., Fig. 6e, $\Delta^{18}O = 4.3‰$).

Tooth enamel samples from pigs (*Suidae*) have an average $\delta^{13}C$ values of −14.8 ± 0.8‰, ranging from −16.3 to −13.6‰ ($n = 18$). This corresponds to reconstructed diet $\delta^{13}C$ values of −27.8 ± 0.8‰, varying from −29.3 to −26.6‰. The $\delta^{18}O$ values for these samples vary widely from −14.0 to −4.9‰, with an average of −8.5 ± 3.2‰. Pigs from Baxian cave had a larger intra-species $\delta^{18}O$ variation (9.1‰) than those from Yugong Cave.

Enamel $\delta^{13}C$ values of bovids (*Leptobos* sp.) vary from −18.7 to −10.0‰, with an average of −14.6 ± 3.9‰ ($n = 34$). The reconstructed diet $\delta^{13}C$ values vary from −32.7 to −24.0‰, averaging to −28.6 ± 3.9‰. The $\delta^{18}O$ values vary from −10.6 to −6.6‰ with an average of −8.1 ± 0.7‰. Large intra-tooth variations are observed in bovids (e.g., Fig. 6g, $\Delta^{18}O = 3.2‰$).

For deer (*Cervus* sp.), the enamel $\delta^{13}C$ values range from −20.0 to −13.1‰ ($n = 2$), corresponding to reconstructed diet $\delta^{13}C$ values of −34.0 to −27.1‰. The $\delta^{18}O$ values vary from −5.9 to −4.7‰, with an average of −5.3 ± 0.8‰.

As for bear (*Ursus thibetanus*), their enamel $\delta^{13}C$ values range from −16.7 to −15.1‰, with an average of −15.8 ± 0.7‰ ($n = 5$). The reconstructed diet $\delta^{13}C$ values vary from −29.7 to −28.1, averaging to −28.8 ± 0.7‰. The $\delta^{18}O$ values for these samples vary from −9.8 to −6.9‰ with an average of −7.9 ± 1.1‰.

## 5. Discussion

### 5.1. Diets and habitats of fossil mammals

The carbon and oxygen isotopic compositions of fossil tooth enamel samples from various mammals found in Yugong Cave and Baxian Cave exhibit significant variations, with $\delta^{13}C$ and $\delta^{18}O$ values varying from −21.2‰ to −4.4‰ and from −14.1‰ to −1.6‰, respectively (Fig. 2; Supplementary Table). These large isotopic variations most likely reflect variations in the diets and habitat preferences of these ancient mammals as well as regional climatic conditions during the late Middle Pleistocene and the early Late Pleistocene.

The reconstructed diet-$\delta^{13}C$ values (after fractionation adjustment) for the Yugong fauna vary from −35.1‰ (pure $C_3$ diet) to −18.4‰ ($C_4$-dominant diet), with the lowest value find in a deer and highest value find in a bovid (Fig. 3a). As shown in Fig. 3, most of the fossil mammals have diet-$\delta^{13}C$ values falling within the range of $C_3$ plants, indicating that these late Middle Pleistocene mammals living in Yugong Cave area had $C_3$-based diets. However, some of these mammals have relatively high $\delta^{13}C$ values, suggesting consumption of small amounts of $C_4$ grasses (Figs. 3a and 5j). In addition, the serial $\delta^{13}C$ values for some mammals including a pig (GJS-15), one deer (GJS-7), and four bovids (GJS-8, GJS-9, GJS-23, GJS-24) exhibit significant (with $\Delta^{13}C > 1.3‰$) seasonal variations (Fig. 5), indicating seasonal intake of some $C_4$ plants. The presence of $C_4$ plants in their diets suggest that $C_4$ grasses were a part of the local ecosystems and likely existed in patches of relatively open habitats (such as wooded grassland or grassland) in an otherwise forested landscape during the late Middle Pleistocene. Meanwhile, the very negative enamel-$\delta^{13}C$ values (Fig. 2a; Fig. 5g and h, as low as −21.2‰) indicate the presence of a densely forested environment. In such an environment, diet-$\delta^{13}C$ values of −27‰ to −25‰ could indicate a mixed $C_3$-$C_4$ diet (with < 44% $C_4$ grasses in diet, assuming end-member $\delta^{13}C$ for pure $C_3$ and $C_4$ diets were −35‰ and −12‰, respectively). In this case, the data imply that dense forests dominated the landscape, but there were patches of open habitats containing some $C_4$ grasses in the Yugong Cave area during the late Middle Pleistocene.

$\delta^{13}C$ values of fossil tooth enamel samples from Baxian Cave exhibit a slightly smaller variation range than that observed in the Yugong fauna. The reconstructed diet-$\delta^{13}C$ values range from −34.0‰ (pure $C_3$) to −23.9‰ (mixed diets) with the highest $\delta^{13}C$ value found in a serial sample from a panda and lowest value found in a deer (Table 1; Fig. 4). Most of the reconstructed diet-$\delta^{13}C$ values for mammals from Baxian Cave fall within the range of $C_3$ plants (Fig. 4), indicating that these early Late Pleistocene mammals had predominantly $C_3$ based diets. However, the diet-$\delta^{13}C$ values of *Ailuropoda melanoleuca* reconstructed using an enrichment factor of 9.7‰ determined by Han et al. (2016) indicate possible consumption of small amounts of $C_4$ plants or some animal matters by a few individuals (Fig. 4). In general, the isotopic signatures indicate that most mammals inhabited a landscape dominated by $C_3$ plants in the Baxian Cave area during the early Late Pleistocene.

Stacklyn et al. (2017) previously reported stable carbon and oxygen isotope data from early Pleistocene mammals discovered in Yanliang Cave in the same region (Fig. 1). Today, Yugong Cave, Baxian Cave and Yanliang Cave are all located within the subtropical climate zone where small amounts of $C_4$ grasses can be found in open areas, though not in dense forests (Ehleringer et al., 1987; Yin and Li, 1997). The available $\delta^{13}C$ data from Pleistocene mammals suggest that small amounts of $C_4$ grasses were present in local habitats in this region, most likely in patches of open areas where dense forests were broken during the early Pleistocene and the late Middle Pleistocene, but the $C_4$ abundance was reduced in the early Late Pleistocene. The most negative diet-$\delta^{13}C$ value reconstructed from enamel-$\delta^{13}C$ values is −32.7‰ for the early Pleistocene Yanliang Cave fauna (Stacklyn et al., 2017), −35.1‰ for the late Middle Pleistocene Yugong fauna, and −34.0‰ for the late Pleistocene Baxian Cave fauna, respectively. Since the atmospheric $CO_2$ $\delta^{13}C$ value was ~1.5‰ higher in pre-industrial times than today (Elsig et al., 2009; Tipple et al., 2010), the very negative diet-$\delta^{13}C$ values of fossil mammals from these three sites could be equivalent to a modern value of −34.2‰ to −36.6‰. This indicates presence of closed canopy forests during the Pleistocene because such low $\delta^{13}C$ values can only be found in understories of closed-canopy forests (Kohn, 2010). In this region today, similar low $\delta^{13}C$ values (< −30‰ to as low as −34.9‰) have been found in sub-canopy plants deep inside a monsoon evergreen broadleaf forest at the Ding Hu Shan Biosphere Preserve (23°08′N,

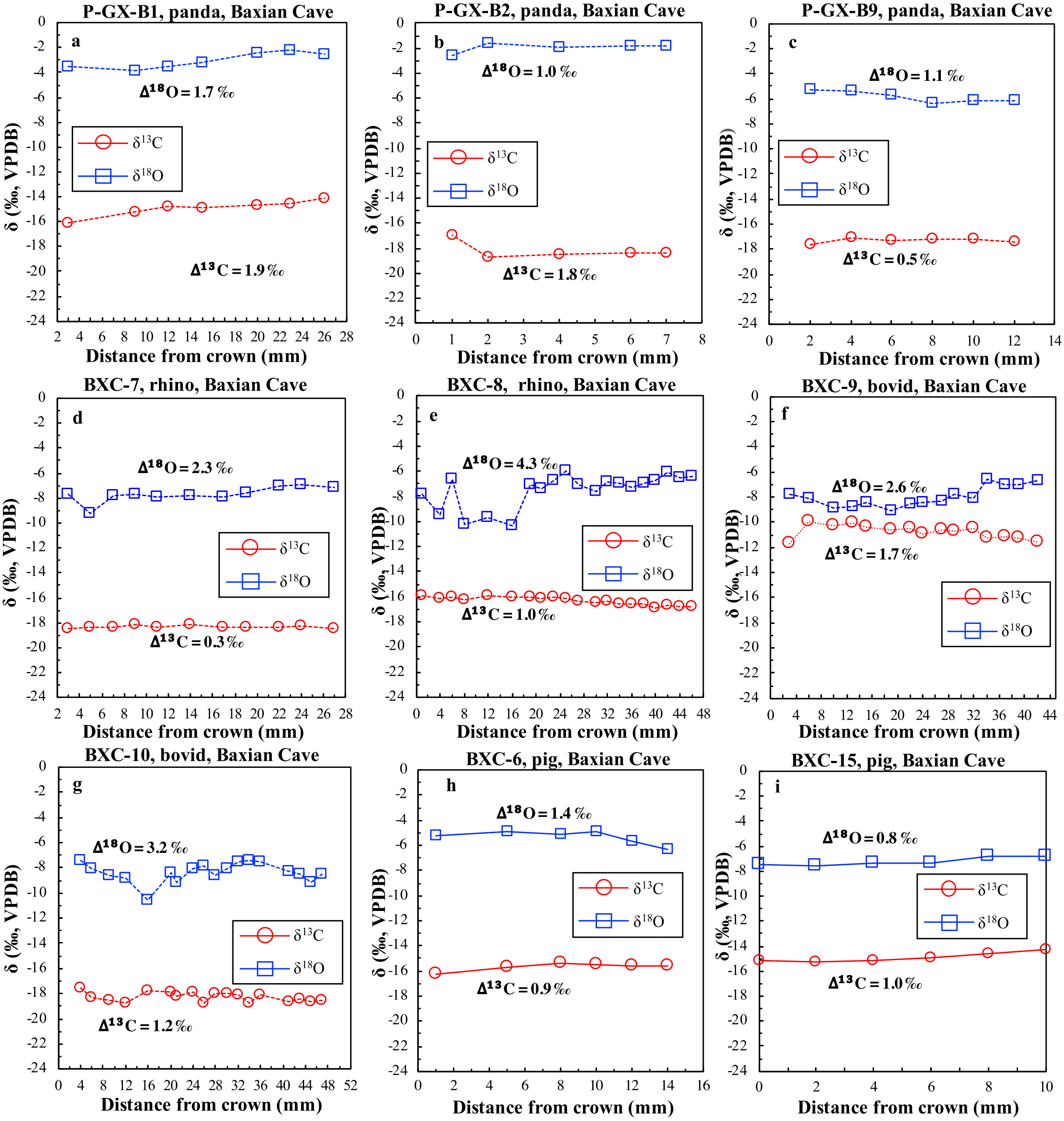

**Fig. 6.** Intra-tooth isotopic variations in selected fossil teeth from Baxian Cave, Chongzuo, Guangxi Province. $\Delta^{13}C$ and $\Delta^{18}O$ values indicate the range of carbon and oxygen isotopic variations, respectively, within each tooth.

112°35′E) in Guangdong Province (Ehleringer et al., 1987).

Variations of diet-$\delta^{13}C$ values among species likely reflect differences in their habitat preferences and eating behaviors (Figs. 3 and 4). Previous studies suggest that deviation of giant panda from ursids could result from enlarged mandibles and the grasping adaptions to the radial sesamoid bone at some time during Miocene (Endo et al., 1996; Hunt, 2004; Jin et al., 2007; Zhang et al., 2007). The primal pandas had crushing cheek teeth and are thought to be carnivores or omnivores (Qiu and Qi, 1989; Jin et al., 2007). The molar and premolar teeth of recently uncovered fossil skull of a 2.0 to 2.4 Ma panda (*Ailuropoda microta*) exhibit a great resemblance to the current extant panda, indicating that pandas should have completed its dietary switch from carnivore to herbivore at that time (Jin et al., 2007). The *Ailuropoda microta* is believed to have switched to a pure vegetarian diet consisting of bamboo during the early Pleistocene (Jin et al., 2007; Stacklyn et al., 2017). Stacklyn et al. (2017) estimated the diet-$\delta^{13}C$ values for *Ailuropoda microta* to be −32.1 ± 0.5‰ using the enrichment factor ($\varepsilon_{enamel\text{-}diet}$) of 13‰ for non-ruminants (Passey et al., 2005). However, a recent study reported a smaller enrichment factor ($\varepsilon_{enamel\text{-}diet}$) of 9.7‰ for panda based on analysis of modern panda tooth enamel and bamboo (Han et al., 2016). Using the panda-specific enrichment factor of 9.7‰ (Han et al., 2016), the estimated mean diet $\delta^{13}C$ values should be −28.8 ± 0.5‰ (rather than −32.1 ± 0.5‰; Stacklyn et al., 2017) for *Ailuropoda microta* from Yanliang Cave. The *Ailuropoda baconi* from Yugong Cave was the largest representative of giant panda lineage. *Ailuropoda baconi* had a relatively higher mean diet-$\delta^{13}C$ value (−26.9 ± 0.9‰) among all the contemporaneous mammals analyzed except bear, indicating a predominantly $C_3$ diet with consumption of some $C_4$ plants or animal matters by a few individuals (Table 1; Fig. 3). In addition, the *Ailuropoda baconi* also had the highest mean $\delta^{18}O$ value among all the contemporaneous mammals analyzed (Table 1; Fig. 3b), suggesting *Ailuropoda baconi* obtained a large proportion of body water from plant water.

*Ailuropoda melanoleuca* from Baxian Cave represents the extant populations of panda. The extant giant panda has more complex cuspate teeth compared to the Miocene panda (Jin et al., 2007). Reconstructed diet-$\delta^{13}C$ values of *Ailuropoda melanoleuca* range from −28.4‰ to −23.9‰, with a mean value of −26.8 ± 0.9‰, indicating that *Ailuropoda melanoleuca* did not live in a closed canopy habitat and some individuals had mixed diets with consumption of small amounts of $C_4$ plants (Fig. 4). Similar to pandas from Yanliang Cave and Yugong Cave, *Ailuropoda melanoleuca* has the highest mean $\delta^{18}O$ value (−4.2 ± 1.4‰) among all the coexisting mammals analyzed from Baxian Cave. This suggests that *Ailuropoda melanoleuca*, like its ancestors, obtained a larger fraction of body water from plants (mainly bamboos) than the other large mammals (Fig. 4).

*Ailuropoda microta* have the lowest diet-$\delta^{13}C$ values (−28.8 ± 0.5‰) and highest mean $\delta^{18}O$ (−4.0 ± 0.7‰) among the panda subspecies. The diet-$\delta^{13}C$ values of *Ailuropoda microta* (−28.8 ± 0.5‰) from Yanliang Cave are significant lower (*t*-test, $p < 0.0001$) than those of *Ailuropoda baconi* (−26.9 ± 0.9‰) and *Ailuropoda melanoleuca* (−26.8 ± 0.9‰), implying that *Ailuropoda microta* preferred a relatively denser habitat. There is no significant difference (*t*-test, $p = 0.87$) in diet-$\delta^{13}C$ values between *Ailuropoda baconi* and *Ailuropoda melanoleuca* (Table 1; Fig. 2). As for oxygen isotopes, the mean enamel-$\delta^{18}O$ (−5.6 ± 0.9‰) value for *Ailuropoda baconi* is significantly lower (*t*-test, $p < 0.0001$) than that of *Ailuropoda microta* (−4.0 ± 0.7‰) and *Ailuropoda melanoleuca* (−4.2 ± 1.4‰) (Fig. 2). This indicates *Ailuropoda baconi* might have drunk more water.

The rhinos analyzed in this study from Yugong Cave and Baxian Cave are *Rhinoceros sondaicus*, also known as the Javan rhino. Modern Java rhinos, which are possibly the rarest large mammal on Earth, reside in dense, low-lying tropical rainforests and prefer areas with abundant water and mud wallows (Dinerstein, 2003). They feed on a variety of plants including leaves, shoots, twigs and fruit, and occasionally graze on grasses (Waters et al., 2000). The rhinos and elephants from Yugong Cave show similar enamel $\delta^{13}C$ values (−16.8 to −14.8‰ and −17.0 to −15.2‰, respectively), indicating that they had predominantly $C_3$-based diets (Figs. 2 and 3). The similarity of the $\delta^{13}C$ values, coupled with the overlap in $\delta^{18}O$ values, suggests that they utilized the same resources. The relatively low enamel $\delta^{18}O$ values of rhinos (−8.4 to −6.4‰) and elephants (−9.1 to −7.1‰) indicate that they obtained a larger proportion of their body water from drinking compared to the majority of other contemporary mammals analyzed in this study (Table 1; Figs. 3 and 4). This is consistent with the ecology and habitat preference of their modern counterparts. Rhinos from Baxian Cave exhibit significantly lower (*t*-test, $p < 0.05$) enamel $\delta^{13}C$ values (−17.0 ± 1.0‰) than those from Yugong Cave (−15.8 ± 0.7‰) and Yanliang Cave (−15.1 ± 0.7‰). This suggests that rhinos from Baxian Cave might have lived in a denser habitat compared to the rhinos from the other two sites although they all had $C_3$-based diets. There is no significant difference between the enamel $\delta^{18}O$ values of *Rhinoceros sondaicus* from Yugong Cave (−7.2 ± 0.8‰) and Baxian Cave (−7.6 ± 1.1‰), but these values are significantly lower (*t*-test, $p < 0.0001$) than those of *Rhinoceros fusuiensis* nov. from Yanliang Cave (−5.7 ± 0.4‰; Stacklyn et al., 2017). This suggests that *Rhinoceros sondaicus* either lived in a wetter (and/or colder) climate or a larger proportion of their body water came from meteoric water compared to their ancestor *Rhinoceros fusuiensis*. Some of the rhinos from Baxian Cave show more pronounced intra-tooth $\delta^{18}O$ variations (Fig. 6d and e) than rhinos from Yanliang Cave and Yugong Cave, suggesting that rhinos from Baxian Cave experienced stronger seasonality during the early Late Pleistocene. It is also likely that the limited serial samples from rhinos from Yugong Cave did not capture the full seasonal variation range (Fig. 5a).

Similar to bovids from Yanliang Cave, bovids from Yugong Cave also had mostly $C_3$ based diets. However, they display a large intra-species $\delta^{13}C$ variation (from −20.0‰ to −4.4‰), large intra-tooth $\delta^{13}C$ variations (Fig. 5j, $\Delta^{13}C = 3.6‰$), and intra-tooth $\delta^{18}O$ variations (Fig. 5g, $\Delta^{18}O = 3.0‰$), indicating that bovids ate a variety of plants and had a wide range of habitats. For instance, the positive excursion at 42 mm from the crown in the $\delta^{13}C$ profile of sample GJS-24 (Fig. 5j) and the gradual increasing trend in the $\delta^{13}C$ values along growth axis suggest that this bovid had ingested a significant amount of $C_4$ grasses. In addition, the very negative $\delta^{13}C$ values of some bovid individuals (Fig. 5g and h) suggest presence of dense forests. The lowest serial enamel-$\delta^{13}C$ value is −20‰, which corresponds to a diet $\delta^{13}C$ value of −34‰, which can only be found deep inside dense forests. This diet-$\delta^{13}C$ value would be equivalent to an even lower modern value when the difference between current and past $\delta^{13}C$ values of atmospheric $CO_2$ is taken into consideration. The variety of diets and wider range of habitats indicate that bovids were more ecologically flexible than other coexisting mammals. Bovids from Baxian Cave display similar $\delta^{13}C$ values to bovids from Yugong Cave. But, the intra-tooth $\delta^{13}C$ variations were smaller than those observed in bovids from Yugong Cave. There were dense forests in the area during the early Late Pleistocene as evidenced by the very negative $\delta^{13}C$ values (Figs. 4 and 6g). Large intra-species $\delta^{13}C$ variation is observed in bovids from Baxian Cave, suggesting their ecological flexibility. Among bovids from the three sites, bovids from Baxian Cave had significantly lower (*t*-test, $p < 0.0001$) $\delta^{18}O$ values than those from Yugong Cave and Yanliang Cave, likely indicating colder temperatures and/or a wetter climate during the early Late Pleistocene.

Bears (*Ursus thibetanus*) from Yugong Cave had the highest mean enamel-$\delta^{13}C$ values (−13.5 ± 0.2‰) among all the coexisting species analyzed (Table 1; Figs. 2 and 3), suggesting these late Middle Pleistocene Asian black bears preferred more open habitats and consumed some $C_4$ plants or animal matter. Modern Asian black bears are known to migrate to different habitats and elevations seasonally (Izumiyama and Shiraishi, 2004), tracking changes of food abundance. Their diets have a great variety and may vary from year to year with differences in food availability. *Ursus thibetanus* are omnivores depending mainly on vegetation (Torii, 1989; Hazumi and Maruyama, 1986) and have a widely varied omnivorous diet throughout their natural range (Izumiyama and Shiraishi, 2004). The relatively higher $\delta^{18}O$ values (−5.7‰) of these ancient bears (*Ursus thibetanus*) indicate that a large proportion of their body water was from plants or animal matter compared to other mammals studied. The overlap of $\delta^{18}O$ values between bears (−5.7 to −5.6‰) and pandas (−6.5 to −5.2‰) suggests they had similar drinking habits. As for bears from Baxian Cave, stable carbon isotope data (−16.7 to −15.1‰, with a mean of −15.8 ± 0.7‰) show that they lived in a denser habitat than bears from Yugong Cave. The lower enamel $\delta^{18}O$ values might indicate a colder and/or wetter climate during the early Late Pleistocene.

Omnivore pigs (*Suidae*) from Yugong Cave had relatively high enamel $\delta^{13}C$ values (−16.7 to −12.4‰, with a mean of −14.7 ± 0.9‰) and low $\delta^{18}O$ values (−9.1 to −5.9‰, with mean of −7.1 ± 0.9‰), indicating these late Middle Pleistocene pigs fed mainly on $C_3$ plants although they consumed a small amount of $C_4$ plants (Fig. 3a). Another possibility for the slightly higher $\delta^{13}C$ values of omnivore pigs and bears may be related to the trophic effect resulting from meat consumption. Because the trophic effect on $\delta^{13}C$ is very small, about 1‰ or less (Lee-Thorp et al., 1989), the slightly higher $\delta^{13}C$ values observed in bears and pigs relative to most of the other animals would require consumption of either large amounts of animal matter or small amounts of meat from animals with a $C_4$ diet, which seems not very likely in a $C_3$ dominated environment (Figs. 3 and 4). The $\delta^{18}O$ data for pigs suggests that a larger portion of their body water came from drinking water compared to panda, bovid, deer and bear (Table 1; Fig. 3). Large intra-species $\delta^{18}O$ variations are observed in pig, suggesting that they had a wide range of water resources. The lower enamel $\delta^{18}O$ values (−8.5 ± 3.2‰) and a larger intra-species $\delta^{18}O$ variation (−14.0 to −4.9‰) for pigs from Baxian Cave than that from Yugong Cave suggest a colder climate and stronger seasonality during the early Late

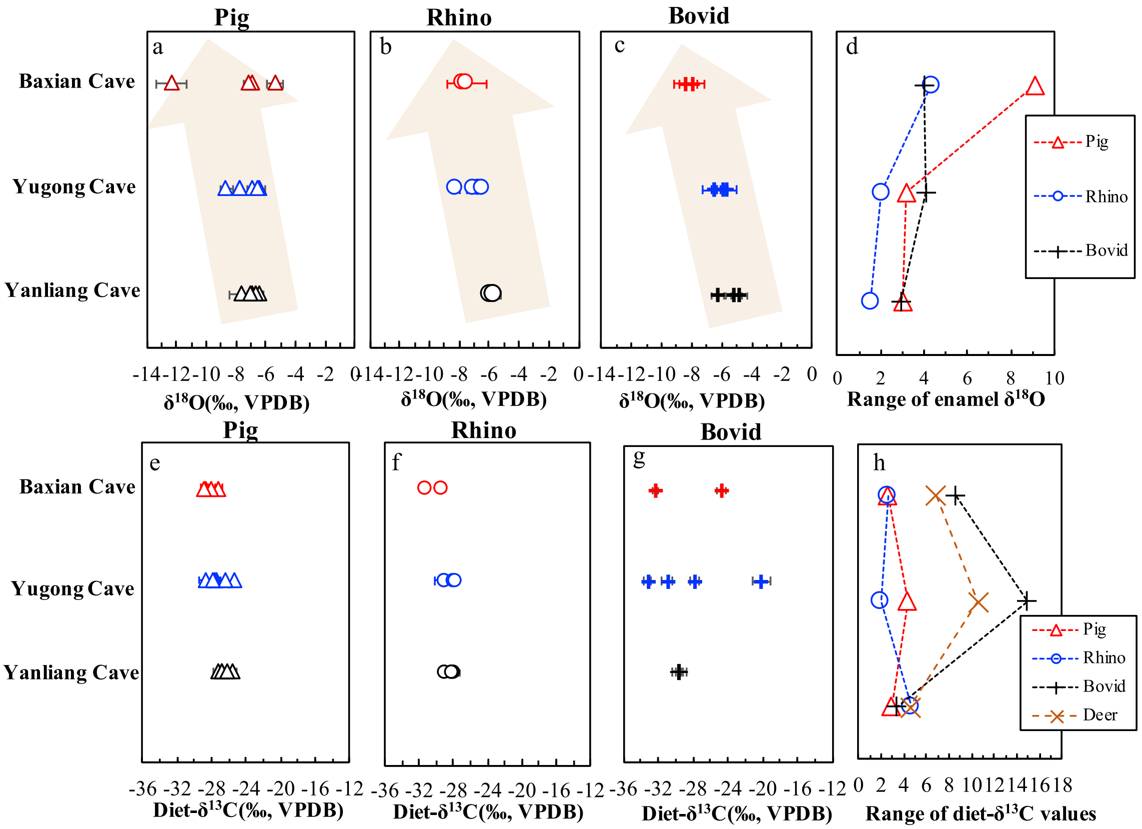

**Fig. 7.** Comparison of enamel $\delta^{18}O$ values (a–c), intra-species enamel $\delta^{18}O$ variability (d), diet-$\delta^{13}C$ values (e–g), and intra-species diet-$\delta^{13}C$ variability (h) of obligate drinkers (pigs, rhinos, and bovids) from the early Late Pleistocene Baxian Cave, the late Middle Pleistocene Yugong Cave, and the Early Pleistocene Yanliang Cave in south China. Each point in a–c and e–g represents the average value of an individual animal. The range for intra-species isotopic variations (in d and h) was determined using all the samples including bulk samples and serial samples.

Pleistocene. Pigs from Yanliang Cave also had higher $\delta^{13}C$ values, indicating consumption of $C_4$ plants (Stacklyn et al., 2017). Pigs from Yanliang Cave had the highest enamel $\delta^{18}O$ values ($-6.9 \pm 0.7$‰) among the pigs from the three fossil sites.

During the Early Pleistocene, deer (*Cervus* sp.) from Yanliang Cave displayed large intra-tooth and intra-species $\delta^{13}C$ variations and were believed to have eaten a variety of food and inhabited a wide range of habitats (Stacklyn et al., 2017). In comparison, deer from Yugong Cave had even larger intra-species and intra-tooth $\delta^{13}C$ variations than observed from Yanlinag Cave (Figs. 3 and 5e). Furthermore, they had the highest mean $\delta^{13}C$ value among deer from the three sites. The relatively high mean $\delta^{13}C$ value, along with large intra-species and intra-tooth $\delta^{13}C$ variations, indicates that these late Middle Pleistocene deer, like their Early Pleistocene counterpart, ingested certain amounts of $C_4$ grasses. Deer from Baxian cave have the highest enamel $\delta^{18}O$ values ($-5.3 \pm 0.8$‰) among deer from the three sites, suggesting that they may have drunk less than the deer from the two sites.

### 5.2. *Reconstruction of paleowater $\delta^{18}O$ and paleoclimatic implications*

Studies have shown that $\delta^{18}O$ values of mammalian tooth enamel from obligate drinkers are strongly correlated with the $\delta^{18}O$ values of local meteoric water (e.g., Kohn and Cerling, 2002; Wang et al., 2008). The $\delta^{18}O$ values of meteoric water are controlled by climatic conditions (Dansgaard, 1964). Precipitation is known to display large seasonal $\delta^{18}O$ variations in response to seasonal variations of climate. Rivers and lakes have a much smaller range of $\delta^{18}O$ variations than precipitation as their water is mostly derived from groundwater that integrates precipitation spatially and temporally over the watershed (Clark and Fritz, 1997). Precipitation isotope data from the IAEA-GNIP (International Atomic Energy Agency Global Network for Isotopes in Precipitation) stations in this area show that summer precipitation is more depleted in $^{18}O$ than winter precipitation (IAEA/WMO, 2018; Stacklyn et al., 2017). This pattern is characteristic of the Asian summer monsoon regime (Johnson and Ingram, 2004). The weighted annual average $\delta^{18}O$ values of precipitation in this region show a general decreasing trend with increasing distance from the ocean (the moisture source) from $-5.8 \pm 1.1$‰ in Guangzhou, $-6.2 \pm 0.9$‰ in Guilin, $-6.5 \pm 0.7$‰ in Liuzhou, to $-6.4 \pm 2.1$‰ in Wuhan and $-7.0 \pm 1.1$‰ in Chengdu (IAEA/WMO, 2018; Stacklyn et al., 2017), which reflects the "continental effect" and the "latitude effect" (Dansgaard, 1964). In summer months, the Asian summer monsoons carry moisture from the ocean to inland, increasing precipitation over continent. Because heavy isotopes are preferentially removed from vapor by condensation, the remaining vapor in an air mass and precipitation produced subsequently become more and more depleted in heavy isotope $^{18}O$ as air mass moves further inland and more vapor condenses to form precipitation. In a given area, the higher the precipitation amount, the lower the $\delta^{18}O$, owing to the "amount effect" (Dansgaard, 1964). $\delta^{18}O$ of precipitation is also affected by temperature, resulting in a strong positive correlation (0.58‰/°C) between precipitation $\delta^{18}O$ and surface air temperature, the so-called "temperature effect", in middle to high latitude regions (Dansgaard, 1964; Rozanski et al., 1993). The temperature effect, however, is much weaker or non-existent in low latitudes and in the Asian monsoon region (Dansgaard, 1964; Rozanski et al., 1993; Johnson and Ingram, 2004).

$\delta^{18}O$ values of paleo-meteoric water can be estimated using the following relationship given in Zhang et al. (2012) which was derived from the enamel/bone phosphate-water $\delta^{18}O$ relationship for obligate drinkers (e.g., rhinos, pigs, bovids, and elephants) (Kohn and Cerling, 2002) and relationship between $\delta^{18}$O of phosphate and structural carbonate components of hydroxyapatite for modern animals (Iacumin et al., 1996):

$$\delta^{18}O_w = [\delta^{18}O_c(\text{VPDB}) - 1.244]/0.891 \quad (1)$$

where $\delta^{18}O_w$ and $\delta^{18}O_c$ are oxygen isotope compositions of water and structural carbonate in enamel, respectively.

Reconstructed paleo-water $\delta^{18}O_w$ values for Yugong Cave and Baxian Cave vary from −10.5‰ to −8.2‰ (averaging −9.4 ± 0.9‰) and from −11.0‰ to −9.9‰ (with an average of −10.5 ± 0.5‰), respectively. These reconstructed $\delta^{18}O_w$ values are lower than those for Yanliang Cave which range from −9.2‰ to −7.5‰, with a mean value of −8.1 ± 0.8‰ (Stacklyn et al., 2017). Both the mean and the most negative enamel-$\delta^{18}$O values of obligate drinkers (pigs, rhinos, and bovid) display a decreasing trend from the Early Pleistocene to the early Late Pleistocene (Fig. 7a to c), reflecting a decrease in the $\delta^{18}O_w$ of local water (Table 1). The decreasing trend in $\delta^{18}O_w$ from the Early Pleistocene to the early Late Pleistocene appears to correspond to an increase in the range of $\delta^{18}$O variability in these mammals (Fig. 7d). This suggests a colder and/or wetter climate with increased seasonality in the late Middle Pleistocene and the early Late Pleistocene than in the Early Pleistocene. The reconstructed diet-$\delta^{13}$C values of pigs and rhinos from Baxian Cave and Yugong Cave are significantly lower (*t*-test, $p < 0.01$) than their counterparts from Yanliang Cave (Fig. 7e–g). This may suggest less $C_4$ in the environment and thus a colder climate in the late Middle Pleistocene and the early Late Pleistocene than in the Early Pleistocene, consistent with the inference from the $\delta^{18}$O data. The decreasing trend in the reconstructed diet-$\delta^{13}$C values from the late Middle Pleistocene to the early Late Pleistocene is accompanied by a decrease in the range of $\delta^{13}$C variation in some of the animals such as bovid and deer (Fig. 7e–h). This suggests that the Baxian Cave fauna may have experienced a colder and/or wetter climate (and thus less $C_4$) in the early Late Pleistocene than the Yugong Cave fauna in the late Middle Pleistocene (Fig. 7e–h). Thus, both the carbon and oxygen isotope data from our fossil enamel samples suggest a colder and/or wetter climate with increased seasonality in the late Middle Pleistocene and the early Late Pleistocene than in the Early Pleistocene, which may be related to the Naynayxungla Glaciation (0.78 to 0.50 Ma) during the Middle Pleistocene and the Penultimate Glaciation (0.30 to 0.13 Ma) during the Late Pleistocene. These two glaciations are the largest Pleistocene glaciations documented in the region (Zheng et al., 2002). It has been hypothesized that these two major glacial events have had a profound effect on panda evolution (Zhao et al., 2013). Fossil records from the region also show that *Gigantopithecus* had a relatively wider distribution during the Early Pleistocene, but withdrew southward to a limited area in the Middle Pleistocene and disappeared during the Late Pleistocene (Zhao and Zhang, 2013). A change in regional climate to colder conditions could be responsible for the extinction of the *Gigantopithecus* in this region. However, due to limited species analyzed in this study and the lack of precise age data for these fossil sites, it is difficult to determine the exact cause of the observed changes in regional climate and their impacts on local faunas. Future research should focus on improving the chronologies of these hominoid-bearing fossil sites and involved additional species of these faunas in isotope analyses.

## 6. Conclusions

Carbon and oxygen isotopic analyses of a variety of mammalian tooth enamel samples from two fossil caves (Yugong Cave and Baxian Cave) in South China show that these Pleistocene mammals had $C_3$-based diets. However, some of the individuals (such as pandas, deer, bovids and pigs) from the late Middle Pleistocene fossil locality consumed small amounts of $C_4$ grasses, similar to mammals from the Early Pleistocene Yanliang Cave in the same region. The carbon isotope data suggest that the cave areas were dominated by $C_3$ habitats including closed canopy forests and woodlands in the late Middle Pleistocene and the early Late Pleistocene, but small amounts of open habitats containing $C_4$ grasses were present likely in patches of open areas. Similar to *Ailuropoda microta* from the Early Pleistocene Yanliang Cave, the late Middle Pleistocene *Ailuropoda baconi* and the early Late Pleistocene *Ailuropoda melanoleuca* preferred relatively open forest habitats and had $C_3$ based diets, but some individuals may have consumed small amounts of $C_4$ plants. Reconstructed $\delta^{18}O_w$ values of paleo-waters were lower than the weighted annual average $\delta^{18}$O value of modern precipitation in the region, suggesting a colder and/or wetter climate during the time periods when these mammals lived in the Pleistocene than today. In addition, the decreasing trend over time in the enamel $\delta^{18}$O values of obligate drinkers from these Pleistocene fossil sites in South China, which is accompanied by increased $\delta^{18}$O variability in these taxa, suggests that the regional climate became colder and/or wetter, with increased seasonality, in the late Middle Pleistocene and the early Late Pleistocene compared to the Early Pleistocene, which may be due to the intensified glaciations.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.03.021.

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