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Isotopic evidence of foraging ecology of Asian elephant (*Elephas maximus*) in South China during the Late Pleistocene



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ABSTRACT

Currently, knowledge of dietary preferences throughout the evolutionary history of the Asian elephant *Elephas maximus* is ambiguous due to the absence of quantified proxy from the Late Pleistocene. In this study, carbon and oxygen stable isotope analysis on the fossilized mammal teeth from the faunal assemblage recovered at Baxian Cave in Guangxi, South China was undertaken in order to reconstruct the dietary behavior and foraging ecology of *Elephas maximus* during the Late Pleistocene. The analyses of X-ray Diffraction (XRD) and Fourier Transform Infrared Spectroscopy (FTIR) on several samples showed that all teeth bioapatite was well-preserved. The isotopic data indicate that all the mammals relied entirely on C₃-based foodstuff, revealing that C₃ vegetation was dominant in this region. Two groups of the Asian elephants are observed in this study on the basis of isotopic difference. This isotopic variation among the Asian elephants evaluated in this study may suggest that they were mixed feeders. The dietary difference of the two groups observed may relate to elephant ages, seasonal variation and/or subspecies differences. In combination with previously published isotopic data, the dietary transition from substantial C₄ plants to C₃ plants of *Elephas* is discussed, indicating flexible dietary behavior throughout the evolution of the genus.

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1. Introduction

As the largest extant terrestrial herbivore, elephants can consume more than 150 kg of plants per day (Shoshani and Eisenberg, 1982). Thus, feeding ecology played a significant role in the evolution of Elephantidae. One of the greatest evolutionary transitions of the elephantids lies in their dental morphology (Maglio, 1973; Lister, 2013). It is generally accepted that the increase of crown height and lamellar frequency of their cheek teeth were an adaptive response to the occurrence and spread of C₄ plants beginning around 10–7 Ma (Quade et al., 1992; MacFadden and Cerling, 1996; Koch et al., 1998).

The Asian elephant (*Elephas maximus*) is one of the only three extant elephant species, and is mainly distributed in Southeast Asia today (Maglio, 1973; Shoshani and Eisenberg, 1982; Shoshani and

Tassy, 1996). *Elephas* appeared in Africa 5–6 Ma and gradually spread to Eurasia beginning approximately 3 Ma, although the exact date and migration route are still unknown (Sukumar, 2006; Kundal and Kundal, 2011; Lister et al., 2013; Bibi and Métais, 2016). Fossil *Elephas* is scarce in Eurasia during the Middle Pleistocene, except for several fossils reported from India (Kundal and Kundal, 2011) and the Middle East (Lister et al., 2013). However, during the Late Pleistocene, fossil materials ascribed to *Elephas* became more abundant in Southeast and South Asia and are regarded as sympatric to anatomically modern humans (*Homo sapiens*) in the region (Tong and Patou-Mathis, 2003; Sukumar, 2006; Liu et al., 2015). Now, they are endangered animals and sparsely distributed in South and Southeast Asia.

Asian elephants are hypsodont herbivores and can adapt to different habitats (Sukumar, 2006). Dental microwear texture analysis of Late Pleistocene Asian elephant fossils from South China shows that they were mixed feeders (Zhang et al., in press). Observations of plant species directly digested by modern Asian elephants in the Nilgiri Biosphere Reserve, south India, suggest that today they are mainly grazers (Baskaran et al., 2010). Conversely,

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modern Asian elephants in Xishuangbanna, South China, are browsers (Chen et al., 2006).

Stable isotope analysis of animal tissues, reflecting the average dietary consumption during individual growth, has been widely applied to investigate the dietary ecology and preference of extinct and extant animals (Quade et al., 1992; Sukumar and Ramesh, 1992, 1995; Koch et al., 1998; Metcalfe and Longstaffe, 2014). Carbon and oxygen isotope analysis of fossil teeth of *Elephas* older than 1 Ma indicates that they relied highly on C₄ grasses (Stern et al., 1994; Cerling et al., 1999, 2015). The great variation of carbon isotope values of bone collagen from modern elephants in India demonstrates that today they are mixed feeders and prefer more browse than grass (Sukumar and Ramesh, 1992, 1995). Young elephants may be an exception, preferring more C₄ grasses than adults (Sukumar and Ramesh, 1992, 1995). Due to the lack of the isotopic studies on *Elephas* from the Middle or Late Pleistocene, the evolution of their foraging ecology is still unclear.

Here, we present a stable isotopic analysis of carbon and oxygen from the tooth enamel of Asian elephants and associated fauna from the Baxian Cave, Guangxi, China, in order to understand the foraging ecology of Asian elephants during the Late Pleistocene. We also present a preliminary discussion of dietary preferences throughout the evolutionary history of the Asian elephants.

2. Carbon and oxygen isotope analysis of enamel bioapatite in fossil teeth

Plants can be classified by photosynthetic pathways. Generally, C₃ plants, including trees, shrubs, herbs and some grasses, have $\delta^{13}\text{C}$ values of -34‰ to -23‰ while C₄ plants, like most grasses, have $\delta^{13}\text{C}$ values ranging from -17‰ to -9‰ (O'Leary, 1981; Farquhar et al., 1989). Due to so-called "canopy effect" that causes the carbon isotopic fractionation in different ecological niches (Ehleringer et al., 1986; Quade et al., 1995; Levin et al., 2004), $\delta^{13}\text{C}$ values of plants growing in closed environments are more negative than those in open environments (Quade et al., 1995). When plants are directly consumed by herbivores, isotopic fractionation occurs during the process of tissue formation. From diet to incorporation into collagen in bones or teeth, carbon isotope values are generally enriched by 5.0‰ (Cerling and Harris, 1999). For large herbivores, enrichment of $\delta^{13}\text{C}$ values from diets to bioapatite in bone or teeth is equal to roughly 14.1‰ (Cerling and Harris, 1999). For omnivores and carnivores, $\delta^{13}\text{C}$ values are enriched by approximately 9‰ (Cerling and Harris, 1999; Bocherens and Drucker, 2007). Therefore, carbon isotope signatures from herbivores are quite useful for reconstructing the palaeodiet and palaeoecology of animals (Ambrose and DeNiro, 1986).

Oxygen isotope values ($\delta^{18}\text{O}$) in mammal tooth enamel are more complicated than carbon isotope values (Longinelli, 1984; Fricke and O'Neil, 1996). $\delta^{18}\text{O}$ values in bioapatite in bone or teeth are mainly determined by water which the animals drink or water in the food they consume (Bryant and Froelich, 1995). For large-sized herbivores that obtain much water input from drinking water, $\delta^{18}\text{O}$ values in their tooth enamel directly reflect those in drinking water and are directly determined by the local temperature, precipitation and humidity (Bryant and Froelich, 1995; Dutton et al., 2005; Metcalfe, 2011).

$\delta^{18}\text{O}$ values in herbivore bioapatite can also be impacted by the preference of the leaves or grass. The transpiration process of plants also causes oxygen isotope fractionation. In general, tree leaves have higher $\delta^{18}\text{O}$ values than grasses because trees undergo greater transpiration of water through the leaves (Quade et al., 1995). Therefore, the mammals mainly consuming such foliage generally have higher $\delta^{18}\text{O}$ values than those that consume grass (Koch et al., 1989; Quade et al., 1995; Sponheimer and Lee-Thorp, 1999b; Wang et al., 2008). Collectively, $\delta^{18}\text{O}$ values in mammal bioapatite can be used as a rough proxy to distinguish diet, drinking behavior and environment (Sponheimer and Lee-Thorp, 1999b).

3. Materials and methods

3.1. Setting and sample selection

In 2014, Baxian Cave ($22^{\circ}34'31.6''\text{N}$, $107^{\circ}21'0.2''\text{E}$) was found at the town of Zuozhou, Chongzuo Municipality, Guangxi Zhuang Autonomous Region of southern China (Fig. 1). The area is characterized by karst and a northern tropical climate. The sediments from Baxian Cave are approximately 5 m thick, and can be divided into five layers from top to bottom. All the fossils in this study were unearthed from the third layer composed of 50 cm of brown-yellow sandy clay with tiny calcareous breccia. Further description of this deposit will be published elsewhere, as the dating of U-series and ESR to determine the absolute date of fossil occupation is still underway. Systematic excavations have uncovered a diverse and rich assemblage of vertebrate fossils. Mammals identified to date include more than 100 individuals of the Asian elephant (*Elephas maximus*) alongside other mammals, including primates (*Pongo* sp., *Macaca* sp., *Namascus* sp., and *Rhinopithecus* sp.), carnivorans (*Ailuropoda baconi*, *Ursus thibetanus*, *Arctonyx collaris* and *Panthera tigris*), stegodonts (*Stegodon orientalis*), perissodactyls (*Rhinoceros sondaicus* and *Megatapirus augustus*), and artiodactyls (*Sus scrofa*, *Muntiacus* sp., *Cervus [Rusa] sp.*, and *Bos [Bibos] sp.*).

The Baxian faunal assemblage, including *E. maximus*, *S. orientalis*, *A. baconi* and *M. augustus*, is most similar to faunas

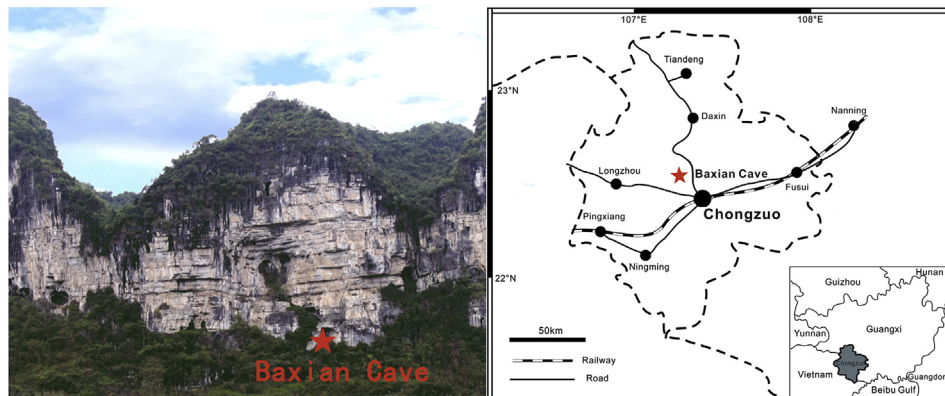


Fig. 1. The geographical location and landscape of the Baxian Cave.

from Zhiren Cave, Chongzuo, dated to 100–113 ka (Jin et al., 2009a; Liu et al., 2010; Cai et al., 2016) and Fuyan Cave, Daoxian, Hunan, dated to 80–120 ka (Liu et al., 2015). Based on the similarity to those faunal assemblages and deposits, the age of the Baxian fauna is currently estimated to be early Late Pleistocene.

Thirty-two samples from partially broken, but well-preserved, fossil teeth were selected for isotopic analysis. We chose those specimens based on both abundance and an effort to sample animals with distinct dietary preferences and body sizes. The samples included Asian elephant (*Elephas maximus*, n = 11), stegodont (*Stegodon orientalis*, n = 2), macaque (*Macaca* sp., n = 1), giant panda (*Ailuropoda baconi*, n = 3), Javan rhino (*Rhinoceros sondaicus*, n = 5), Bacon's giant tapir (*Megatapirus augustus*, n = 1), wild boar (*Sus scrofa*, n = 3), muntjac (*Muntiacus* sp., n = 3), sambar deer (*Cervus [Rusa] sp.*, n = 2), and gaur (*Bos [Bibos] sp.*, n = 1). The samples of 11 elephant teeth included 4 dp4s, 4 M1s, and 3 M2s and were selected in order to evaluate potential dietary difference of the subadults and adults. Considering the incompleteness of individual specimens available, no systematic strategy for tooth sampling was utilized and samples were not consistently derived from homologous positions on the teeth. Therefore, the results presented here represent a broad overview of the isotopic ecology preserved in mammal teeth from Baxian Cave. The lab number and species list for selected samples is shown in Table 1.

Table 1
Sample information, FTIR peak and isotope data.

Sample	Taxon	BPI	PCI	CO ₂ %wt	δ ¹³ C (‰)	δ ¹⁸ O (‰)	Tooth
01	<i>Elephas maximus</i>				-14.5	-9.0	M2
02	<i>Elephas maximus</i>				-16.6	-6.8	M1
03	<i>Elephas maximus</i>	0.34	4.4	4.1	-16.1	-6.3	M1
04	<i>Elephas maximus</i>				-16.8	-6.6	dp4
05	<i>Elephas maximus</i>				-15.4	-8.4	M1
06	<i>Elephas maximus</i>				-17.6	-6.8	dp4
07	<i>Elephas maximus</i>				-15.8	-5.9	M2
08	<i>Elephas maximus</i>	0.31	3.8	3.8	-14.3	-8.5	M1
09	<i>Elephas maximus</i>	0.32	4.3	3.9	-17.2	-7.2	dp4
10	<i>Elephas maximus</i>	0.17	5.3	2.4	-15.1	-6.4	M2
11	<i>Elephas maximus</i>				-14.5	-8.2	dp4
12	<i>Cervus (Rusa.) sp.</i>				-19.3	-7.3	Tooth fragment
13	<i>Cervus (Rusa.) sp.</i>	0.25	5.1	3.2	-17.0	-7.1	Tooth fragment
14	<i>Muntiacus sp.</i>	0.25	5.2	3.2	-14.4	-7.1	Tooth fragment
15	<i>Muntiacus sp.</i>				-15.6	-4.6	Tooth fragment
16	<i>Muntiacus sp.</i>				-15.5	-5.8	Tooth fragment
17	<i>Sus scrofa</i>				-15.7	-7.8	Tooth fragment
18	<i>Sus scrofa</i>				-14.6	-6.9	Tooth fragment
19	<i>Sus scrofa</i>				-12.9	-6.7	Tooth fragment
20	<i>Rhinoceros sondaicus</i>	0.28	4.8	3.5	-17.1	-7.3	Tooth fragment
21	<i>Rhinoceros sondaicus</i>	0.28	4.9	3.5	-16.3	-5.5	Tooth fragment
22	<i>Rhinoceros sondaicus</i>				-17.2	-6.8	Tooth fragment
23	<i>Rhinoceros sondaicus</i>	0.29	4.0	3.6	-18.1	-9.2	Tooth fragment
24	<i>Rhinoceros sondaicus</i>	0.33	4.3	4.0	-16.3	-8.5	Tooth fragment
25	<i>Megatapirus augustus</i>	0.18	5.1	2.5	-17.5	-6.1	Tooth fragment
26	<i>Stegodon orientalis</i>				-15.9	-8.4	Tooth fragment
27	<i>Stegodon orientalis</i>				-15.5	-8.2	Tooth fragment
28	<i>Bos (Bibos) sp.</i>				-14.7	-6.6	Tooth fragment
29	<i>Macaca sp.</i>				-15.9	-7.1	Tooth fragment
30	<i>Ailuropoda baconi</i>				-15.9	-8.0	Tooth fragment
31	<i>Ailuropoda baconi</i>				-18.0	-7.1	Tooth fragment
32	<i>Ailuropoda baconi</i>				-17.3	-6.4	Tooth fragment

3.2. Bioapatite preparation

A technique proposed by Lee-Thorp et al. (1989) was followed to prepare the bioapatite from the tooth enamel. First, contaminants adhering to tooth surfaces were carefully cleaned off with a diamond-tipped dental burr and the tooth enamel was then drilled until about 10 mg powder was collected. Second, each of the powder samples was separately put in a 1.5 ml centrifuge tube and soaked in 50% sodium hypochlorite (NaOCl) for about 48 h at

4 °C to eliminate organic matter. Third, the remains were centrifuged at 3200 rpm 5 times and the supernatants were removed and cleaned with distilled water at least three times to neutralize the pH. Then, 1 mol/l acetic acid was added to each sample for about 24 h to remove diagenetic carbonate, following the same centrifugation and neutralization procedure as in the third step. Finally, the remains were freeze-dried and ground into powder again.

3.3. Preservation assessments of bioapatite

Although tooth enamel is the most resistant structure in the vertebrate body, it is still susceptible to contamination during long-term interment (Person et al., 1995). Thus, it is better to assess preservation before isotopic analysis, if possible. In this study, 11 of 32 samples, which had relatively high bioapatite yields, were selected for X-ray Diffraction (XRD) and Fourier Transform Infrared Spectroscopy (FTIR) analysis to partially assess the bioapatite preservation.

The finely-ground bioapatite powder was put on the glass slide and measured in the Rigaku MiniFlex II Desktop X-ray Diffractometer. The phase compositions of the bioapatite were identified through the XRD peaks by MDI Jade 6.5 software. The XRD patterns of the samples were drawn by Origin Pro 8.0 (see Fig. 2).

Additionally, the bioapatite powder was mixed with potassium bromide (1:100) to make the KBr pallet for FTIR analysis in the Fourier Transform Infrared Spectroscopy (NICOLET 6700, made by Thermo Scientific). The infrared spectra of 11 samples were calibrated in OMNIC 8.0, and plotted in Origin Pro 8.0 (see Fig. 3). The bioapatite crystallinity index, e.g., PCI (phosphate crystallinity index) and BPI (carbonate-phosphate index), were calculated according to protocols addressed by previous studies (Sponheimer and Lee-Thorp, 1999a; Michel et al., 1995), and are listed in Table 1.

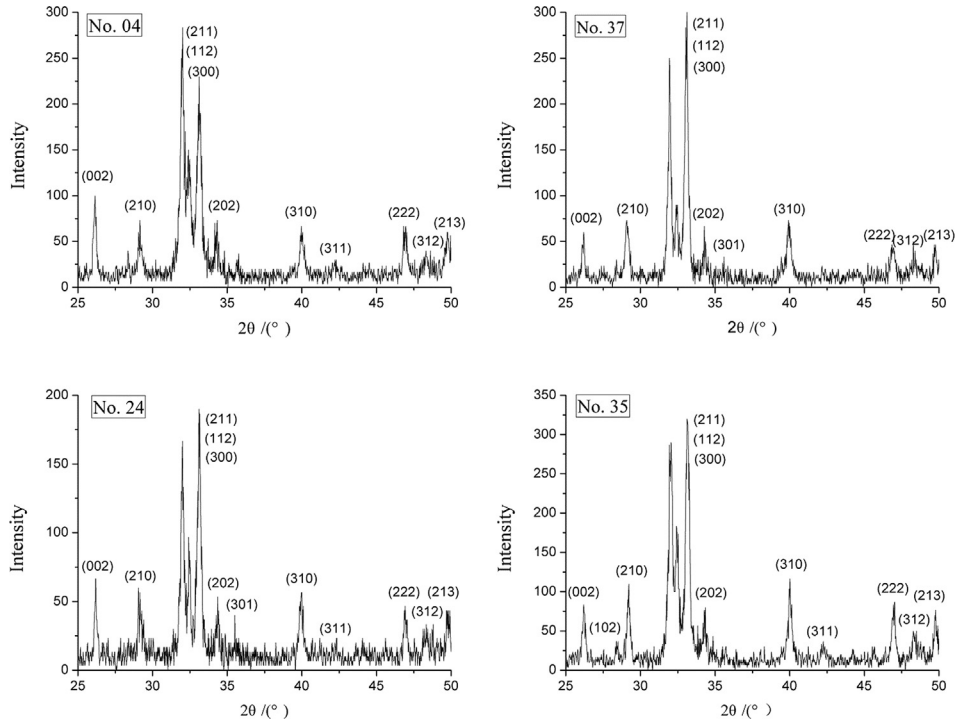


Fig. 2. X-ray diffraction diagram of some fossil specimens.

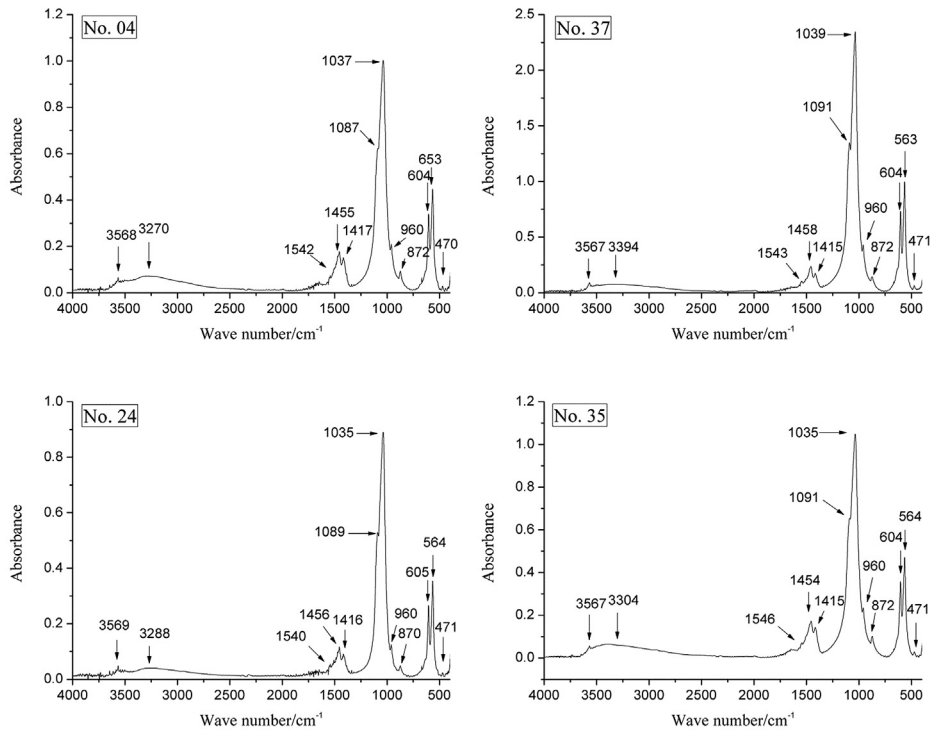


Fig. 3. FTIR spectra of some fossil specimens.

Carbon and oxygen isotope ratios were measured by an Iso-prime 100 Isotope Ratio Mass Spectrometry (IRMS) coupled with a multi-flow system at the Stable Isotope Laboratory in Department of Archaeology and Anthropology, University of Chinese Academy of Sciences. The bioapatite powder of every sample was packed into sealed glass tubes and flushed with high-purity helium. Then 1 ml

of ultrapure phosphoric acid (H_3PO_4) at 70 °C was injected into every tube using a disposable medical injector. After the reaction was maintained at 80 °C for an hour, the carbon dioxide released in the tube was eventually transported by helium as carrier gas to IRMS. The standards of IAEA CO-8 and NBS 19 were used for isotopic calibration. A standard of NBS 18 was inserted while running

samples as reference for monitoring the measurement stability. Carbon and oxygen isotope values are expressed to $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values relative to V-PDB. The long-term measurement precisions were better than $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$.

4. Results

4.1. Preservation assessment of bioapatite

XRD patterns of the fossil teeth-derived bioapatite only show the typical peaks of hydroxyl apatite (e.g., 002, 210, 211, 112, 300, 202, 310, 222 and 213, see Fig. 2). The sharp peaks also indicate that the enamel bioapatite has high crystallinity that is resistant to the diagenesis.

The commonly used method to assess the preservation of bioapatite crystallinity in FTIR is PCI and BPI (Sponheimer and Lee-Thorp, 1999a; Michel et al., 1995). PCI is used to monitor the crystal alternation of phosphate in the bioapatite, which ranges from 3.5 to 3.8 in modern animals (Sponheimer and Lee-Thorp, 1999a). The PCI in our study ranges from 3.7 to 5.2, values that are a little higher than in modern animals. However, the carbon and oxygen isotope values were measured in the carbonate of the bioapatite and can be evaluated by the BPI. Sponheimer and Lee-Thorp (1999a) found that the BPI of modern animals range from 0.16 to 0.35, representing carbonate contents in the bioapatite between 2.3% and 4.2%. In our study, the BPI of all samples fall in the range of 0.17–0.34 and stand for the carbonate contents between 2.4% and 4.1%, which is located within the range of modern animals. Due to the fact that all the fossils are from a similar depositional environment, it is reasonable to infer that all samples studied here can be regarded as retaining the *in vivo* isotopic signature of the bioapatite carbonate despite the fact that our assessments were only undertaken for a subsample.

4.2. Isotope data of the animals

The results of isotopic analyses for the samples from the Baxian Cave fossil fauna are presented in Fig. 4. Sampled herbivores included the sambar deer, muntjac, gaur, Bacon's giant tapir, Javan rhino, Asian elephant and stegodont. Although both are cervids, the sambar deer and muntjac preserved different isotopic data. The former has lower mean $\delta^{13}\text{C}$ value ($-18.2 \pm 1.6\text{‰}$, $n = 2$) and $\delta^{18}\text{O}$ value ($-7.2 \pm 0.1\text{‰}$, $n = 2$) than the latter with mean $\delta^{13}\text{C}$ value ($-15.1 \pm 0.7\text{‰}$, $n = 3$) and $\delta^{18}\text{O}$ value ($-5.8 \pm 1.3\text{‰}$, $n = 3$), suggesting that the sambar deer from Baxian Cave mainly inhabited a

relatively closed environment and ate the grasses with smaller $\delta^{18}\text{O}$ values. The gaur shows similar isotopic data to the muntjac, suggesting a similar ecological preference.

The Bacon's giant tapir, Javan rhino, stegodont and Asian elephant were large hindgut fermenters, and their isotopic values show some differences from the ruminants. For the Bacon's giant tapir, $\delta^{13}\text{C}$ (-17.5‰) and $\delta^{18}\text{O}$ values (-6.1‰) lie between the sambar deer and muntjac. The Javan rhino has relatively lower $\delta^{13}\text{C}$ values with a mean of $-17.0 \pm 0.8\text{‰}$ ($n = 5$) and the most negative $\delta^{18}\text{O}$ values with a mean of $-7.5 \pm 1.4\text{‰}$ ($n = 5$). This may imply that these taxa mainly inhabited a closed environment. Samples of stegodont had higher $\delta^{13}\text{C}$ values ($-15.7 \pm 0.3\text{‰}$, $n = 2$) than Javan rhino, possibly indicating inhabitation of a relatively open environment. Samples of Asian elephant have high $\delta^{13}\text{C}$ values with a mean of $-15.8 \pm 1.2\text{‰}$ ($n = 11$) and low $\delta^{18}\text{O}$ values with a mean of $-7.3 \pm 1.0\text{‰}$ ($n = 11$). Their isotopic data indicate that they occupied relatively open environment.

Omnivores, including wild boar ($n = 3$) and macaque ($n = 1$), preserve different carbon isotope values although their $\delta^{18}\text{O}$ values are similar (see Fig. 4). The higher $\delta^{13}\text{C}$ values of the wild boar ($-14.4 \pm 1.4\text{‰}$) compared to the macaque suggest that they occupied a more open environment.

There was only one carnivoran sampled in this study: giant panda ($n = 3$). They have relatively higher $\delta^{13}\text{C}$ values ($-17.0 \pm 1.1\text{‰}$) and lower $\delta^{18}\text{O}$ values ($-7.2 \pm 0.8\text{‰}$) similar to the Javan rhino (see Fig. 4), suggesting that they occupied a more closed environment and consumed more resources with lower $\delta^{18}\text{O}$ values.

5. Discussions

5.1. Foraging ecology of the fauna from Baxian Cave

Several studies show that the $\delta^{13}\text{C}$ bioapatite values of grazers with a diet consisting of pure C_4 grasses are over -4‰ whereas those of grazers or browsers with pure C_3 diets are lower than -15‰ (Cerling and Harris, 1999; Pushkina et al., 2010). Additionally, carnivores living in C_4 habitats have $\delta^{13}\text{C}$ bioapatite values more positive than -6‰ and in C_3 habitats more negative than -13‰ (Pushkina et al., 2010). Therefore, we use those $\delta^{13}\text{C}$ values as the threshold to preliminarily interpret the ecology and dietary preferences of the faunal assemblage evaluated in this study.

Altogether, the herbivores from this study have an average $\delta^{13}\text{C}$ value of $-16.2 \pm 1.3\text{‰}$ ($n = 25$), strongly suggesting that they inhabited a region of predominantly C_3 vegetation. Moreover, the $\delta^{13}\text{C}$ bioapatite values of the omnivores (wild boars and macaque) and the giant panda has a mean of $-15.8 \pm 1.7\text{‰}$ ($n = 7$), also suggesting the presence of C_3 vegetation in areas they inhabited. The isotopic data from the animal remains are consistent with an interpretation of a predominantly C_3 environment in Guangxi during the Late Pleistocene, which is congruent with other faunal studies in the region (Wang et al., 2007; Jin et al., 2008, 2009a,b).

As mentioned above, the $\delta^{18}\text{O}$ values of animal bioapatite can be used to broadly differentiate the drinking behaviors of browsers from grazers (Sponheimer and Lee-Thorp, 1999b). Low $\delta^{18}\text{O}$ values in herbivores indicate grazing and/or consumption of meteoric water. On the contrary, relatively higher $\delta^{18}\text{O}$ values in herbivores indicate reliance on browsing and/or less consumption of water (Quade et al., 1995; Sponheimer and Lee-Thorp, 1999b). In general, large herbivores, including Javan rhino, Asian elephant and stegodont, have low $\delta^{18}\text{O}$ values (see Fig. 4) given the fact that most of their drinking water came from the meteoric water and/or that they relied on graze. On the contrary, higher $\delta^{18}\text{O}$ values are observed in other animals with small or middle body sizes, which might be caused by less reliance on the meteoric water and/or more consumption of water through browse directly or indirectly. We

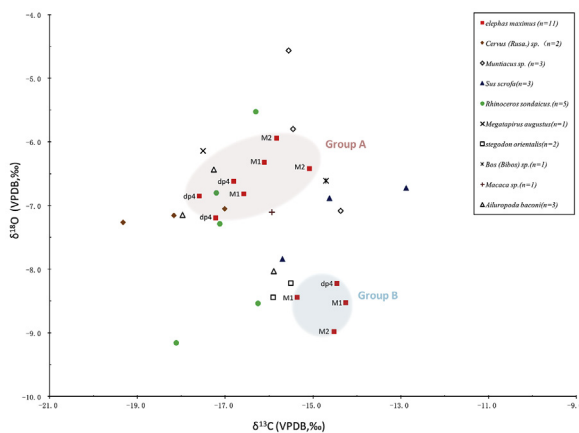


Fig. 4. The scatter plot of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of fauna fossils from Baxian Cave.

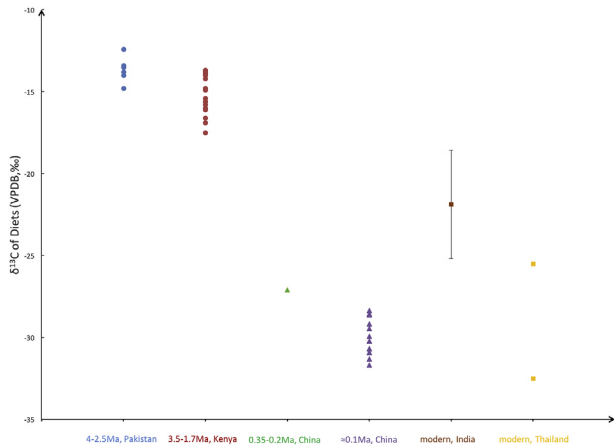


Fig. 5. Summary of carbon isotope results of *Elephas* through time. Summary includes data from both collagen and tooth enamel, and $\delta^{13}\text{C}$ here is for diet. We calculated them respectively depleted 14.1‰ and 5.5‰ because of different fractionation factors. The data are successively from: Stern et al. (1994; n = 5) in Pakistan and 1 sample from Cerling et al. (1999) from the same area; Cerling et al. (1999; n = 19) in Kenya, Africa; this study (n = 11); Wang et al. (2007; n = 1) in south China; Sukumar and Ramesh (1992; n = 56) in India; Pushkina et al. (2010; n = 2) in Thailand.

observed large variation of $\delta^{18}\text{O}$ values in Javan rhino, indicating that they consumed both browse and grass and should be classified as mixed feeders. For Asian elephants, the large variation of their $\delta^{18}\text{O}$ values along with $\delta^{13}\text{C}$ values, indicates that they were also mixed feeders, which is consistent with the results of dental microwear texture analysis on several Asian elephants at the same site (Zhang et al., in press).

5.2. Dietary variations of Asian elephants

It is notable that there are meaningful variations in the stable isotopic signature from the Asian elephants at Baxian Cave (see Fig. 4) and can be divided into two groups according to their isotopic differences. Group A has higher mean $\delta^{18}\text{O}$ value ($-6.6 \pm 0.4\text{‰}$, n = 7) and lower mean $\delta^{13}\text{C}$ value ($-16.5 \pm 0.9\text{‰}$, n = 7) whereas group B has much lower mean $\delta^{18}\text{O}$ values ($-8.5 \pm 0.3\text{‰}$, n = 4) and higher mean $\delta^{13}\text{C}$ value ($-14.6 \pm 0.5\text{‰}$, n = 4). An independent T-test indicates that the differences in isotope data between the two groups are significant ($\delta^{13}\text{C}$ values, $p = 0.004$; $\delta^{18}\text{O}$ values, $p < 0.01$). When considered with the isotopic results for other animals in this study, we infer that the elephants of group A lived in more closed forests and possibly fed on more tree leaves, while the elephants of group B inhabited in more open environments and consumed more grasses. Thus, it seems that significant dietary plasticity among Asian elephants existed in Guangxi during the Late Pleistocene.

Although our sampling of bulk teeth only provides broad information about the foraging ecology of elephants during a partial lifetime, we can still explore other possible factors, such as age,

seasonality and subspecies of elephants, which might be relevant for explaining the dietary variations.

Previous studies on modern Asian elephants show that young elephants incorporate more C_4 grasses in their diet than the adults (Sukumar and Ramesh, 1992, 1995). Both isotopic groups in our study include dp4s, M1s and M2s, representing both pre-adulthood (dp4 and M1) and adulthood (M2). Therefore, the dietary difference between two groups seems unlikely to be related to changes in dietary habits throughout the life of an individual. However, we acknowledge that the uneven sample numbers between two groups may render it insufficient to compare the dietary difference between the young and adult elephants.

Observations of feeding strategy of modern Asian elephants in India indicate that different dietary behavior existed between dry and wet seasons (Olivier, 1978; Baskaran et al., 2010). Thus, it is quite possible that the dietary variations observed here resulted from the seasonal and habitat change during the growing cycle of elephant teeth. Future sequential sampling of elephant teeth is needed to clarify the presence or absence of such a pattern, as has been observed in other fossil proboscideans (e.g., mammoths and mastodonts, Koch et al., 1998; Feranec and MacFadden, 2000; Baumann and Crowley, 2015).

One may speculate that different populations or subspecies of Asian elephants might also have produced the isotopic patterns we observed. There are at least four subspecies among modern Asian elephants, including *E. m. indicus*, *E. m. maximus*, *E. m. sumatranus* and *E. m. bengalensis* (Shoshani and Eisenberg, 1982; Shoshani and Tassy, 1996; Lister et al., 2013). Potential differences in ecological and dietary preferences among living subspecies should be tested as a reference in the near future.

5.3. Dietary evolution of Elephas

Carbon data for *Elephas* from previous studies (Sukumar and Ramesh, 1992; Stern et al., 1994; Cerling et al., 1999; Wang et al., 2007; Pushkina et al., 2010) and this study are summarized in Table 2 and plotted in Fig. 5 in order to facilitate preliminary discussion of the dietary evolution of *Elephas* through time and space. Before 1 Ma, $\delta^{13}\text{C}$ values of fossil *Elephas* in both Africa and Asia show that their diets contained substantial C_4 plants (Fig. 5). Apparently, the morphological evolution of *Elephas* from the brachyodont to hypsodont molars reflects their adaptation to the radiation of C_4 plants (Lister, 2013), a factor that may have been necessary for them to successfully disperse beyond Africa and into Eurasia. However, the diets shift towards C_3 plants in Pleistocene and modern times (Fig. 5) in some regions, specifically in South and Southeast Asia where C_3 ecosystems prevailed during those timeframes (Wang et al., 2007; Jin et al., 2008; Pushkina et al., 2010; Qu et al., 2014). Adaptations to tropical vegetation mainly composed of C_3 plants indicate a dietary flexibility that likely allowed populations of *Elephas* in South and Southeast Asia to survive the end-Pleistocene megafauna extinctions.

Table 2
Previous research on *Elephas*.

Lab number	Taxa	Age (Ma)	Site	Locality	$\delta^{13}\text{C}$ (tissues)	$\delta^{13}\text{C}$ (diets)	Reference
M12	<i>Elephas</i> sp.	2.53	Mirpur 6	Pakistan	-0.7	-14.8	Stern et al., 1994
M7	<i>Elephas</i> sp.	2.53	Ghanda Paik	Pakistan	0.3	-13.8	Stern et al., 1994
M5	<i>Elephas</i> sp.	2.53	Ghanda Paik	Pakistan	0.6	-13.5	Stern et al., 1994
M4	<i>Elephas</i> sp.	2.69	Mirpur 4	Pakistan	0.1	-14	Stern et al., 1994
M6	<i>Elephas</i> sp.	3.97	Ghanda Paik	Pakistan	0.7	-13.4	Stern et al., 1994
ROT-191	<i>Elephas</i> sp.	4	Upper Siwaliks	Pakistan	1.7	-12.4	Cerling et al., 1999
ER 767	<i>Elephas recki recki</i>	1.7	Turkana basin	Kenya	-3.4	-17.5	Cerling et al., 1999
ER 1693	<i>Elephas recki atavus</i>	1.9	Turkana basin	Kenya	-1.5	-15.6	Cerling et al., 1999
ER 1691	<i>Elephas recki ileretensis</i>	1.9	Turkana basin	Kenya	0.2	-13.9	Cerling et al., 1999

(continued on next page)

Table 2 (continued)

Lab number	Taxa	Age (Ma)	Site	Locality	$\delta^{13}\text{C}$ (tissues)	$\delta^{13}\text{C}$ (diets)	Reference
ER 927	<i>Elephas recki ileretensis</i>	1.9	Turkana basin	Kenya	-2.8	-16.9	Cerling et al., 1999
ER-1302	<i>Elephas recki ileretensis</i>	1.9	Turkana basin	Kenya	0.3	-13.8	Cerling et al., 1999
ER-1302	<i>Elephas recki ileretensis</i>	1.9	Turkana basin	Kenya	0.4	-13.7	Cerling et al., 1999
ER-1302	<i>Elephas recki ileretensis</i>	1.9	Turkana basin	Kenya	0.4	-13.7	Cerling et al., 1999
ER-1700	<i>Elephas recki shungurensis</i>	1.9	Turkana basin	Kenya	-0.7	-14.8	Cerling et al., 1999
ER-1700	<i>Elephas recki shungurensis</i>	1.9	Turkana basin	Kenya	-0.8	-14.9	Cerling et al., 1999
ER-4102	<i>Elephas recki shungurensis</i>	2	Turkana basin	Kenya	-0.1	-14.2	Cerling et al., 1999
ER-4113	<i>Elephas recki shungurensis</i>	2	Turkana basin	Kenya	0.1	-14	Cerling et al., 1999
ER-5871	<i>Elephas recki shungurensis</i>	2	Turkana basin	Kenya	0.3	-13.8	Cerling et al., 1999
ER-2894	<i>Elephas recki brumpti</i>	3	Turkana basin	Kenya	-1.9	-16	Cerling et al., 1999
ER-2895	<i>Elephas recki brumpti</i>	3	Turkana basin	Kenya	-2.0	-16.1	Cerling et al., 1999
ER-3191	<i>Elephas recki brumpti</i>	3	Turkana basin	Kenya	-1.3	-15.4	Cerling et al., 1999
ER-4106	<i>Elephas recki brumpti</i>	3	Turkana basin	Kenya	0.2	-13.9	Cerling et al., 1999
KP 30173	<i>Elephas ekorensis</i>	3.5	Turkana basin	Kenya	-1.7	-15.8	Cerling et al., 1999
WT 3570	<i>Elephas ekorensis</i>	3.5	Turkana basin	Kenya	-1.5	-15.6	Cerling et al., 1999
WT 3614	<i>Elephas ekorensis</i>	3.5	Turkana basin	Kenya	-2.5	-16.6	Cerling et al., 1999
UPC-A	<i>Elephas</i> sp.	0.35–0.2	Bubing Cave	China	-13	-27.1	Wang et al., 2007
Unknown	<i>Elephas maximus</i>	Modern		Thailand	-11.4	-25.5	Pushkina et al., 2010
Unknown	<i>Elephas maximus</i>	Modern		Thailand	-18.4	-32.5	Pushkina et al., 2010
Unknown	<i>Elephas maximus</i>	Modern	Nilgiri-Eastern Ghats region	India		-21.9 ± 3.3 , n = 56	Sukumar and Ramesh, 1992

Noted: all the data are from bioapatite, except Sukumar and Ramesh (1992). In Sukumar and Ramesh (1992), only calculated mean and standard deviation were given.

6. Conclusion

In this study, carbon and oxygen isotope analyses of 32 fossil teeth representing 10 taxa were conducted to preliminarily understand the dietary preferences and foraging ecology of Asian elephants and other taxa unearthed from Baxian Cave, Guangxi, China. The isotopic signatures indicate that all animals inhabited in C₃ ecosystem and that elephants were likely mixed feeders. We cannot completely exclude the possibility that the isotope record of the elephant population considered here might be related to age, seasonality and/or subspecies differences. Regardless, the variation of isotope data for fossil *Elephas* through time suggests a strong dietary flexibility throughout the evolution of the genus.

As a final, cautionary note, this paper represents a preliminary study which lacked a high-resolution, systematic sampling method, as a result of logistical constraints. Future systematic sequential sampling of additional elephant teeth in future will undoubtedly provide more clues to the evolution of foraging ecology in the Asian elephants, and either support or refute the interpretations presented here.

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