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.

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,
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 values of bone collagen from modern elephants in India demonstrates that today they are mixed feeders and prefer more browse (Cerling and Harris, 1999; Drucker, 2007). Therefore, the mammals mainly consuming such foliage generally have higher δ18O values than those that consume grass (Koch et al., 1989; Quade et al., 1995; Sponheimer and Lee-Thorp, 1999b; Wang et al., 2008). Collectively, δ18O 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°34′31.6″N, 107°21′0.2″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., *Namus* sp., and *Rhinopithecus* sp.), carnivorans (*Ailuroproda bacoa*, *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. baco* and *M. augustus*, is most similar to faunas

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