

## Enamel carbon isotope evidence of diet and habitat of *Gigantopithecus blacki* and associated mammalian megafauna in the Early Pleistocene of South China

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Enamel stable carbon isotope analyses were conducted on the large fossil ape *Gigantopithecus blacki* and an associated mammalian megafauna from Longgudong Cave in Jiashi and Juyuandong Cave in Liucheng, South China. The range in  $\delta^{13}\text{C}$  values ( $-18.8\text{‰}$  to  $-14.1\text{‰}$ ) indicates that *G. blacki* and other large mammals fed on solely  $\text{C}_3$  biomass, and lived in forest habitats, and not open country or savannas. These results are consistent with other faunal and floral analyses for that time. The diet and habitat of *G. blacki* were significantly different from those of early hominins (*Australopithecus* and *Paranthropus*) from South and East Africa. Extinction of *G. blacki* probably was a result of forest habitat fragmentation and deterioration.

### *Gigantopithecus blacki*, diet, enamel stable carbon isotopes, habitat

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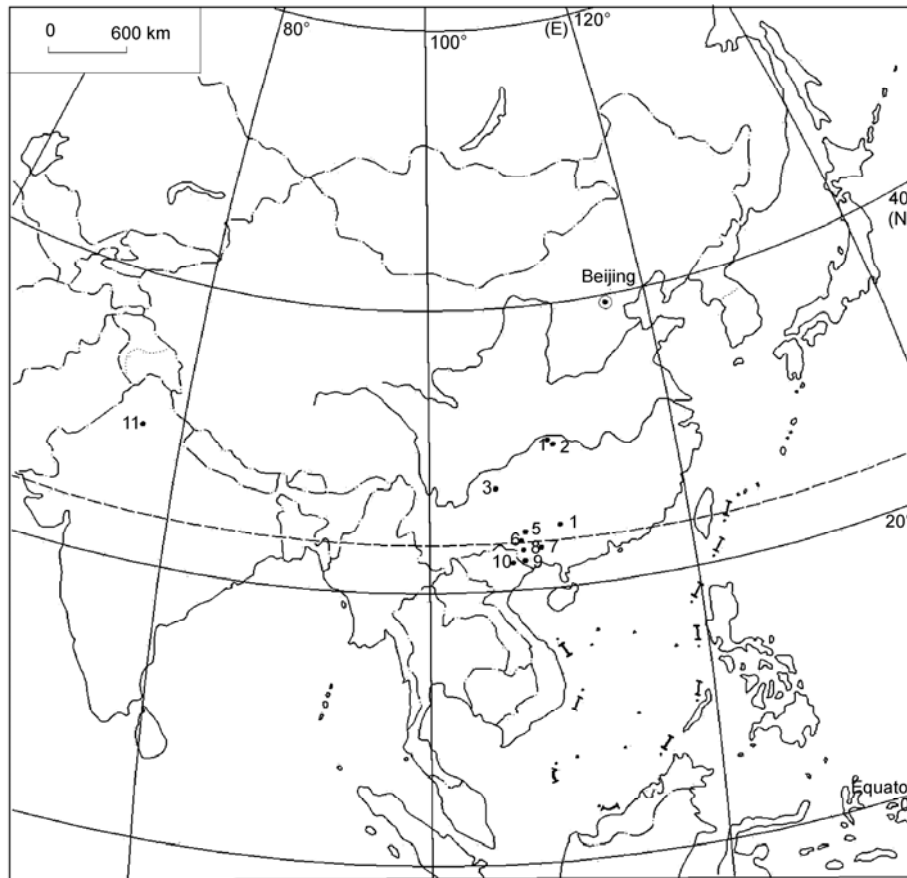
*Gigantopithecus blacki* was a species of large hominoids that dominated the Pleistocene of South China (Figure 1). The characteristics of this species include a large mandible and massive buccal teeth with very thick enamel, and some features similar to hominins [1–4]. Information regarding its diet and habitat requirements is of interest to both paleoanthropologists and the general public.

Based on the associated fauna, most scholars believe that *G. blacki* lived in subtropical forest environments [5–7]. However, open-country grasslands also have been hypothesized to have been used by *Gigantopithecus bilaspurensis* of North India and *G. blacki* of South China. Pilbeam suggested that it is most likely that *Gigantopithecus* species spent most of their time on the ground, foraging for their

food in open country, similar to the gelada baboon in Ethiopia today [8]. The massive mandible, large postcanine teeth and thick enamel characteristics resemble the powerful mastication evident among *Gigantopithecus*, *Paranthropus* and *Australopithecus*, and may imply a similar diet and habitat use. However, the precise habitat of *Gigantopithecus* is still unknown.

Analysis of stable carbon isotopes is a powerful method [9–11] for exploring the diet and habitat use of extinct herbivorous mammals, including early hominins in South and East Africa [12–21]. This method is based on the fact that the carbon isotope composition is significantly different between plants that use different photosynthetic pathways, such as  $\text{C}_3$  plants ( $\delta^{13}\text{C}$  from  $-22\text{‰}$  to  $-35\text{‰}$ ) and  $\text{C}_4$  plants (from  $-8\text{‰}$  to  $-16\text{‰}$ ). Furthermore, the stable carbon isotope composition of enamel is dependent on the diet

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**Figure 1** Fossil sites of *G. blacki* (1–10) and *G. bilaspurensis* (11). 1, Longgupo of Wushan; 2, Longgudong of Jianshi; 3, Baeryan of Bijie; 4, Juyuangong of Liucheng; 5, Nongmoshan of Bama; 6, Mohuidong of Bubing; 7, Lalishan of Wuming; 8, Heidong of Daxin; 9, Sanhedadong of Chongzuo; 10, Than Khuyen in northern Vietnam; 11, Haritalyangar in northern India.

components throughout the food chain. In this paper, we analyze enamel stable carbon isotope values, diets and habitat use of *G. blacki* and the associated mammalian megafauna from two sites in South China.

## 1 Materials and methods

Longgudong Cave (30°40'N, 110°05'E, altitude 740 m) of Jianshi in Hubei Province is an early Pleistocene hominin site, from where more than 100 teeth of *Gigantopithecus* and 6 teeth of hominins have been identified as *Australopithecine* [22] or *Meganthropus* [7]. Dating of the associated fauna and paleomagnetic dating have placed the geological age of these teeth findings as Early Pleistocene. The geological age of Juyuangong Cave (24°40'N, 109°15'E, altitude 200 m) of Liucheng in Guangxi also is Early Pleistocene, but earlier than that of the Longgudong site, where 3 mandibles and about 1000 teeth of *Gigantopithecus* have been discovered.

A total of 32 tooth samples were investigated in the present study. Four teeth of *G. blacki* and 24 teeth of associated large mammals were analyzed from Longgudong Cave,

Jianshi. The other 4 teeth of *G. blacki* were taken from Juyuangong Cave of Liucheng (Figure 1). The large mammals included 9 species: *Sus* sp., *Leptobos* sp., *Cervus* sp., *Equus* sp., *Rhinoceros sinensis*, *Tapirus sinensis*, *Pachycrocuta licenti*, *Ursus* sp., *Ailuropoda wulingshanensis* (Table 1).

The clean enamel fragments were ground into powder. The powder was allowed to react in 5% sodium hypochlorite overnight to eliminate bacterial protein and humates, and then in 6% acetic acid overnight to remove diagenetic carbonates. Clean and dry CO<sub>2</sub> was produced by reaction of enamel samples in 100% phosphoric acid hydrolysis. Carbon isotopes were measured on a Finnigan Mat252 mass spectrometer at the Stable Isotope Laboratory in the State Key Laboratory of Lithospheric Evolution of Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China. The analytical precision of the  $\delta^{13}\text{C}$  values (PDB) was better than 0.1‰.

## 2 Results and discussion

### 2.1 Enamel $\delta^{13}\text{C}$ values and diet

A total of 32 enamel powder samples from 32 individual

teeth were prepared. A total of 42 enamel powder samples were analyzed for stable carbon isotopes ( $\delta^{13}\text{C}$ ), of which 2–3 parallel samples were taken for 9 tooth samples (Table 1). The most enriched  $\delta^{13}\text{C}$  value was  $-14.1\%$ , and the most depleted was  $-18.8\%$ . An enrichment of  $14\%$  for  $\delta^{13}\text{C}$  was observed between food types and enamel [23]. The  $\delta^{13}\text{C}$  values of food sources should be from  $-32.8\%$  to

$-28.1\%$ , which is within the  $\delta^{13}\text{C}$  range of  $\text{C}_3$  biomass and far too negative for that of  $\text{C}_4$  biomass. It is clear that *Gigantopithecus* and the affiliated megafauna (e.g. browsers (*Cervus* sp. and *Tapirus sinensis*), grazers (*Equus* sp. and *Leptobos* sp.) and carnivores (*Pachyrocata licenti* and *Ursus* sp.)) all derived their carbon from solely  $\text{C}_3$  biomass sources.

**Table 1** Enamel stable carbon isotope ratios ( $\delta^{13}\text{C}$  in PDB) of *Gigantopithecus blacki* and an associated large mammalian fauna

Taxon	Specimen	Tooth type	Site	$\delta^{13}\text{C}$ (‰)	Mean $\pm$ SD
Specimen from Juyuangong of Liucheng in Guangxi					
<i>G. blacki</i>	19	Lower molar	5704C	-17.5	
<i>G. blacki</i>	20	Lower molar	5704B	-17.3	-17.3 $\pm$ 0.3
<i>G. blacki</i>	21	Upper molar	5704C	-17.5	
<i>G. blacki</i>	22	Lower molar	5704C	-16.8	
Specimen from Longgudong of Jianshi in Hubei					
<i>G. blacki</i>	23	Upper molar	70016 E11	-17.2	
<i>G. blacki</i>	24	P <sub>3</sub>	70016E11	-15.9	-16.4 $\pm$ 1.8
<i>G. blacki</i>	25	Upper molar	70016W4	-18.2	
<i>G. blacki</i>	26	Lower molar	70016 W7	-14.2	
<i>Leptobos</i> sp.	1A <sup>a)</sup>			-15.8	
	1B	P <sub>3</sub>	70016 E11	-15.7	
	1C			-15.8	-15.9 $\pm$ 0.8
<i>Leptobos</i> sp.	2	M <sub>3</sub>	70016 E11	-15.4	
<i>Leptobos</i> sp.	3	M <sup>3</sup>	70016 E11	-17.1	
<i>Leptobos</i> sp.	4	Upper premolar	70016 E11	-15.3	
<i>Cervus</i> sp.	5	M <sub>3</sub>	70016 E11	-16.8	
<i>Cervus</i> sp.	6	M <sub>3</sub>	70016 E11	-17.8	-16.7 $\pm$ 1.2
<i>Cervus</i> sp.	7	M <sup>3</sup>	70016 E11	-15.5	
<i>Tapirus sinensis</i>	8	Lower molar	70016 E11	-16.6	
<i>Tapirus sinensis</i>	9A			-17.6	
	9B	Lower molar	70016 E11	-17.7	-16.7 $\pm$ 0.7
<i>Tapirus sinensis</i>	10	Upper molar	70016 E11	-16.3	
<i>Tapirus sinensis</i>	11	Lower molar	70016 E11	-16.1	
<i>Rhinoceros sinensis</i>	12	M <sup>1</sup>	70016 E11	-14.4	
<i>Rhinoceros sinensis</i>	13	M <sub>3</sub>	70016 E11	-15.8	
<i>Rhinoceros sinensis</i>	14	M <sub>1</sub>	70016 E11	-14.9	
<i>Rhinoceros sinensis</i>	15	M <sup>3</sup>	70016 E11	-15.8	-15.2 $\pm$ 0.6
<i>Rhinoceros sinensis</i>	32A			-15.4	
	32B	Lower molar	70016 E11	-15.4	
<i>Pachyrocata licenti</i>	16	Upper premolar	70016 E11	-14.1	-14.1
<i>Ursus</i> sp.	17	Lower molar	70016 E11	-15.9	-15.9
<i>Ailuropoda wulingshanensis</i>	18A			-18.3	
	18B	Lower molar	70016 E11	-18.3	-18.3
<i>Equus</i> sp.	27A			-18.8	
	27B	Lower molar	70016 E11	-18.8	
<i>Equus</i> sp.	28A			-17.5	
	28B	Upper premolar	70016 E11	-17.6	
<i>Equus</i> sp.	29A			-18.4	
	29B	Lower molar	70016 E11	-18.4	-18.0 $\pm$ 0.7
<i>Equus</i> sp.	30A			-17.3	
	30B	Lower molar	70016 E11	-17.3	
<i>Sus</i> sp.	31A			-16.0	
	31B	Lower molar	70016 E11	-16.1	-16.1

a) A, B and C under the same number represent parallel powder samples from the same tooth.

**2.2 Diet and habitat**

Results indicate that the living environment of *G. blacki* and the associated mammalian megafauna was vegetation dominated by C<sub>3</sub> plants from a dense forest or possibly an open savanna environment in a cold or cool climate.

C<sub>4</sub> plants were commonly distributed in the subtropical region of South China [24]. The Three Gorges region of Yangtze River, where the Jianshi site is located, is mainly covered by subtropical forest flora today. In this region, C<sub>4</sub> photosynthesis species constitute only about 2.5% of the total 2685 vascular plant species, and *Gramineae* are the leading C<sub>4</sub> species and constitute about 36% of the total grasses. 95% C<sub>4</sub> species can be found at 500–800 m altitude [25]. Surveys of a subtropical monsoon evergreen broad-leaved forest in South China have shown that C<sub>4</sub> plants survive only in open ground areas, and cannot be found in dense forests [26]. If *Gigantopithecus* lived in an open environment at the Jianshi site, where C<sub>4</sub> grasses should have been common, the associated grazers, such as *Equus* and *Leptobos*, would have consumed C<sub>4</sub> grasses as well. In fact, both of these taxa consumed a pure C<sub>3</sub> diet. In addition, both fauna and flora show evidence indicating the typical subtropical forest environment of the Jianshi Site [7,27]. However, Early Pleistocene *Equus* from Yuanmou human sites consumed as much as 70% C<sub>4</sub> grasses in their diets, and lived in an open habitat, as evidenced by their carbon isotope signatures [28]. Thus, all the above data support a subtropical dense forest for the habitat of *G. blacki* and the associated large mammals.

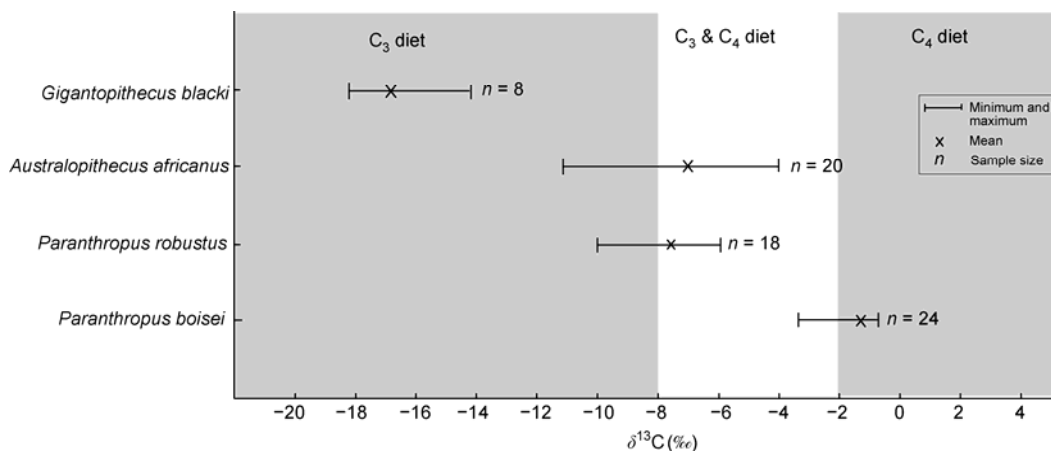
If *Gigantopithecus* lived in dense forest habitats, what was their diet? Identification of opal phytoliths bonded to the enamel surface of *G. blacki* indicates this giant ape had a varied diet of grasses and fruits [29]. Compared with the dental microwear of living anthropoids, *G. blacki* was intermediate between folivorous forms and hard-object specialists, and was most similar to the predominantly frugivorous *Pan troglodytes* species [30]. A high frequency of

dental caries indicates that the diet of *G. blacki* was rich in sugar or starch [1,31,32]. The large molars with high crowns and thick enamel indicate an adaptation of strong grinding to hard food.

**2.3 Comparison to extant apes and early hominins**

As the extant hominoids, *G. blacki* lived in forest habitats, and had a solely C<sub>3</sub> biomass diet. This species is different from some early hominins, such as *Australopithecus africanus*, *Paranthropus robustus* and *Paranthropus boisei* in Africa (Figure 2). Stable carbon isotope evidence indicates that *A. africanus* from Makapansgat [14], Sterkfontein [15,17] and *P. robustus* from Swartkrans [12,15] in South Africa had a mixed diet of C<sub>3</sub> and C<sub>4</sub> biomass, and *P. boisei* from East Africa consumed a high proportion of C<sub>4</sub> biomass (almost 80% of its diet) [16,18]. The data indicate these early hominins could live in open habitats and consume a high proportion of C<sub>4</sub> biomass, consisting of tropical/savannah grasses and certain sedges, and/or animal eating C<sub>4</sub> foods. Thus, Leo-Thorp et al. [13] recently suggested that engagement with C<sub>4</sub> food resources may mark a fundamental transition in the evolution of hominin lineages in the Pliocene. However, earlier hominins, such as *Ardipithecus ramidus*, preferred C<sub>3</sub> biomass diets and woodland habitats [33].

The present fossil record indicates that *G. blacki* was distributed widely in South China during the Early Pleistocene (Figure 1), but it was limited to the south of Guangxi Province in the Middle Pleistocene. No fossil record has been discovered for the Late Pleistocene *Gigantopithecus* until now. It is unclear what may have caused the extinction of this giant ape. Analysis of Pleistocene sporopollen floras in China has shown that there was a significant transformation of vegetation during 1.6–0.8 Ma, and during this period the climate became cold and dry. This environmental change may have been related to the uplift of the Tibetan Plateau [34]. Primates are sensitive to climate and environmental



**Figure 2** Comparison of diet and enamel stable carbon isotopes ( $\delta^{13}C$ ).

change, and are likely to be threatened by any situation that involves competition or conflict with humans. The most common and persistent factor that adversely affects populations of wild primates is loss of usable habitat. For example, the only extant great ape in Asia, the orangutan, had been widely distributed in South China during the Pleistocene, and now is only found in Borneo and Sumatra. In 1900, the population of orangutans was estimated to be in excess of 300000 individuals, and in 1997 the total population had dropped to only 27000 individuals [35]. The lesser ape, the black-crested gibbon, is now only found on Hainan Island, in southern and central Yunnan in China and northern Vietnam, although its historic distribution extended to South China [36]. Compared with orangutans and gibbons, *G. blacki* might have been more sensitive to climatic and environmental change as well as habitat contraction from human activity during the Pleistocene. Study on dental development indicates that *G. blacki* had a longer and slower and more delayed growth pattern [37]. This implies a lower reproduction rate, which did not appear to bode well for its population development when the forest habitat became fragmented and deteriorated.

### 3 Conclusions

Stable carbon isotope analyses indicate that *G. blacki* from South China had a diet of pure C<sub>3</sub> biomass resources, and lived in dense forest habitats. The diet and habitat of *G. blacki* was significantly different from that of early hominins in Africa, such as *Australopithecus* and *Paranthropus*, which could live in open habitats and consume both C<sub>3</sub> and C<sub>4</sub> resources. Dependence on forest habitat might be an important factor that drove *Gigantopithecus* extinction when the climate and environment changed dramatically during the Pleistocene.

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