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New fossil evidence and diet analysis of *Gigantopithecus blacki* and its distribution and extinction in South China

L.X. Zhao [a,b,*], L.Z. Zhang [a,b]

[a] Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, Beijing 100044, China
[b] Laboratory of Human Evolution, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, China

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ABSTRACT

The present paper reports the recently discovered fossil teeth of Early Pleistocene *Gigantopithecus blacki* and associated mammalian fauna from Baeryan Cave, Bijie County in Guizhou Province, and also reviews briefly the known fossil sites of *Gigantopithecus* in south China of Pleistocene. In Early Pleistocene, *Gigantopithecus* had a wider distribution, but withdrew southward in Middle Pleistocene to a limited area mainly in South China, and it disappeared in the Late Pleistocene according to the present fossil records. Diet and habitat analysis from carbon isotope evidence is used to investigate the reasons for the extinction of *Gigantopithecus*, which fed on a pure C_3 diet and lived in a forest habitat. It was clearly different from early hominins in South and East Africa, such as *Australopithecus africanus*, *Paranthropus robustus* and *Paranthropus boisei,* which had C_4 diets. The extinction of *Gigantopithecus* was also related to the great changes of climate and environment of the Pleistocene, especially the last one million years, during which *Homo* became more and more prosperous and exerted great pressure on *G. blacki*.

1. Introduction

Pleistocene *Gigantopithecus blacki* is the largest species of extinct and extant primates. What this giant ape ate, what kind of habitat it lived in, and how it evolved and went extinct during the Pleistocene, are unsolved questions of interest, not only for paleoanthropologists and also for the public. New fossil evidence and further analysis on *Gigantopithecus* could be helpful in investigating the above issues. This paper reports on the recently discovered fossils of *Gigantopithecus* and associated mammalian fauna from a cave site, Baeryan cave, Bijie, South China. The diet and habitat was discussed based on the enamel carbon isotope evidence along with other information as fauna, flora, dental caries, and microwear of *Gigantopithecus* in two sites, Longgudong cave in Jianshi and Juyuandong cave in Liucheng. A brief review is included of the known fossil sites of *Gigantopithecus* and the geographical distribution change in South China during the Pleistocene, followed by attempt to investigate the reasons for its extinction.

2. New fossil evidence of *G. blacki* from Baeryan cave, Bijie

The Baeryan cave fossil site (27°22′12″N, 105°15′16″E) located in Bijie County, Guizhou Province, was exposed when a local farmer made excavations in the 1980s (Xu and Cai, 1984). In 2001–2004, *Gigantopithecus* teeth and other mammalian fossils were uncovered and collected by the quarry worker Mr. Peng, and the amateur Mr. FP Zhao and family. Unfortunately, the fossil deposits had been destroyed by quarrying. The bottom of the deposits measures 1630 m above sea level, and 40 m above the nearby river surface.

2.1. Teeth of *G. blacki*

Five isolated teeth of *G. blacki* were discovered, one lower right central incisor GBB1-4, one lower right lateral incisor GBB1-5, one lower left canine GBB1-2, one lower right first molar GBB1-3 and an upper left second molar GBB1-1 (Fig. 1). All teeth crowns are well-preserved, especially the three anterior teeth with almost complete roots. The anterior teeth and the lower first molar are moderately worn with exposed dentine holes. The upper second molar is slightly worn, with flat protocone and blunt paracone, metacone and hypocone.

Compared with the large assemblage (IVPP laboratory, Beijing) of *Gigantopithecus* teeth from Juyuandong cave 5704C site, Liucheng county, Guangxi Autonomous Region, described in detail by Woo (1962), the morphology features of Baeryan *Gigantopithecus* teeth show no difference in features, so they are not described here in detail. Measurements of tooth size are presented in Table 1. Compared with the tooth size data of Juyuandong 5704C, the sizes of the Baeryan specimens are within the variation. *G. blacki* is a primate

* Corresponding author. Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Xi-Zhi-Men-Wai 142, Beijing 100044, China.
E-mail address: zhaolingxia@ivpp.ac.cn (L.X. Zhao).

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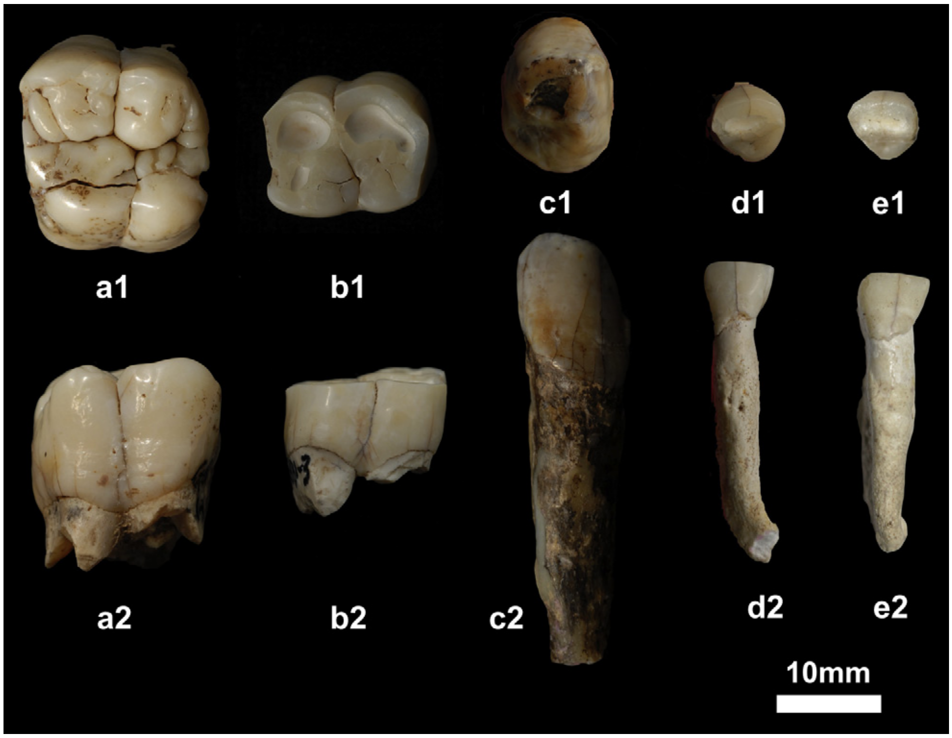

Fig. 1. Fossil teeth of *Gigantopithecus blacki* from Baeryan cave, Bijie county, Guizhou Province. 1-occlusal view 2-lateral view; a GBB-1 l M^2; b GBB-3 r M_1; c GBB-2 l C_1; d GBB-5 r I_2; e GBB-4 r I_1.

with sexual dimorphism in the sizes of teeth and mandible. Woo (1962) divided the tooth assemblage 5704C into two groups, large and small, which might imply male and female respectively. Accordingly, the upper second molar GBB1-1 should lie within the large type, and the other four teeth belong to the small type.

Non-destructive micro-CT based methodology was used to investigate the enamel thickness features of the upper second molar GBB1-1, which is less worn. From the plane coursing through the mesial cusps (Fig. 2), the two-dimensional average enamel thickness (2DAET) and two-dimensional relative enamel thickness (2DRET) are calculated as 2.45 mm, and 20.31. The three-dimensional thickness 3DAET is 2.50 mm, and the 3 DRET is 20.41. Clearly, the great thickness of enamel (not only by absolute thickness measurements AET, but also relative thickness index RET concerning the tooth size) is a typical feature of *G. blacki* among the primates, including humans. Thick enamel is a special adaptation to its diet.

2.2. Associated mammalian fauna and geological age

A total of 21 species were identified from the mammalian fossil assemblage of Baeryan Cave site, including *G. blacki*, *Ailuropoda microta*, *Pachycrocuta licneti*, *Cuon dubius*, *Ursus thibetanus primitinus*, *Panthera* sp., *Dicoryphocheorus ultimus*, *Muntiacus* sp., *Cervavitus fenqii*, *Cervus* cf. *unicolor*, *Budorcas* sp., Caprinae gen. et sp. indet., *Gazella* sp., *Leptobos* sp., *Tapirus sanyuanensis*, *Nestoritherium* sp., *Rhinoceros sinensis*, *Rhinopithecus* sp., *Stegodon orientalis*, *Rhizomys* sp., and *Hystrix subcristata*.

In terms of the compositions of mammalian fauna, the Baeryan fauna include the typical elements of the early Pleistocene fauna in South China, such as *A. microta*, *P. licneti*, *C. dubius*, *T. sanyuanensis*, *Nestoritherium*, *D. ultimus*, and *Leptobos*, and it is most similar to those of Juyuandong cave, Liucheng (Pei, 1960), Longgupo cave, Wushan (Huang and Fang, 1991), and Mohui and Chuifeng caves of

Table 1
Tooth measurements (mm) of *Gigantopithecus blacki* from Baeryan cave.

Specimen	Tooth	MD	LB	Crown height	Root length	Type group
GBB1-1	upper left M^2	19.0	22.0	>17.0		Large type
GBB1-2	lower left C	11.6	15.0	>16.3	>29	Small type
GBB1-3	lower right M_1	16.0	14.0	>7.7		Small type
GBB1-4	lower right I_1	6.5	7.4	>8.2	17	Small type
GBB1-5	lower right I_2	7.2	8.1	>8.2	21	Small type

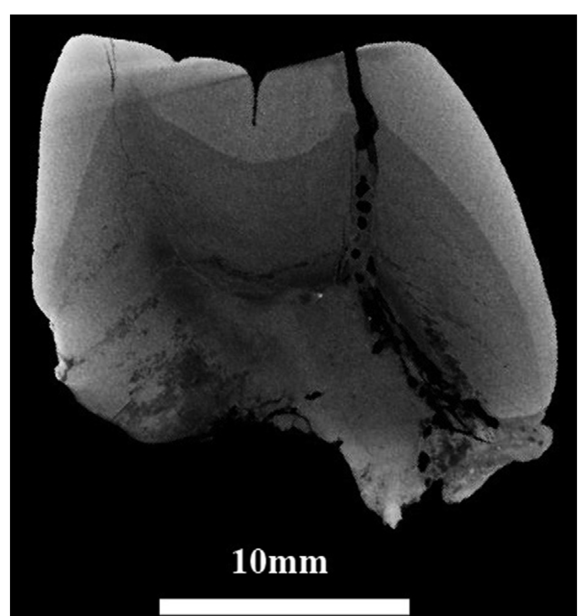

Fig. 2. Micro-CT section through mesial cusps of the upper second molar GBB1-1.

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Tiandong (Wang et al., 2007; Wang, 2009). Therefore, the Baeryan Fauna is early Early Pleistocene. It is earlier than those of Longgudong cave in Jianshi, Sanhe Cave in Chongzuo, Heidong cave in Daxin, Lalishan cave in Wuming, and Nongmoshan cave in Bama.

The new fossils of *Gigantopithecus* from Baeryan Cave widen its distribution in the geographical and geological record. Baeryan is located in the Yunnan-Guizhou Plateau, and is the highest site in altitude among known sites of *G. blacki*. It provides evidence for exploring the evolution and extinction, which is discussed in the following context.

3. Diet and habitat analysis of *G. blacki*

As the largest species of extinct and extant primates, the diet and habitat of *G. blacki* are interesting. Open-country grassland had been suggested for the living environments of *Gigantopithecus bilaspurensis* from North India (Simons and Chopra, 1969) and *G. blacki* from South China (Pilbeam, 1972). However, the associated mammalian fauna of *G. blacki* from south China shows a dominant forest environment (Pei, 1960; Hsu et al., 1974; Zheng, 2004). Enamel stable carbon isotope analysis on *Gigantopithecus* from two key sites is used to attempt to explore its diet and habitat directly.

A total of 8 teeth of *G. blacki* were analyzed, with 4 teeth from the Longgudong Cave, Jianshi County, Hubei Province, and 4 teeth from Juyuandong Cave, Liucheng County, Guangxi Autonomous Region. Longgudong cave (30°40′N, 110°05′E, altitude 740 m) is an Early Pleistocene hominin site, where more than 100 teeth of *G. blacki* were discovered and also 6 hominin teeth, probably belonging to Australopithecine or *Meganthropus* (Gao, 1975; Zheng, 2004). Its geological age is Early Pleistocene, from fauna and palaeomagnetic data. In Juyuandong cave (24°40′N, 109°15′E, altitude 200 m), 3 mandibles and nearly 1000 teeth of *G. blacki* were discovered (Woo, 1962). Its geological age is also Early Pleistocene, but earlier than Longgudong, based on the fauna analysis.

During laboratory treatments and analysis, the clean enamel fragments were ground into powder. The powdered enamel samples were reacted 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_2 was produced by reaction of enamel powder samples in 100% phosphoric acid hydrolysis. Carbon isotopes were measured on the Finnigan Mat252 mass spectrometer at the Stable Isotope Laboratory, Institute of Geology and Geophysics, Chinese Academy of Sciences. The analytical precision of $\delta^{13}C$ values (PDB) is better than 0.1‰.

The $\delta^{13}C$ results (Table 2) show slight differences between the same specimen with no treatment and after treatment, which might imply a small enrichment effect of diagenetic carbonates in the enamel. The $\delta^{13}C$ range of the samples before and after treatment is respectively from −13.0‰ to −16.8‰, and from −14.2‰ to −18.2‰. Concerning the enrichment (about 14‰) of $\delta^{13}C$ values from food to enamel (Lee-Thorp and van der Merwe, 1987; Cerling and Harris, 1999), the $\delta^{13}C$ values of food resource should be in the range −27.0‰ to −30.8‰, or −28.1‰ to −32.8‰, both completely within the range of C_3 plants ($\delta^{13}C$ from −22‰ to −35‰) and far from the range of C_4 plants (from −8‰ to −16‰). The results indicate a pure C_3 diet for *G. blacki* and a habitat where C_3 plants should be dominant.

What kind of habitat did *G. blacki* live in? C_3 plants include trees, shrubs forbs and herbs. C_4 species are predominantly tropical and subtropical grasses and sedges. A floral survey indicates C_4 plants are distributed in South China (Yin and Li, 1997). If *G. blacki* lived in an open environment, the associated typical grazers such as *Equus* and *Sus* should have had C_4 grasses in their diets. However, both grazers and browsers, and even carnivorous predators such as *Pachycrocuta,* all had a pure C_3 diet (Zhao, 2006b). A survey of a subtropical monsoon evergreen broad-leaved forest in South China showed that C_4 plants only survive in open areas, and cannot be found in the dense forest (Ehleringer et al., 1987). The Longgudong site is located in the Three Gorges region of the Yangtze River, where a subtropical forest flora is dominant nowadays. C_4 photosynthesis species in this region are only about 2.5% of the total of 2685 vascular plant species. Most C_4 species can be found at 500–800 m altitude, and *Gramineae* are the leading C_4 taxa, about 36% of the total (Wang, 2003). The Yuanmou fauna is nearly of contemporary age with the Jianshi and Liucheng *Gigantopithecus* fauna, and the carbon isotope evidence indicates the grazer *Equus* had a diet of 70% C_4 grasses and lived in an open habitat (Biasatti et al., 2011). All the above evidence supports a subtropical forest habitat of *G. blacki*. The isotope evidence is consistent with associated mammal fauna (Hsu et al., 1974; Zheng, 2004) and flora analysis (Cheng and Gao, 2004).

The diet and habitat of *G. blacki* is clearly different from that of early hominins from Africa such as *Paranthropus* and *Australopithecus*, even though the massive mandible and large postcanine teeth and thick-enamel characteristics show some similarly powerful mastication between *Gigantopithecus* and *Paranthropus*. Their $\delta^{13}C$ values are clearly separate do not overlap (Table 3). Isotope evidence indicated that *Australopithecus africanus* from Sterkfontein and Makapansgat, *Paranthropus robustus* from Swartkrans and Kromdraai in South Africa had a diet with more than 30% C_4 resources (Sponheimer et al., 2005). *Paranthropus boisei* from East Africa had a diet with 80% C_4 resources (van der Merve et al., 2008; Cerling et al., 2011). Both *Paranthropus* and *Australopithecus* could live in an open habitat and had C_4 grasses in their diets. Adaptation to open habitats was essential for the early hominins to survive in the changing climate and environment during the Pliocene to Pleistocene. However, *G. blacki* seemed to be limited to forest habitat. The morphological similarity between *Gigantopithecus* from East Asia and *Paranthropus* from Africa, with massive mandibles, large molars and thick-enamel features, does not mean they are adapted to similar diet and habitat.

Table 2
Enamel stable carbon isotope ratios $\delta^{13}C$ of *Gigantopithecus blacki* (‰ PDB).

Specimen	Tooth type	$\delta^{13}C^a$	$\delta^{13}C^b$
Specimens from Juyuandong cave			
19	Lower molar	−15.4	−17.5
20	Lower molar	−16.0	−17.3
21	Upper molar	−16.1	−17.5
22	Lower molar	−15.5	−16.9
Specimens from Longgudong cave			
23	Upper molar	−15.2	−17.2
24	P_3	−14.7	−15.9
25	Upper molar	−16.8	−18.2
26	Lower molar	−13.0	−14.2
Mean(sd)		−14.9 (1.1)	−16.8 (1.2)

[a] Enamel powder without chemical treatment.
[b] Enamel powder after treatment.

Table 3
Comparison of enamel carbon isotope $\delta^{13}C$ (‰ PDB) between *Gigantopithecus*, *Paranthropus*, and *Australopithecus*.

	n	Mean (sd)	Minimum	Maximum	Diet
Gigantopithecus blacki	8	−14.9 (1.1)	−16.8	−13.0	C_3 diet
		−16.8 (1.2)	−18.2	−14.2	
Paranthropus boisei	24	−1.3 (0.9)	−3.4	0.7	Dominant C_4 diet
Paranthropus robustus	18	−7.6 (1.1)	−10.0	−5.9	Mixed C_3 and C_4 diet
Australopithecus africanus	20	−7.0 (1.8)	−11.3	−4.0	Mixed C_3 and C_4 diet

What kinds of C_3 food did *G. blacki* eat? The high frequency of caries indicates a diet rich in carbohydrates or starch (Woo, 1962; Han and Zhao, 2002; Zhao, 2006a). Fifteen carious teeth were identified from the total of 62 molars discovered in Longgudong cave (Zhao, 2006a). Thick enamel and blunt-cusp morphology of buccal teeth are related to the adaptation to feeding on hard objects, such as seeds and nuts. Both pits and scratches of micro-wear were commonly present on the occlusial surface under SEM (Fig. 3), which implies an omnivorous diet. The microwear evidence and the morphological features suggest *G. blacki* had a frugivorous and highly fibrous diet (Daegling and Grine, 1994). Identification of opal phytoliths bonded to the enamel surface of the teeth indicated that *G. blacki* had a varied diet of grasses and fruits (Ciochon et al., 1990). It was also likely *Gigantopithecus* fed on bamboo (C_3 plant) as part of its diet. More detailed analysis is necessary for further interpretation of the diet of the giant ape.

To date, 12 *G. blacki* sites (Pei and Woo, 1956; Woo, 1962; Zhang et al., 1973; Hsu et al., 1974; Zhang et al., 1975; Huang and Fang, 1991; Ciochon et al., 1996; Zheng, 2004; Zhao et al., 2006; Jin et al., 2008; Li et al., 2008; Zhao et al., 2008) have been reported (Fig. 4, Table 4). Mainly based on the biostratigraphical analysis of associated mammalian fauna, their geological ages were estimated as early Early Pleistocene, middle or late Early Pleistocene, and Middle Pleistocene (Table 4, Fig. 4). The typical species of early Early Pleistocene mammalian fauna include *A. microta*, *Cuon dudius*, *Tapirus peii* (in Juyuandong) and *T. sanyuanensis*. In middle to late Early Pleistocene, *Ailuropoda melanoleuca wulingshanensis*, *Cuon javanicus antiquus* and *Tapirus sinensis* are present in Longgudong cave, and Sanhe cave in Chongzuo. *Ailuropoda melanoleuca baconi* and *Megatapirus augustus* are present in Middle Pleistocene fauna such as in Heidong cave, Daxin.

The present fossil records indicate that *Gigantopithecus* was distributed widely during the Early Pleistocene (Fig. 1), not only in the Guangxi area of South China (such as Juyuandong cave in Liucheng, Mohui cave and Chuifeng cave in Tiandong, Sanhe cave in Chongzuo), but north to the Three Gorges Area of the Yangtze River (such as Longgupo site in Wushan and Longgudong cave in Jianshi), and also in the Guizhou Plateau, such as the Baeryan site in Bijie. In the Middle Pleistocene, *Gigantopithecus* withdrew southward to a limited area of South China, mainly in Guangxi Province (Heidong cave in Daxin, Bulalishan cave in Wuming, Nongmoshan cave in Bama), and more southward to Hainan island (Xinchong cave) and North Vietnam (Tham Khuyen cave). No fossil record of Late Pleistocene *Gigantopithecus* has been discovered.

Climate changes of the Pleistocene, and geographical and geological environmental change might have had a strong influence on *Gigantopithecus*. Analysis of Pleistocene sporopollen flora 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 (Tong et al., 1999). Based on the spatial and temporal distribution of the Xigeda and Yuanmou Formations, it was suggested that Yunnan Plateau had risen ~1600 m in the past ca. 1 Ma (Yang et al., 2010). Considering that the Bijie region is located in Guizhou Plateau, connected with the Yunnan Plateau (together called Yun-Gui Plateau), it would have had an altitude much lower in Early Pleistocene than the present 1600 m. A similar situation might also occur in the Three Gorges area, located in the transitional zone from the west Plateau to the east lowland plain. The climate and

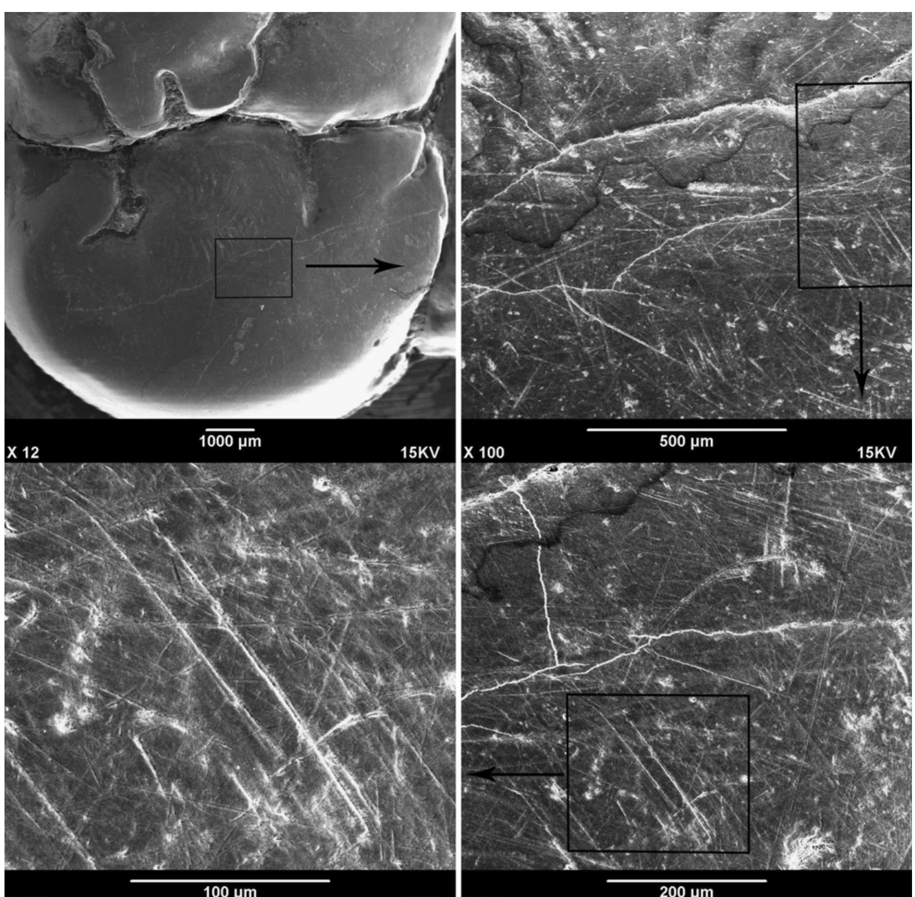

Fig. 3. Microwear by SEM showing the pits and scratches on the protoconid surface of a lower first molar of *Gigantopithecus blacki* from Juyuandong cave.

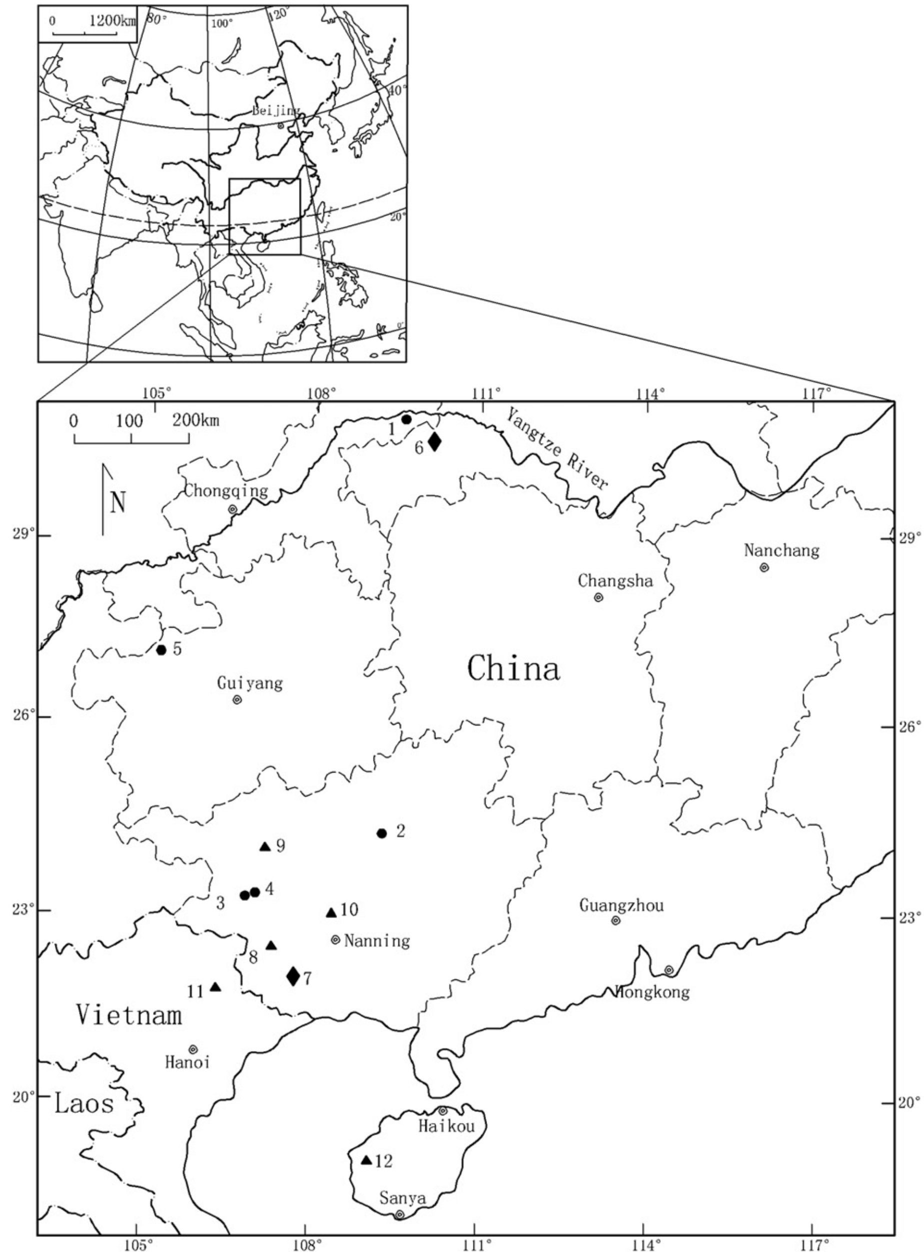

Fig. 4. Distribution map of *Gigantopithecus blacki*: ● early Early Pleistocene ◆ late Early Pleistocene ▲ Middle Pleistocene. 1 Longgupo of Wushan; 2 Juyuandong cave of Liucheng; 3 Chuifeng cave of Tiandong; 4 Mohui cave of Tiandong; 5 Baeryan cave of Bijie; 6 Longgudong cave of Jianshi; 7 Sanhe cave of Chongzuo; 8 Heidong cave of Daxin; 9 Nongmoshan cave of Bama; 10 Bulalishan cave of Wuming; 11 Than Khuyen cave in Vietnam; 12 Xinchong cave of Changjiang.

Table 4
Gigantopithecus blacki sites and their geological age.

Site	Region	Species	Geological age
Juyuandong cave	Liucheng County Guangxi AR	*Ailuropoda microta*	early Early Pleistocene
Longgupo cave	Wushan County Chongqing	*Ailuropoda microta*	early Early Pleistocene
Mohui cave	Tiandong County Guangxi AR	*Ailuropoda microta*	early Early Pleistocene
Chuifeng cave	Tiandong County Guangxi AR	*Ailuropoda microta*	early Early Pleistocene
Baeryan cave	Bijie County Guizhou Province	*Ailuropoda microta*	early Early Pleistocene
Longgudong cave	Jianshi County Hubei Province	*Ailuropoda melanoleuca wulingshanensis*	middle Early Pleistocene
Sanhe cave	Chongzuo County Guangxi AR	*Ailuropoda melanoleuca wulingshanensis*	late Early Pleistocene
Heidong cave	Daxin county Guangxi AR	*Ailuropoda melanoleuca baconi*	Middle Pleistocene
Bulalishan cave	Wuming County Guangxi AR	*Ailuropoda melanoleuca baconi*	Middle Pleistocene
Nongmoshan cave	Bama County Guangxi AR	*Ailuropoda melanoleuca baconi*	Middle Pleistocene
Xinchong cave	Changjiang County Hainan Province	*Ailuropoda melanoleuca baconi*	Middle Pleistocene
Tham Khuyen cave	Lang Son Province northern Vietnam	*Ailuropoda melanoleuca baconi*	Middle Pleistocene

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environmental change during the late Early Pleistocene might have had a strong effect on the habitat and diet of *Gigantopithecus*, and made it withdraw southward into the subtropical forest where the climate was warm and wet.

Study of dental development indicates that *G. blacki* had a longer and slower and more delayed growth pattern, and this implies a lower reproduction rate (Zhao, 2006b), which did not appear to bode well for its population development when the forest habitat became fragmented and deteriorated. The reasons for the extinction of *Gigantopithecus* might also involve humans. *Homo* had evolved and existed in South China since the Early Pleistocene, and several Early Pleistocene sites have been found, such as *Homo erectus* in Yuanmou, and in Jianshi where *Gigantopithecus* fossils coexisted. Enlarging *Homo* populations with increasing intelligence and abilities in tool-making and fire-controlling might apply competitive pressure on *Gigantopithecus* for territory and resources. It is interesting that giant pandas usually coexisted with *Gigantopithecus*, although the territory of giant pandas became larger while *Gigantopithecus* went extinct through the middle to late Pleistocene.

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