



Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

New 400–320 ka *Gigantopithecus blacki* remains from Hejiang Cave, Chongzuo City, Guangxi, South China

Yingqi Zhang^{a,*}, Changzhu Jin^a, Yanjun Cai^b, Reiko Kono^c, Wei Wang^d, Yuan Wang^a, Min Zhu^a, Yaling Yan^a

^a Key Laboratory of Vertebrate Evolution and Human Origin of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

^b State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710075, China

^c Division of Human Evolution, Department of Anthropology, National Museum of Nature and Science, Tsukuba 305-0005, Japan

^d Guangxi Museum of Nationalities, Nanning 530021, China

ARTICLE INFO

Article history:

Available online xxx

ABSTRACT

Gigantopithecus blacki is a typical member of the *Stegodon*–*Ailuropoda* faunal complex (*sensu lato*) that inhabited southern China or, more broadly, mainland Southeast Asia during the Early and Middle Pleistocene. Current evidence indicates that the giant ape became extinct during the Middle Pleistocene. Recently, new remains of *G. blacki* and associated mammalian fossils have been unearthed from a karst cave site, Hejiang Cave, in Chongzuo City, Guangxi, South China. The age of the *Gigantopithecus*-bearing depositional unit is estimated to be 400–320 ka using ²³⁰Th–²³⁴U disequilibrium U-series dating of flowstone samples bracketing the deposits. These finds document the latest occurrence of *Gigantopithecus* and provide potential insights regarding its extinction. Comparisons of dental dimensions between the Hejiang *G. blacki* remains, more than four hundred isolated teeth from Early Pleistocene localities, and over ninety isolated teeth from local drugstores show that the Hejiang teeth are slightly larger in their buccolingual dimensions. In addition, the crowns of the three unerupted upper premolars differ from those of all of the other *Gigantopithecus* material in having more complex crenulations. The differences in dental dimensions and morphology are possibly reflective of dietary responses to environmental changes that eventually led to the extinction of *Gigantopithecus*.

© 2013 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Nearly eighty years have passed since the Dutch paleoanthropologist G. H. R. von Koenigswald first found a huge human-like fossil tooth among the “dragon bones” in a Hong Kong drugstore and named it *Gigantopithecus blacki* (Von Koenigswald, 1935). In the intervening years, three jaws and thousands of teeth of this giant ape species have been collected from cave deposits, mostly in South China, and a wealth of articles have been published by paleoanthropologists on various aspects its paleobiology and evolutionary relationships. The most critical question is its phylogenetic placement. Two principal views have been expressed among earlier workers as to the affinities of *Gigantopithecus*: (1) that it is an aberrant pongine with distinctive dental features (Pei and Woo,

1956; Tung, 1962; Simons and Pilbeam, 1965; Simons and Chopra, 1969; Pilbeam, 1970; Simons and Ettel, 1970; Corruccini, 1975; Szalay and Delson, 1979; Martin, 1990; Kelley, 2002; Cameron, 2003); and more contentiously (2) that the genus is either ancestral to later hominins (Weidenreich, 1945; Eckhardt, 1973, 1975; Robinson and Steudel, 1973; Wang et al., 1981) or an extinct hominin side branch that existed in South East Asia contemporary with *Australopithecus* and *Homo* in Africa (Von Koenigswald, 1952, 1958; Dart, 1960; Woo, 1962; Frayer, 1973; Gelvin, 1980). The evolutionary relationships of *Gigantopithecus* remain unresolved, in large part because of a lack of critical evidence from its cranial and postcranial anatomy. Furthermore, the classical “homoplasy” problem continues to be an impediment to resolving hominoid relationships, especially in regard to *Gigantopithecus* (Wood and Harrison, 2011). In addition, diverse approaches have been applied to reveal other aspects of the paleobiology of *Gigantopithecus*, such as diet (Ciochon et al., 1990; Daegling and Grine, 1994; Kupczik and Dean, 2008; Zhao et al., 2011; Zhao and Zhang, 2013), habitat (White, 1975; Cheng et al.,

* Corresponding author. Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China.
E-mail address: zhangyingqi@ivpp.ac.cn (Y. Zhang).

2006; Zhao et al., 2011), dental caries (Han and Zhao, 2002), body mass (Johnson, 1979), and change in dental size (Zhang, 1982). However, morphological change through time has been largely neglected, mainly as a result of inadequate dating of the cave deposits and difficulties in chronological seriation. Nevertheless, *G. blacki* has been generally thought to survive from the Early to the Middle Pleistocene, a period of more than 1 million years. This raises the question of to what degree the morphology of *Gigantopithecus* changed during this time interval, when other genera in the *Stegodon*–*Ailuropoda* fauna underwent speciation events, such as *Ailuropoda* (Jin et al., 2007) and *Tapirus* (Tong, 2005). Recently, a newly discovered and well-dated *Gigantopithecus*-bearing cave site, Hejiang cave, in Guangxi Zhuang Autonomous Region, South China, provides an opportunity to better understand the evolution and extinction of *G. blacki*.

2. Location and geological context of Hejiang Cave

Guangxi Zhuang Autonomous Region, South China is famous for the discovery of *G. blacki* fossils. In late 1950s Chinese paleontologists from the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica carried out systematic field investigation to collect *in situ* *Gigantopithecus* remains instead of those being purchased from Chinese dispensaries. Meanwhile, three teeth of *Gigantopithecus* were found *in situ* for the first time from a cave in Daxin County (Pei and Woo, 1956), and three mandibles and more than 1000 isolated teeth were unearthed from the *Gigantopithecus* Cave in Liucheng (Pei, 1957a; Pei and Li, 1958; Woo, 1962). The latter collection is still the largest sample of *G. blacki* from a single cave site. Recently, a series of Pleistocene *Gigantopithecus*-bearing cave sites has been discovered in Guangxi (Wang et al., 2005, 2007a,b; Zhao et al., 2008; Jin et al., 2009; Wang, 2009). Hejiang Cave, one of these new sites, was discovered and excavated in 2009. Hejiang Cave (22°17'15.6"N, 107°30'50.6"E) is located on the same Mulan Mountain as Zhiren Cave (Jin et al., 2009; Liu et al., 2010), about 100 km north of the China–Vietnam

boundary, and 100 km southwest of Nanning City, Guangxi Zhuang Autonomous Region in South China (Fig. 1).

The landscape of the Chongzuo area is characterized by a typical and spectacular geomorphology, consisting of peak cluster karst and peak forest karst (Fig. 2A). The so-called “tower karsts” or “inselbergs”, with a maximum elevation ranging from about 240 m to 400 m above sea level (asl), developed in monotonous Devonian–Triassic limestone beds, more than 3000 m thick (Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region, 1997). Numerous caves developed in the limestone at different elevations, most of which contain fossiliferous deposits.

Mulan Mountain is made up of a peak cluster with several karst towers connected together at the base. The opening of the Hejiang Cave is on the northwest side of the mountain at an altitude of 179.4 m asl, about 35 m higher than the Hejiang River valley floor. The cave itself is small, but consists of two distinct chambers. The outer cave is a straight corridor about 6 m long. The inner cave is a small chamber nearly filled with sediments. Initially, they probably belonged to two different cave systems, and were later linked by the penetration of a small opening at the end of the outer cave. The original entrance to the inner cave is thought to be somewhere on the southeast side of the karst tower, but there is no way to know because the passage to the inner cave chamber is filled. Accordingly, the sediments in the inner cave and outer cave are derived from different sources. The sediments of the inner cave would have been transported from the original entrance, not from the outer cave corridor. Only a small block of deposits is left hanging on the cave wall of the outer cave directly below the upper calcitic surface (Fig. 2B, C).

3. Description of the sedimentary deposits

The sedimentary deposits in the inner cave consist of the superimposition of three distinct units (Fig. 2C). Unit 1 is made up of five interbedded layers of argillaceous yellowish-brown sand and grayish-green silt with a total thickness of more than 1.8 m. The

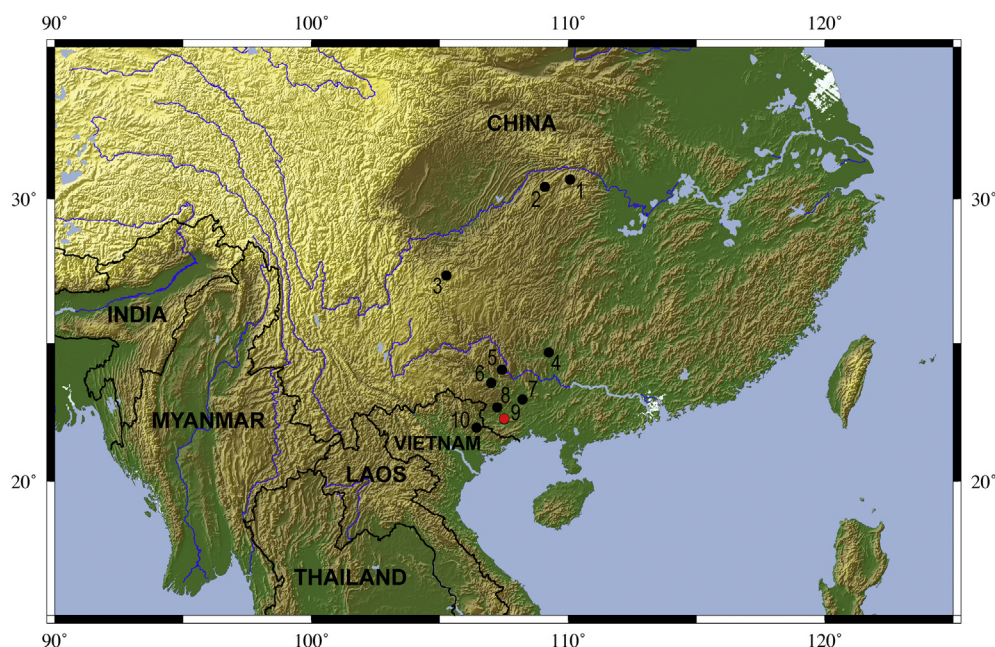


Fig. 1. Location map of Hejiang Cave and the other *Gigantopithecus blacki* localities. 1. Longgudong, Jianshi, Hubei Province (Zheng, 2004); 2. Longgupo, Wushan, Chongqing (Huang and Fang, 1991); 3. Baeryan, Bijie, Guizhou Province (Zhao et al., 2006); 4. *Gigantopithecus* Cave, Liucheng, Guangxi Autonomous Region (Pei, 1957a; Woo, 1962); 5. Nomoshan, Bama, Guangxi Autonomous Region (Chang et al., 1975); 6. Chui Feng Cave (Wang, 2009) and Mohui Cave (Wang et al., 2005), Tiandong, Guangxi Autonomous Region; 7. Bulalishan, Wuming, Guangxi Autonomous Region (Chang et al., 1973); 8. Heidong, Daxin, Guangxi Autonomous Region (Pei and Woo, 1956); 9. Hejiang Cave and Sanhe Cave (Jin et al., 2009), Chongzuo, Guangxi Autonomous Region; 10. Than Khuyen Cave, Lang Son Province, Vietnam (Ciochon et al., 1996).

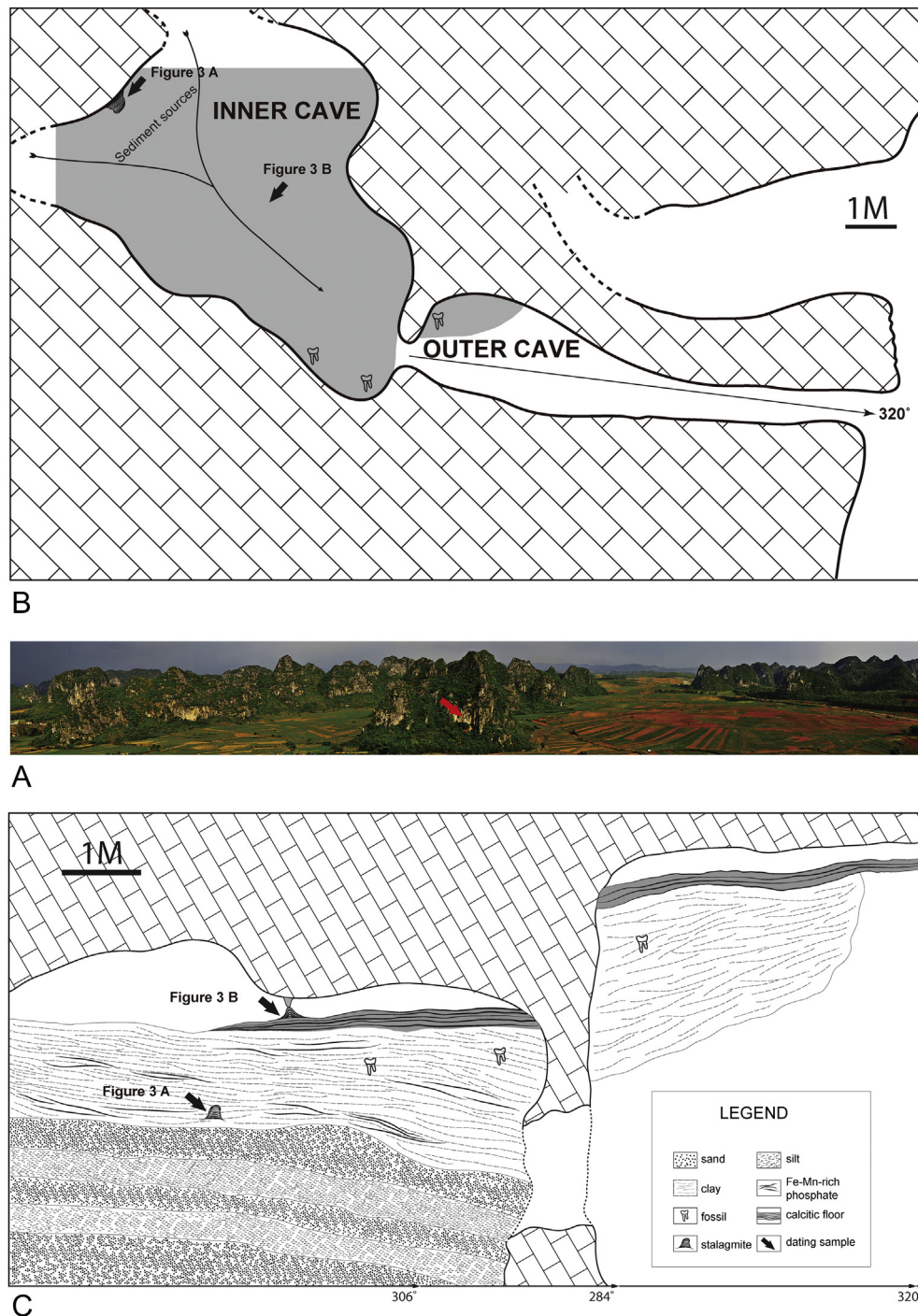


Fig. 2. Landscape of the Mulan Mountain area (A), and plan (B) and section (C) of the Hejiang Cave. A: The arrow points to the location of the entrance of the Hejiang Cave. B and C: The grey areas are the excavation area; the line with arrow heads represents the inferred moving direction of the sediment sources; the two black arrows show the sampling position for the ^{230}Th – ^{234}U Disequilibrium U-series dating (see Fig. 3).

sand and silt beds dip to the northwest at a low angle. There is a paucity of fossils in the basal unit, so excavation did not extend to the bottom of this unit. The presence of a well-developed unit of interbedded sands and silts at the base of the cave and the absence of pebbles or coarse-grained sediments suggest that there was very little water circulation inside the cave. Unit 2 is a fossiliferous brownish-red clay that overlies Unit 1, with a thickness of 0.9–1.9 m. Abundant dark-colored Fe–Mn-rich phosphate strips and pisoliths can be seen in this unit. The base of Unit 1 and the overlying Unit 2 appear to be superimposed conformably without a

major erosional event. All of the paleontological remains, mostly fossil teeth, come from Unit 2. Fe–Mn-rich pisoliths, arenitic material, as well as fossil teeth, suggest that powerful water flows transported them into the cave. At the bottom of Unit 2, a stalagmite adhering to the south wall, about 20 cm above the lower boundary, was sampled for dating. Unit 3 is a layer of calcite encrusting Unit 2, with a maximum thickness of about 25 cm, and linked to the cave ceiling by speleothems at the center of the inner cave chamber. Another dating sample was collected where Unit 3 meets the ceiling.

The outer cave deposits consist of two sedimentary units (Fig. 2B, C). Unit 1 is a small block of arenitic brownish-red clay with calcareous breccia adhering to the cave wall directly below Unit 2, which is a layer of calcite containing no remains with a maximum thickness of about 20 cm. Only one broken molar of *Stegodon* and several teeth of *G. blacki* were recovered from Unit 1 (Table 2).

(Fig. 3A, Table 1), in which the youngest date provides a maximum age of ~400 ka for Unit 2. The Unit 2 sediments are capped by a series of calcite deposits in which few stalagmites formed, and these joined together with the flowstone and stalactites from above (Fig. 3B, Table 1). U-series dates obtained from the lowest stalagmite yielded ages correlated with marine isotope stage (MIS) 9–8

Table 1
The dating results.

Sample number	^{238}U (ppb)	^{232}Th (ppt)	$^{230}\text{Th}/^{232}\text{Th}$ (atomic $\times 10^{-6}$)	$^{230}\text{Th}/^{238}\text{U}$ (activity)	$\delta^{234}\text{U}^a$ (measured)	^{230}Th Age (ka) (uncorrected)	$\delta^{234}\text{U}_{\text{initial}}^b$ (corrected)	^{230}Th Age (ka BP) ^c (corrected)
HJ-3A-1	51.1 $\pm$ 0.1	722 $\pm$ 2	1267 $\pm$ 7	1.0843 $\pm$ 0.0054	107.1 $\pm$ 3.7	325.4 $\pm$ 12.2	268.3 $\pm$ 13.5	325.0 $\pm$ 12.2
HJ-3A-2	48.8 $\pm$ 0.1	989 $\pm$ 2	880 $\pm$ 4	1.0806 $\pm$ 0.0047	105.3 $\pm$ 4.1	322.9 $\pm$ 11.6	261.9 $\pm$ 13.6	322.3 $\pm$ 11.6
HJ-3A-3	77.8 $\pm$ 0.1	1615 $\pm$ 4	802 $\pm$ 4	1.0081 $\pm$ 0.0045	88.6 $\pm$ 3.2	257.2 $\pm$ 5.7	183.0 $\pm$ 7.2	256.5 $\pm$ 5.7
HJ-S-1	107.9 $\pm$ 0.3	6799 $\pm$ 137	275 $\pm$ 6	1.0493 $\pm$ 0.0038	54.4 $\pm$ 2.4	409.2 $\pm$ 19.9	171.9 $\pm$ 12.3	407.6 $\pm$ 19.9
HJ-S-2	64.1 $\pm$ 0.1	65,481 $\pm$ 1311	17.1 $\pm$ 0.3	1.0583 $\pm$ 0.0034	48.4 $\pm$ 2.5	513.7 $\pm$ 50.0	190.6 $\pm$ 25.9	485.5 $\pm$ 50.0
HJ-S-3	65.3 $\pm$ 0.1	20,835 $\pm$ 417	53.5 $\pm$ 1.1	1.0357 $\pm$ 0.0024	31.1 $\pm$ 2.7	532.4 $\pm$ 59.3	136.2 $\pm$ 24.9	523.8 $\pm$ 59.3

The chemical procedures were similar to those described in Edwards et al. (1987) and accomplished in the clean lab of Minnesota Isotope Laboratory. The measurements were run on inductively coupled plasma mass spectrometers, Thermo Finnigan Neptune, using procedures described in Cheng et al. (2009a, 2009b). Analytical errors are 2 of the mean.

^a $\delta^{234}\text{U} = ([^{234}\text{U}/^{238}\text{U}]_{\text{activity}} - 1) \times 1000$.

^b $\delta^{234}\text{U}_{\text{initial}}$ was calculated based on ^{230}Th age (T), i.e., $\delta^{234}\text{U}_{\text{initial}} = \delta^{234}\text{U}_{\text{measured}} \times e^{\lambda^{234}\text{U} \cdot T}$. Corrected ^{230}Th ages assume the initial $^{230}\text{Th}/^{232}\text{Th}$ atomic ratio of $4.4 \pm 2.2 \times 10^{-6}$. Those are the values for a material at secular equilibrium, with the bulk earth $^{232}\text{Th}/^{238}\text{U}$ value of 3.8. The errors are arbitrarily assumed to be 50%.

^c B.P. stands for "Before Present" where the "Present" is defined as the year 1950 A.D.

4. ^{230}Th – ^{234}U Disequilibrium U-series dating

The stalagmite intercalated between Unit 3 and Unit 2 in the Inner Cave provided three successive U-series dates of 407.6 ± 19.6 ka, 485.5 ± 43.9 ka and 523.8 ± 54.9 ka from the top

(i.e., 325.0 ± 12.1 ka, 322.4 ± 11.6 ka and 256.6 ± 5.6 ka). The oldest age, from the bottom of the stalagmite, provides a date of 325.0 ± 12.1 ka, which bounds a minimum age for Unit 2 of ~320 ka. Therefore, we can conclude that the fossil remains were buried during the period from ~400 ka to 320 ka.

Table 2
Faunal list and specimen.

Species	IVPP no.	N	Specimen (field no.)
<i>The Inner Cave</i>			
Primates			
<i>Gigantopithecus blacki</i>	PA1573	47	LDP ³ (97), LDP ⁴ (88), RDP ⁴ (91), LI ¹ (87), LP ³ (90), RP ³ (76), RP ⁴ (75), LM ¹ (93), LP ₃ (89), LM ₂ (22), LM ₁ (165.1), RM ₁ (165.2), RM ₂₋₃ (165.3)
<i>Nomascus</i> sp.	V18903	1	LM ^{1/2} (3)
<i>Macaca</i> sp.	V18904	26	LM ₁ (4, 12, 78), RM ₂ (85, 94), RM ₃ (28, 92, 153), LM ₃ (9), RM ₁ (10), RM ₂ (17), RM _{1/2} (77), LM ₂ (156), LC ¹ (27, 14, 131.7), RC ₁ (80, 81), RP ₃ (79), RP ⁴ (95, 84), LP ⁴ (8), LP ₃ (2), LC ₁ (18), LI ₁ (20), RC ₁ (144.2)
<i>Trachypithecus</i> sp.	V18905	7	RM ₁ (36, 32), LM ^{1/2} (16), LM ₃ (11), LP ₄ (33), LM ₃ (15), RM ₃ (30, 31)
Proboscidea			
<i>Stegodon orientalis</i>	V18906	2	Molar fragments (42.1, 42.2)
Carnivora			
<i>Ursus</i> sp.	V18907	1	RC ₁ (61.2)
<i>Panthera pardus</i>	V18908	8	LP ₃ (127.6), RP ₃ (108.6), LP ⁴ (129), RP ⁴ (39.1, 108.5), RP ₄ (39.2), RC ₁ (39.3, 127.5),
<i>Panthera tigris</i>	V18909	2	RP ⁴ (44), RC ₁ (127.5)
<i>Hyaena</i> sp.	V18910	1	RP ₃ (138)
<i>Ailuropoda baoni</i>	V18911	1	LM ¹ (61.1)
<i>Meles</i> sp.	V18912	3	LP ₃ (137), LM ₁ (139.1), LP ⁴ (117.1)
<i>Melogale</i> sp.	V18913	1	Right mandible corpus fragment (54)
Perissodactyla			
<i>Tapirus sinensis</i>	V18914	1	RM ₂ (98)
<i>Rhinoceros sinensis</i>	V18915	11	RDP ₃ (123.1, 40.3), RP ₃ (119.5), LM ₁ (116.2), LM ₂ (116.1), RM ₂ (40.1, 40.2), RDP ¹ (118), RDP ³ (126.2, 40.4), RM ¹ (126.1),
Artiodactyla			
<i>Sus scrofa</i>	V18916	51	RM _{1/2} (37.6), LM ₃ (37.4), LM ₃ (37.1, 101.1, 119.1, 119.2), RM ₃ (119.3), LM ^{1/2} (37.7, 64.8, 141.2, 144.1, 108.1), RM ^{1/2} (37.8, 73.2), LM ₃ (37.5, 37.9), RM ₃ (37.2, 37.3, 109, 141.1), LC ₁ (122), RC ₁ (37.14), LP ₁ (108.3), RP ₁ (131.4), LP ₂ (108.2), RP ₂ (127.4), RP ₃ (131.1), LP ₄ (120.1, 127.1, 43.4), RP ₄ (37.17, 64.11, 131.2, 131.5, 43.1), LI ₁ (64.12, 64.13), RI ₁ (73.6, 43.7), LI ¹ (141.3), LP ₃ (141.4, 43.2), RP ¹ (64.10), RP ² (139.2, 141.5), RP ₁ (101.2), LP ₃ (45.2), LP ⁴ (103.1, 73.3), RP ⁴ (103.3, 45.1),
<i>Sus xiaozhu</i>	V18917	6	LM _{1/2} (37.11), RM _{1/2} (37.12, 127.2), RM ^{1/2} (103.4, 64.9, 62.4),
<i>Muntiacus</i> sp.	V18918	24	LP ₂ (45.3), RP ₃ (150.10), LM ₁ (41.7, 41.9, 41.16), RM ₁ (41.13), LM ₂ (41.8), LM ₃ (120.4), RM ₃ (62.2), LP ² (41.2), LP ₃ (41.20), RP ⁴ (59.1), LM ² (41.4), RM ² (41.10, 41.17, 130.5, 130.6), LM ₃ (150.5, 41.11, 64.6), RM ₃ (150.8, 41.14, 159, 73.8),

Table 2 (continued)

Species	IVPP no.	N	Specimen (field no.)
<i>Rusa cf. unicolor</i>	V18919	32	RDP ² (41.15), LP ₂ (43.3, 43.5), RP ₂ (41.3, 131.3), RDP ₄ (130.1, 120.3), LP ₄ (41.1), LM ₁ (41.6, 150.7, 64.1, 64.2, 38.3, 121.1), RM ₂ (150.3, 64.3, 38.4, 38.6, 140), LM ₃ (41.5), RM ₃ (150.1, 150.2), LDP ⁴ (130.7), RDP ⁴ (130.2, 106), RP ³ (64.5), LM ¹ (143.1, 121.2), LM ² (150.4, 130.4), RM ² (62.1), RM ³ (130.3),
<i>Babulus</i> or <i>Bibos</i> sp.	V18920	18	LDP ₄ (38.8), LP ₃ (151), LP ₄ (38.5), LM _{1/2} (38.9, 38.10, 38.12), RM _{1/2} (105.3, 105.6), LM ₃ (106.3, 38.15),
<i>Megalovis</i> <i>guangxiensis</i>	V18921	2	RM ₃ (132), RDP ² (38.11), LP ³ (105.1), LM ^{1/2} (106.4, 38.16), RM ^{1/2} (106.1, 106.2, 38.14),
<i>The Outer Cave</i>			
Proboscidea		1	
<i>Stegodon orientalis</i>	V18922	1	Molar fragment (74 with 2 plates)
Primates		4	
<i>Gigantopithecus blacki</i>	PA1574	4	LI ² (26), RI ² (25), RC ₁ (24), RP ₃ (23),

5. Fauna

The Hejiang Cave fauna includes primates (i.e., macaques, colobines, gibbons and *G. blacki*), a range of ungulates (i.e., cervids, bovids, suids, tapir and rhino), carnivores (i.e., mustelids, hyena, tiger, leopard, bear and giant panda), and *Stegodon* (Table 2, Figs. 4 and 5). It is typical of the *Stegodon*–*Ailuropoda* faunal complex,

which is conventionally thought to be indicative of the Middle Pleistocene (Matthew and Granger, 1923; Colbert and Hooijer, 1953; Pei, 1957b; Kahlke, 1961). The numerical dating results, which bracket the age of the Hejiang Cave fauna between ~400 ka and ~320 ka, are consistent with this conclusion. The fauna is almost entirely represented by isolated teeth, some of which, especially the roots, were evidently gnawed by porcupines. Although porcupines are not represented in the fauna, they are the most likely accumulating agent for the bone assemblage. Secondary washing of fossil material into the original cave or porcupine burrows in the deeper parts of cave are also likely to have contributed to the accumulation of bones. The presence of *Stegodon*, *Rhinoceros*, and *Tapirus* in the fauna indicates that the environment was a mixed woodland, while the occurrence of giant panda and colobine monkey suggests some more densely forested areas.

6. *G. blacki* remains

A total of 17 specimens from Hejiang Cave are assigned to *G. blacki*. Except for 165.3, a fragmentary right mandibular corpus with M₂₋₃, all other specimens are isolated teeth. Measurements of the teeth are presented in Table 3.

Table 3

Measurements of *G. blacki* remains.

Tooth	No.	MD	MAXOB	MAXMD	BL	PP
LdP ³	97	15.5			18.6	
LdP ⁴	88	18.8			19.3	
RdP ⁴	91	18.5				
LI ¹	87	4.7			16.42	
LI ²	26	9.4			10.7	
LI ₂	25	8.8			10.6	
RC ₁	24		16.8			11.9
LP ³	90			17.1		
RP ³	76			16.5		
RP ⁴	75	16.1				
RP ₃	23		22.0			16.5
LP ₃	89		25.0			20.1
LM ^{1/2}	93	21.1			26.8	
LM ₂	22					
LM ₁	165.1	24.5			24.7	
RM ₁	165.2	23.7			23.2	
RM ₂	165.3	24.4			24.3	
RM ₃	165.3	24.7			24.4	

MD, mesiodistal length; BL, buccolingual breadth; MAXMD, maximum mesiodistal diameter of P³ taken at buccal crown; MAXOB, maximum oblique diameter of crown; PP, maximum diameter perpendicular to MAXOB.

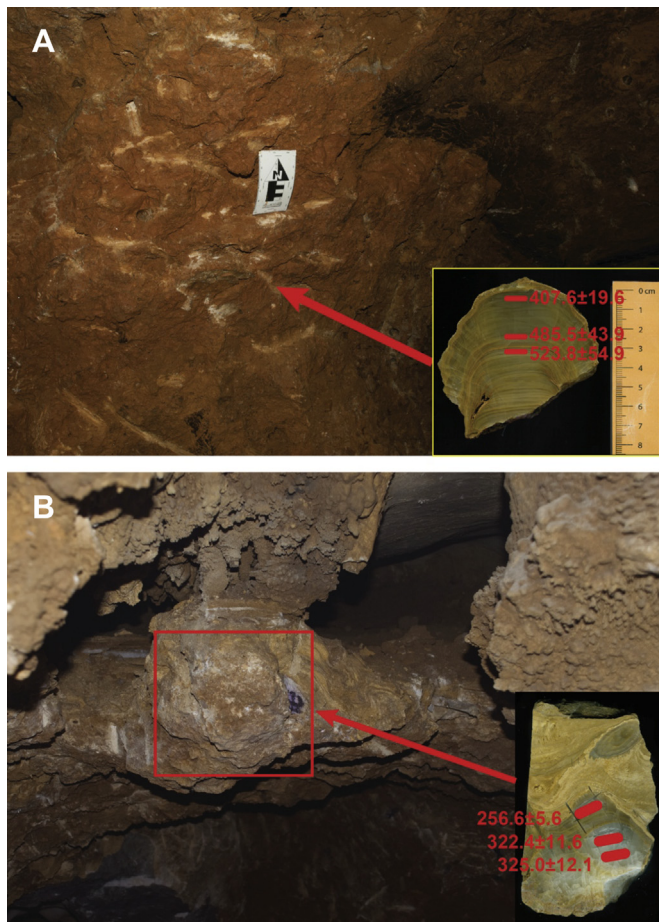


Fig. 3. Positions and ages of the U-series dating samples in the section. A. stalagmite collected below Unit 2. B. calcite deposits and stalagmites overlying Unit 2. It is stratigraphically parallel to Unit 3. The insets show the section of the stalagmites, the position of dating samples and the ages. The samples were measured by using the new generation ²³⁰Th–²³⁴U dating method on Thermo-Finnigan Neptune and all of the ages are in stratigraphic order within the dating error (2σ).

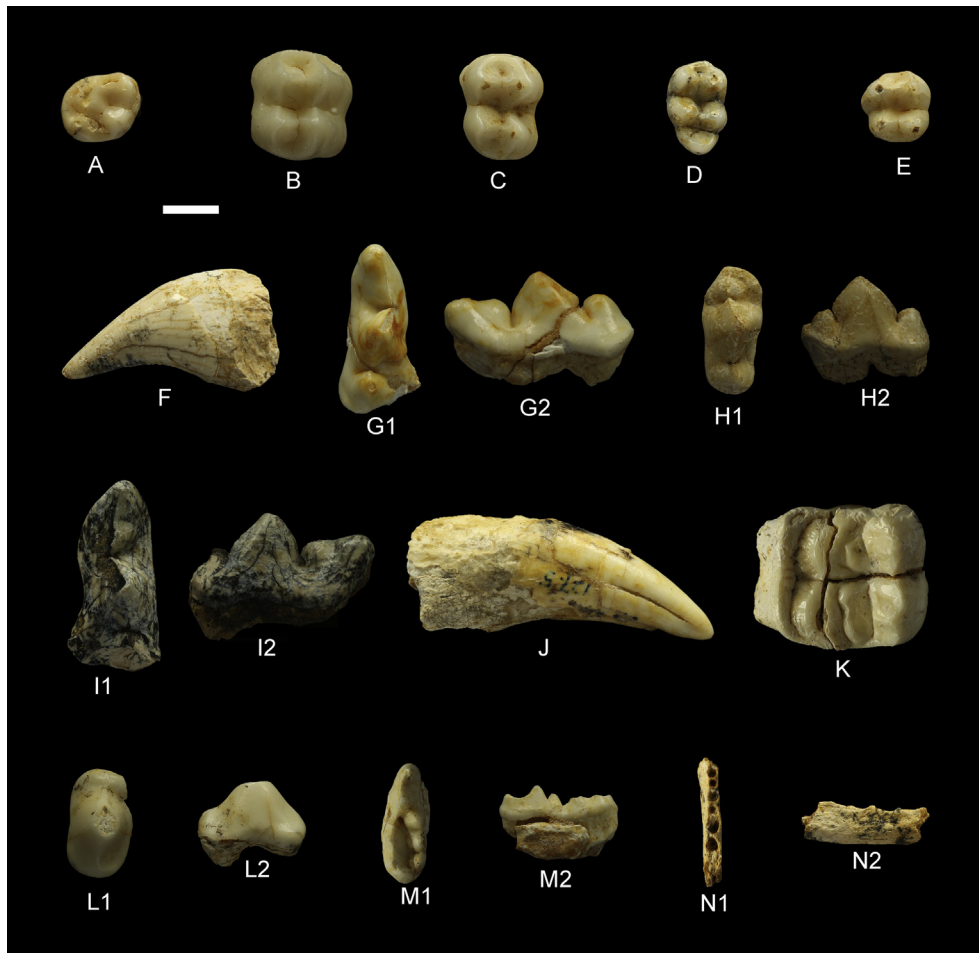


Fig. 4. Representative specimens from the Hejiang Cave fauna: Primates and Carnivora (scale bar = 0.5 cm for A–E, 1 cm for the others). A. *Nomascus* sp.: LM^{1/2} (3), B. *Macaca* sp.: RM² (85), C. *Macaca* sp.: RM_{1/2} (77), D. *Trachypithecus* sp.: RM₃ (30), E. *Trachypithecus* sp.: RM¹ (36), F. *Ursus* sp.: RC₁ (61.2), G. *Panthera pardus*: LP⁴ (129), H. *Panthera pardus*: RP₄ (39.2), I. *Panthera tigris*: RP⁴ (44) [1. occlusal view, 2. buccal view], J. *Panthera tigris*: RC¹ (127.5), K. *Ailuropoda baoni*: LM¹ (138), L. *Hyaena* sp.: RP₃ (138), M. *Meles* sp.: LM₁ (139.1), N. *Melogale* sp.: right mandible corpus fragment (54).

Deciduous teeth ($n = 3$): The three roots of the left dP³ (97) are well preserved. They diverge widely with the distal two roots fused together. Three of the four cusps, with the exception of the metacone, have been worn and expose dentine. The mesial fovea is well developed, with the mesial margin expanded mesially. Both the left and right dP⁴ (88 and 91, respectively) only have part of the crown preserved. The morphology is similar to that of the upper molars, but they are smaller. A secondary cusplet is developed between the paracone and the protocone, which, together with the mesial fovea, make the occlusal outline of the tooth trapezoidal. Both dP⁴s are in the early stage of wear, with dentine exposure only at the tip of the protocone.

Incisors ($n = 3$): The left I¹ (87), an unerupted germ, is concave in lingual view. Well-developed ridges run along the mesial and distal margins of the lingual face of the crown. Several minor ridges interrupt the mesial and distal marginal ridges at their bases. Three small mammelons can be seen on the incisal edge. The left I² (26) is heavily worn, but the vestige of the lingual cingulum can still be observed. The left I₂ (25) has a sloping incisal edge toward the cervix on the distal half. There is no cingulum, fovea, or marginal ridges.

Lower canine ($n = 1$): The right lower canine (24) of a presumptive female individual with moderate wear is buccolingually compressed, relatively small in size and low crowned. No distinct mesial and distal ridges are observed. On the disto-

buccal wall, there is a distal fovea filled with interlaced wrinkles basally, and a honing facet for the upper canine on the apical aspect.

Upper premolars ($n = 3$): All three upper premolars, left P³ (90), right P³ (76), and right P⁴ (75), are unerupted germs at an early stage of root formation. They all have the same basic morphology with the paracone much larger and more elevated than the protocone, and the enamel surface heavily wrinkled. The mesially protruding parastyle makes the occlusal outline of the two P³s triangular, while that of the P⁴ is oval.

Lower premolars ($n = 2$): The two P₃s vary greatly in size, with the left P₃ (89) being much larger than the right P₃ (23), and is probably indicative of sexual dimorphism. The P₃s are bicuspid. The protoconid and the metaconid are subequal in size, and separated by a mesio-distally oriented groove. The groove terminates at the talonid basin distally and at the anterior fovea mesially. The roots of the right P₃ have been completely gnawed by porcupines, while more than 1 cm of those of the right P₃ (89) are preserved after porcupine gnawing.

Upper molars ($n = 1$): The only upper molar, a left M¹ (93), was freshly erupted with only slight wear, but all four cusp have suffered damage by dental caries and/or erosion to various degrees, and this has created a cavity that penetrated the enamel in the middle of the paracone and metacone. The roots are nearly completely gnawed by a porcupine.

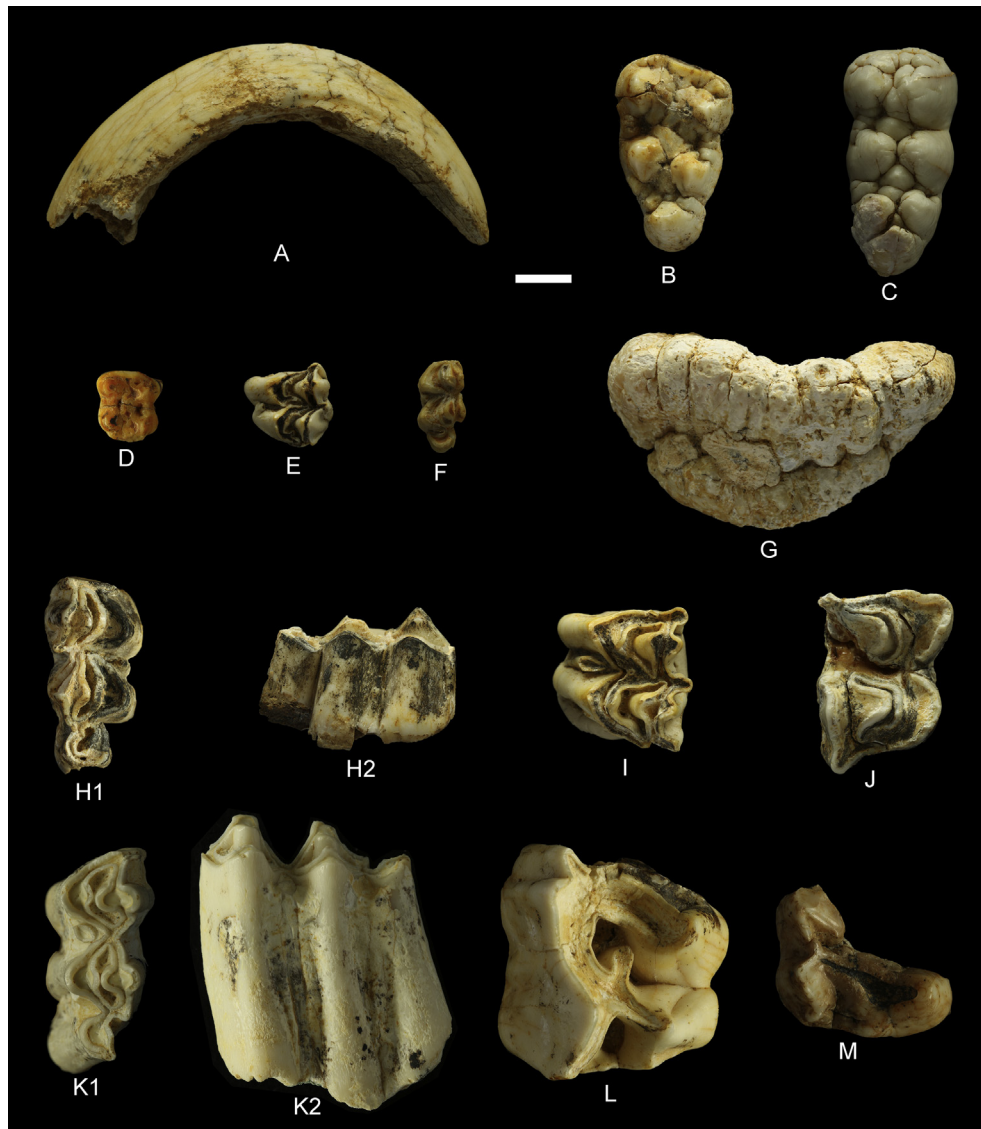


Fig. 5. Representative specimens from the Hejiang Cave fauna: Artiodactyla, Perissodactyla and Proboscidea (scale bar = 1 cm). A. *Sus scrofa*: LC₁ (122), B. *Sus scrofa*: RM³ (37.2), C. *Sus scrofa*: LM₃ (119.2), D. *Sus xiaozhu*: RM_{1/2} (37.12), E. *Muntiacus* sp.: LM³ (150.5), F. *Muntiacus* sp.: LM₃ (120.4), G. *Stegodon orientalis*: molar fragment (42.1), H. *Rusa* cf. *unicolor*: RM₃ (150.1), I. *Rusa* cf. *unicolor*: LM² (130.4), J. *Megalotis guangxiensis*: RM¹ (105.2), K. *Babulus* or *Bibos* sp.: RM₃ (132), L. *Rhinoceros sinensis*: RM¹ (126.1), M. *Tapirus sinensis*: RM² (98).

Lower molars ($n = 5$): The left M₂ (22) has only its crown preserved. Among the cuspids, the protoconid has been damaged, and the enamel on the protoconid and the hypoconid has been penetrated by wear with exposure of dentine. The left M₁ (165.1) has undergone moderate wear with dentine exposure at the tip of the protoconid. The occlusal outline is somewhat rectangular. The metaconid is the largest and most elevated cuspid. Lingual bulging and buccal flare are weak. On the buccal side, the enamel surface becomes slightly roughened because of dental caries and/or erosion. The roots of this tooth have been gnawed by a porcupine and only a small remnant remains near the cervix. The right M₁ (165.2) bears nearly the same morphology as 165.1, but the crown is more worn with dentine exposure at the tips of the protoconid and hypoconid, and the roots are preserved. Dental caries and/or erosion only occur at the bucco-distal corner of the tooth. The right M₂ and M₃ (165.3) are preserved in the fragmentary mandibular corpus. The occlusal surface and the buccal face of the crown are damaged by heavy dental caries and/or erosion, but wear can still be observed on the undamaged portion of the cuspids. Dentine

exposure only occurs on the protoconid of M₂, and at least the metaconid, hypoconulid and entoconid of M₃ are unworn. The wear on the protoconid and hypoconid are not clear because of dental caries and/or erosion. Buccal flare is weak. Lingual bulging tends to increase from M₂ to M₃. Porcupine gnawing marks are evident on the ventral side of the corpus, and only a small portion of bone is preserved below M₂₋₃. All of the roots of M₂₋₃ have been gnawed by porcupine to varying degrees.

7. Comparisons and discussion

The Hei (literally means “black”) Cave, Daxin, Guangxi (Pei and Woo, 1956) is famous for its first discovery of *in situ* *G. blacki* specimens. Rink et al. (2008) dated the Hei Cave faunal assemblage using the coupled ESR/²³⁰Th/²³⁴U methods at 380–310 ka, based on a primate tooth sample, DX3a. They considered the results to document the last known occurrence of *G. blacki*. However, there is no way to be certain if the date for the DX3a sample can be used to restrict the age of *G. blacki* from Hei Cave, because it is possible that

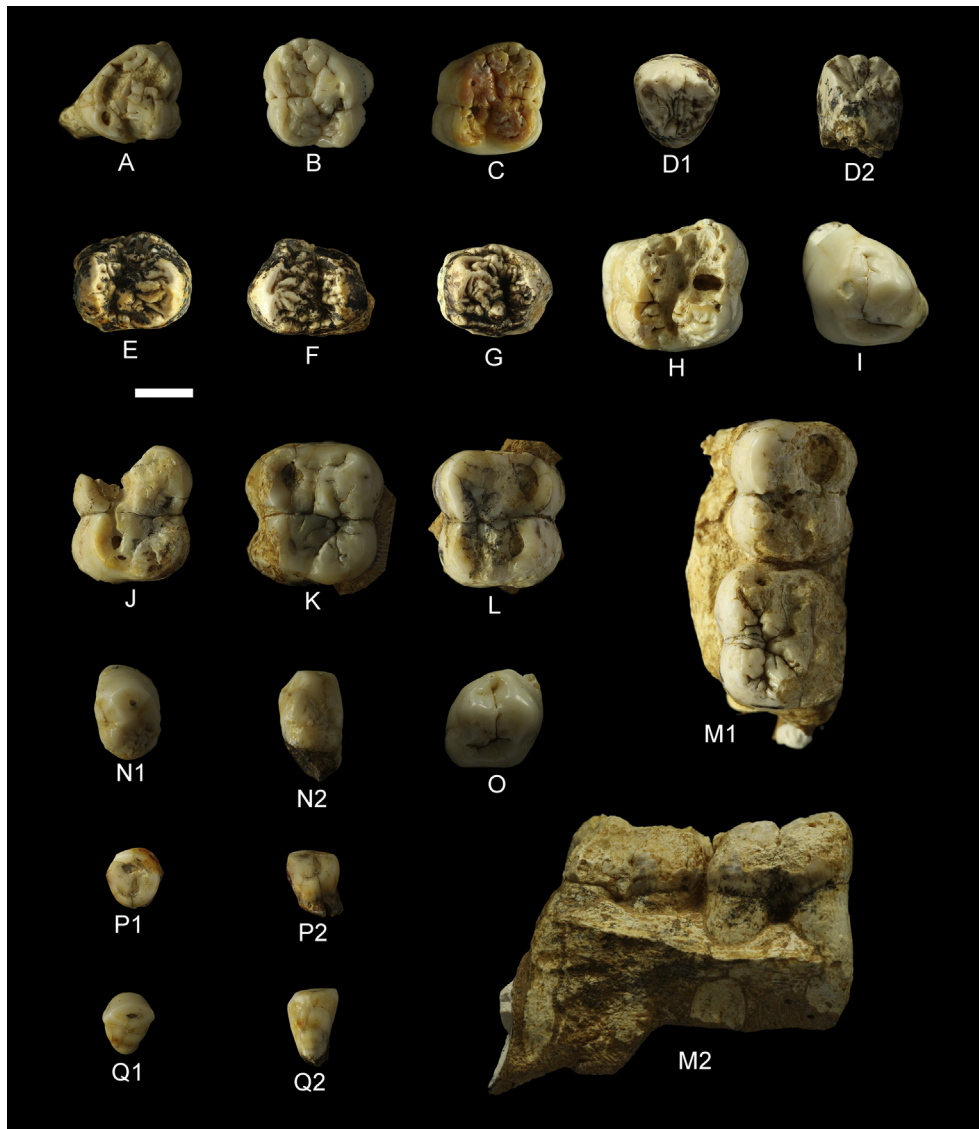


Fig. 6. *Gigantopithecus blacki* specimens from the Hejiang Cave (scale bar = 1 cm). Inner cave: A. LDP³ (97), B. LDP⁴ (88), C. RDP⁴ (91), D. LI¹ (87) [1. occlusal view, 2. lingual view], E. LP³ (90), F. RP³ (76), G. RP⁴ (75), H. LM¹ (93), I. LP³ (89), J. LM₂ (22), K. LM₁ (165.1), L. RM₁ (165.2), M. RM₂₋₃ (165.3) [1. occlusal view, 2. lingual view] Outer cave: N. RC₁ (24) [1. occlusal view, 2. distal view], O. RP₃ (23), P. LI² (26) [1. occlusal view, 2. lingual view], Q. RI² (25) [1. occlusal view, 2. lingual view].

the DX3a tooth came from a different stratigraphic unit. Rink et al. (2008) also dated the Bulalishan Cave faunal assemblage of Wuming (Chang et al., 1973), another well known Middle Pleistocene *G. blacki* site, at 720–480 ka using the same methods. The dating results for the Bulalishan faunal assemblage have the same problem as those for Hei Cave. The well-dated ~400–320 ka *G. blacki* deposits from the Hejiang Inner Cave provide firm evidence to support a late Middle Pleistocene occurrence. It is now possible to infer that the latest occurrence of this giant ape is at least 75 ky younger than the 475 ka *G. blacki* remains from Tham Khuyen Cave in Vietnam (Ciochon et al., 1996). These new results provide additional insight into the timing of the extinction of *Gigantopithecus*.

Comparisons of dental dimensions can be made between *G. blacki* from the Hejiang Inner Cave and those from the early Pleistocene sites of Sanhe Cave, Chongzuo, Guangxi (Zhao et al., 2008; Jin et al., 2009), Longu Cave, Jianshi, Hubei (Hsu et al., 1974; Zheng, 2004), *Gigantopithecus* Cave, Liucheng, Guangxi (Pei, 1957a; Pei and Li, 1958; Woo, 1962). In addition to excavated materials, *Gigantopithecus* specimens of unknown age and provenance

from local drugstores in Guangxi, Guangdong and Hubei (Pei and Woo, 1956; Hsu et al., 1974) have been remeasured and included in the comparisons. The results (Fig. 7) show that the teeth of *G. blacki* from the Hejiang Inner Cave are slightly larger in their buccolingual dimensions than those from the three Early Pleistocene localities. The drugstore collection displays a similar pattern of larger buccolingual dimensions than that found in Early Pleistocene specimens, except that there is one specimen from the Guangdong drugstore collection (Fig. 7D) that is larger in its buccolingual dimension than one of the three Hejiang Inner Cave M_{1/2}s. Zhang (1982) argued that the dental dimensions of *G. blacki* tends to become larger from Early Pleistocene to Middle Pleistocene based on statistical analysis of the *G. blacki* teeth from Liucheng and later localities. The present results support this argument, but further analyses are needed to reach a definitive conclusion.

No evident morphological differences can be observed on the molars of *G. blacki* from the Hejiang Inner Cave compared to other specimens. However, distinctions may be obscured by heavy wear (Fig. 6J, K, L) or dental erosion (Fig. 6H, M1). Nevertheless, the

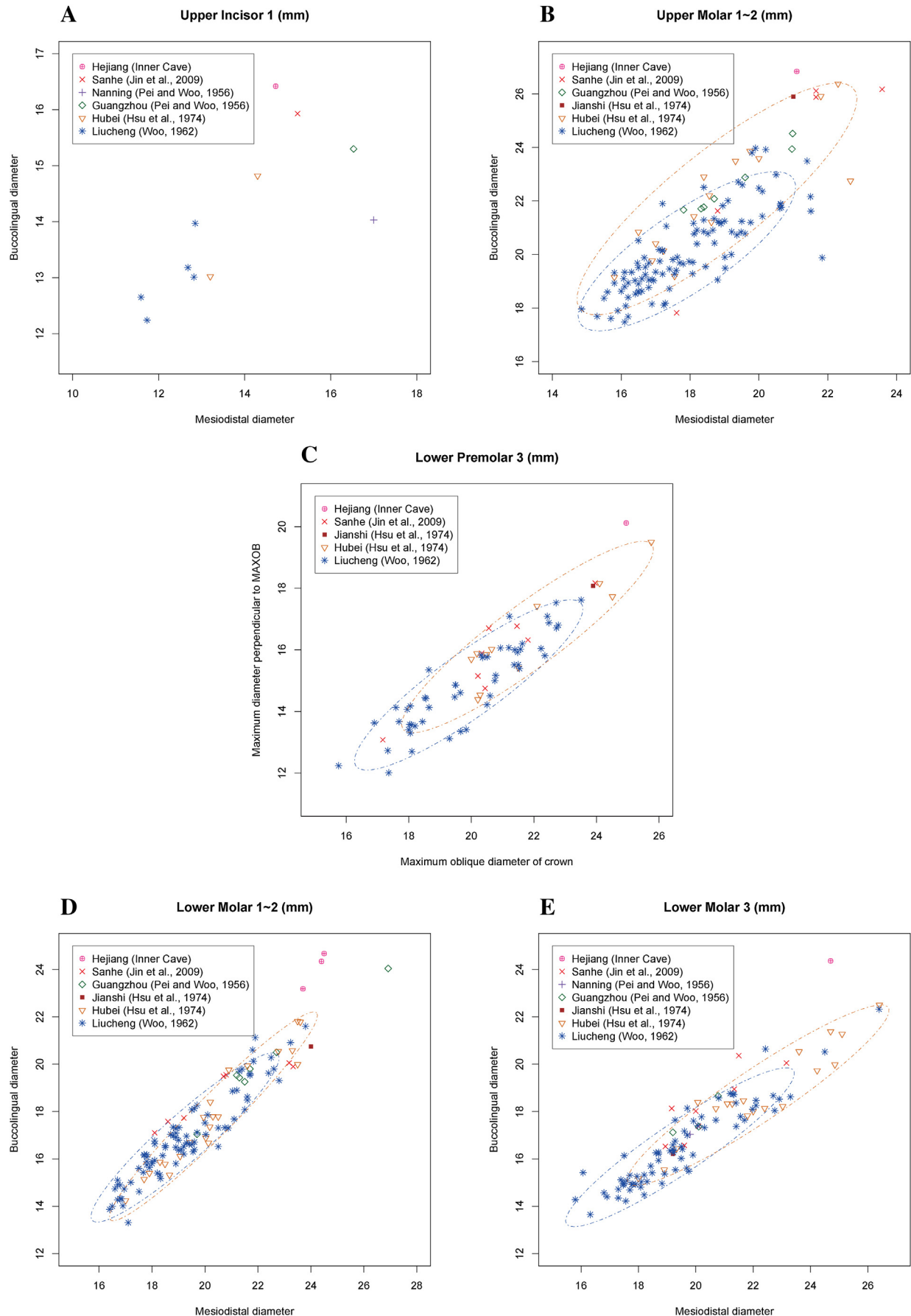


Fig. 7. Comparisons of dental dimensions of *Gigantopithecus blacki* from the Hejiang Cave and those from other localities.

crowns of the three unerupted upper premolars are distinctive in having more complex crenulations. The greater complexity of the upper premolar morphology of *G. blacki* from Hejiang Inner Cave probably indicates a morphological difference from earlier samples. Several previous workers have proposed that the extinction of *G. blacki* occurred at ~380–310 ka (Rink et al., 2008), 0.3 Ma (Wang, 2009), or at the end of the Middle Pleistocene (Zhao and Zhang, 2013). If this is indeed the case, the well-dated ~400–320 ka *G. blacki* material from the Hejiang Cave is sampling a population that was nearing its extinction. The morphological changes that can be observed on the teeth at this time might possibly be reflective of a dietary response to environmental changes that eventually led to the extinction of this giant ape.

Acknowledgments

We thank Yi-Hong Liu, Zhi-Lu Tang, Qiu-Yuan Wang, Fu-qiao Shi, Wei-Min Zheng for their hard work during the excavation of Hejiang Cave. The excavations at Hejiang Cave and the work in this paper have been supported by the Key Research Program of the Chinese Academy of Sciences (kzzd-ew-03), the National Science Fund for Talent Training in Basic Science (J1210008), National Natural Science Foundation of China (41072013) and the Program of China Geological Survey (1212011220519).

References

- Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region, 1997. Stratigraphy (Lithostratigraphy) of Guangxi Zhuang Autonomous Region. China University of Geosciences Press, Wuhan.
- Cameron, D.W., 2003. A functional and phylogenetic interpretation of the late Miocene Siwalik hominid *Indopithecus* and the Chinese Pleistocene hominid *Gigantopithecus*. *Himalayan Geology* 24, 19–28.
- Chang, Y., Wu, M., Liu, C., 1973. New discovery of *Gigantopithecus* teeth from Wuming, Kwangsi. *Chinese Science Bulletin* 18, 130–133.
- Chang, Y., Wang, L., Dong, X., Chen, W., 1975. Discovery of a *Gigantopithecus* tooth from Bama District in Kwangsi. *Vertebrata Palasiatica* 13 (3), 148–154.
- Cheng, J., Zheng, S., Gao, Z., Zhang, Z., Feng, X., Wang, X., 2006. Natural environment during the living period of the early human and gigantic ape in west Hubei. *Acta Geologica Sinica* 80 (4), 473–480.
- Cheng, H., Fleitmann, D., Edwards, R.L., Wang, X.F., Cruz, F.W., Auler, A.S., Mangini, A., Wang, Y.J., Kong, X.G., Burns, S.J., Matter, A., 2009a. Timing and structure of the 8.2 kyr BP event inferred from $\delta^{18}\text{O}$ records of stalagmites from China, Oman, and Brazil. *Geology* 37, 1007–1010.
- Cheng, H., Edwards, R.L., Broecker, W.S., Denton, G.H., Kong, X., Wang, Y., Zhang, R., Wang, X., 2009b. Ice Age terminations. *Science* 326, 248–252.
- Ciochon, R.L., Long, V.T., Larick, R., González, L., Grün, R., de Vos, J., Yonge, C., Taylor, L., Yoshida, H., Reagan, M., 1996. Dated co-occurrence of *Homo erectus* and *Gigantopithecus* from Tham Khuyen Cave, Vietnam. *Proceedings of the National Academy of Sciences of the United States of America* 93, 3016–3020.
- Ciochon, R.L., Piperno, D.R., Thompson, R.G., 1990. Opal phytoliths found on the teeth of the extinct ape *Gigantopithecus blacki*: implications for paleodietary studies. *Proceedings of the National Academy of Sciences of the United States of America* 87, 8120–8124.
- Colbert, E.H., Hooijer, D.A., 1953. Pleistocene mammals from the limestone fissures of Szechwan, China. *Bulletin of the American Museum of Natural History* 102 (1), 1–134.
- Corruccini, R.S., 1975. *Gigantopithecus* and hominids. *Anthropologischer Anzeiger* 35 (1), 55–57.
- Daegling, D.J., Grine, F.E., 1994. Bamboo feeding, dental microwear, and diet of the Pleistocene ape *Gigantopithecus blacki*. *South African Journal of Science* 90 (10), 527–532.
- Dart, R.A., 1960. The status of *Gigantopithecus*. *Anthropologischer Anzeiger* 24, 139–145.
- Eckhardt, R.B., 1973. *Gigantopithecus* as a hominid ancestor. *Anthropologischer Anzeiger* 34, 1–8.
- Eckhardt, R.B., 1975. *Gigantopithecus* as a hominid. In: Tuttle, R.L. (Ed.), *Paleoanthropology, Morphology and Paleoeology*. Mouton, The Hague, pp. 105–127.
- Edwards, R.L., Chen, J.H., Wasserburg, G.J., 1987. ^{238}U - ^{234}U - ^{232}Th systematics and the precise measurement of time over the past 500,000 years. *Earth Planet Science Letters* 81 (2–3), 175–192.
- Frazer, D.W., 1973. *Gigantopithecus* and its relationship to *Australopithecus*. *American Journal of Physical Anthropology* 39 (3), 413–426.
- Gelvin, B.R., 1980. Morphometric affinities of *Gigantopithecus*. *American Journal of Physical Anthropology* 53 (4), 541–568.
- Han, K., Zhao, L., 2002. Dental caries of *Gigantopithecus blacki* from Hubei Province of China. *Acta Anthropologica Sinica* 21 (3), 191–197.
- Hsu, C., Han, K., Wang, L., 1974. Discovery of *Gigantopithecus* teeth and associated fauna in Western Hubei. *Vertebrata Palasiatica* 12 (4), 293–309.
- Huang, W., Fang, Q., 1991. Wushan Hominid Site (in Chinese). China Ocean Press, Beijing.
- Jin, C., Qin, D., Pan, W., Tang, Z., Liu, J., Wang, Y., Deng, C., Zhang, Y., Dong, W., Tong, H., 2009. A newly discovered *Gigantopithecus* fauna from Sanhe Cave, Chongzuo, Guangxi, South China. *Chinese Science Bulletin* 54 (5), 788–797.
- Jin, C., Ciochon, R.L., Dong, W., Hunt Jr., R.M., Liu, J., Jaeger, M., Zhu, Q., 2007. The first skull of the earliest giant panda. *Proceedings of the National Academy of Sciences of the United States of America* 104 (26), 10932–10937.
- Johnson Jr., A.E., 1979. Skeletal estimates of *Gigantopithecus* based on a gorilla analogy. *Journal of Human Evolution* 8 (6), 585–587.
- Kahlke, H.D., 1961. On the complex of the *Stegodon-Ailuropoda*-fauna of southern China and the chronological position of *Gigantopithecus blacki* von Koenigswald. *Vertebrata Palasiatica* 1 (2), 83–108.
- Kelley, J., 2002. The hominoid radiation in Asia. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 369–384.
- Kupczik, K., Dean, M.C., 2008. Comparative observations on the tooth root morphology of *Gigantopithecus blacki*. *Journal of Human Evolution* 54 (2), 196–204.
- Liu, W., Jin, C.Z., Zhang, Y.Q., Cai, Y.J., Xing, S., Wu, X.J., Cheng, H., Edwards, R.L., Pan, W.S., Qin, D.G., An, Z.S., Trinkaus, E., Wu, X.Z., 2010. Human remains from Zhirendong, South China, and modern human emergence in East Asia. *Proceeding of National Academy of Sciences of the United States of America* 107 (45), 19201–19206.
- Martin, R.D., 1990. *Primate Origins and Evolution: a Phylogenetic Reconstruction*. Princeton University Press, Princeton.
- Matthew, W.D., Granger, W., 1923. New fossil mammals from the Pliocene of Szechuan, China. *Bulletin of the American Museum of Natural History* 48, 563–598.
- Pei, W., 1957a. Discovery of *Gigantopithecus* mandible and other material in Liu-cheng district of central Kwangsi in South China. *Vertebrata Palasiatica* 1 (2), 65–72.
- Pei, W.C., 1957b. The zoogeographical divisions of Quaternary mammalian faunas in China. *Vertebrata Palasiatica* 1 (1), 9–24.
- Pei, W., Li, Y., 1958. Discovery of a third mandible of *Gigantopithecus* in Liu-Cheng, Kwangsi, South China. *Vertebrata Palasiatica* 2 (4), 193–200.
- Pei, W.C., Woo, J.K., 1956. New materials of *Gigantopithecus* teeth from South China. *Acta Palaeontologica Sinica* 4 (4), 477–490.
- Pilbeam, D., 1970. *Gigantopithecus* and the origins of Hominidae. *Nature* 225, 516–519.
- Rink, W.J., Wang, W., Bekken, D., Jones, H.L., 2008. Geochronology of *Ailuropoda-Stegodon* fauna and *Gigantopithecus* in Guangxi Province, southern China. *Quaternary Research* 69, 377–387.
- Robinson, J.T., Steudel, K., 1973. Multivariate discriminant analysis of dental data bearing on early hominid affinities. *Journal of Human Evolution* 2 (6), 509–527.
- Simons, E.L., Chopra, S.R.K., 1969. *Gigantopithecus* (Pongidae, Hominoidea) a new species from North India. *Postilla* 138, 1–18.
- Simons, E.L., Ettel, P.C., 1970. *Gigantopithecus*. *Scientific American* 222 (1), 76–85.
- Simons, E.L., Pilbeam, D.R., 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthropeidae). *Folia Primatologica* 3 (2–3), 81–152.
- Szalay, F.S., Delson, E., 1979. *Evolutionary History of the Primates*. Academic Press, New York.
- Tong, H., 2005. Dental characters of the Quaternary tapirs in China, their significance in classification and phylogenetic assessment. *Geobios* 38, 139–150.
- Tung, T.C., 1962. The taxonomic position of *Gigantopithecus* in primates. *Vertebrata Palasiatica* 6 (4), 375–383.
- Von Koenigswald, G.H.R., 1952. *Gigantopithecus blacki* von Koenigswald, a giant fossil hominoid from the Pleistocene of Southern China. *Anthropological Papers of the American Museum of Natural History* 43 (4), 292–325.
- Von Koenigswald, G.H.R., 1958. *Gigantopithecus* and *Australopithecus*. *The Leech* 28, 101–105.
- Wang, W., Potts, R., Hou, Y., Chen, Y., Wu, H., Yuan, B., Huang, W., 2005. Early Pleistocene hominid teeth recovered in Mohui Cave in Buling Basin, Guangxi, South China. *Chinese Science Bulletin* 50 (23), 2777–2782.
- Wang, W., Potts, R., Yuan, B., Huang, W., Cheng, H., Edwards, R.L., Ditchfield, P., 2007a. Sequence of mammalian fossils, including hominid teeth, from the Buling basin caves, South China. *Journal of Human Evolution* 52, 370–379.
- Wang, W., Tian, F., Mo, J.Y., 2007b. Recovery of *Gigantopithecus blacki* fossils from the Mohui Cave in the Buling Basin, Guangxi, South China. *Acta Anthropologica Sinica* 26 (4), 329–343.
- Wang, W., 2009. New discoveries of *Gigantopithecus blacki* teeth from Chuifeng Cave in the Buling Basin, Guangxi, south China. *Journal of Human Evolution* 57, 229–240.
- Wang, L., Fang, K., Zheng, Y., 1981. An application of Bayes discriminant analysis in determining the systematic position of *Gigantopithecus*. *Vertebrata Palasiatica* 19 (3), 269–275.
- Weidenreich, F., 1945. Giant early man from Java and South China. *Anthropological Papers of the American Museum of Natural History* 40 (1), 1–134.
- White, T.D., 1975. Geomorphology to paleoecology: *Gigantopithecus* reappraised. *Journal of Human Evolution* 4 (3), 219–233.
- Woo, J.K., 1962. The mandibles and dentition of *Gigantopithecus*. *Paleontologica Sinica New Series D* 11 (146), 1–94.
- Wood, B., Harrison, T., 2011. The evolutionary context of the first hominins. *Nature* 470, 347–352.

- Zhang, Y., 1982. Variability and evolutionary trends in tooth size of *Gigantopithecus blacki*. *American Journal of Physical Anthropology* 59, 21–32.
- Zhao, L., Jin, C., Qin, D., Pan, W., 2008. Description of new fossil teeth of *Gigantopithecus blacki* from Sanhe Cave, Chongzuo, Guangxi in Southern China with comments on evolutionary trends in *Gigantopithecus* dental size. *Quaternary Sciences* 28 (6), 1138–1144.
- Zhao, L., Tong, H., Xu, C., Yuan, Z., Cai, H., 2006. New discovery of *Gigantopithecus blacki* tooth fossil from Bijie, Guizhou and its significance. *Quaternary Sciences* 26 (4), 548–554.
- Zhao, L., Zhang, L., 2013. New fossil evidence and diet analysis of *Gigantopithecus blacki* and its distribution and extinction in South China. *Quaternary International* 286, 69–74.
- Zhao, L., Zhang, L., Zhang, F., Wu, X., 2011. Enamel carbon isotope evidence of diet and habitat of *Gigantopithecus blacki* and associated mammalian megafauna in the Early Pleistocene of South China. *Chinese Science Bulletin* 56 (33), 3590–3595.
- Zheng, S., 2004. *Jianshi Hominid Site* (in Chinese). Science Press, Beijing.