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The Early Pleistocene *Gigantopithecus-Sinomastodon* fauna from Juyuan karst cave in Boyue Mountain, Guangxi, South China

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A B S T R A C T

As one of the most important Quaternary mammalian faunas in southern China, the *Gigantopithecus-Sinomastodon* fauna has received much attention. The large-primate fossil teeth newly collected from Juyuan karst cave in Boyue Mountain, Guangxi Zhuang Autonomous Region of southern China, can be identified as *Gigantopithecus blacki*. The morphology and size of these *G. blacki* teeth differ from those of the middle Pleistocene *Gigantopithecus* teeth which hold evidently larger dental dimensions and more complex crenulations from Hejiang Cave also in Guangxi and Tham Khuyen Cave in Vietnam. However, the *G. blacki* teeth from Juyuan Cave are relatively similar to those from Early Pleistocene Mohui Cave and Liucheng *Gigantopithecus* Cave both in Guangxi, which suggests that the three cave sites have similar age. The Juyuan fauna associated with *Gigantopithecus blacki*, consisting of 45 mammalian species (such as *Sinomastodon yangziensis*, *Ailuropoda wulingshanensis*, *Stegodon huananensis*, and *Rhinoceros fusuiensis*), is a typical Early Pleistocene *Gigantopithecus-Sinomastodon* fauna of southern China. The Juyuan fauna is mostly similar to Mohui fauna, also implying their contemporaneity. Paleomagnetic analyses demonstrate that the fossil-bearing sediments in Juyuan Cave are dominated by normal polarity. Combining the faunal analysis and magnetostratigraphic evidence, the Juyuan sediments can be best correlated with the Olduvai normal subchron, giving an estimated age of 1.8 Ma.

1. Introduction

As the largest primate ever to have lived, *Gigantopithecus blacki* is an extinct giant ape and a typical member of the Pleistocene fauna known from southern China or, more broadly, mainland Southeast Asia. *Gigantopithecus blacki* was initially erected based on the isolated teeth collected from traditional Chinese pharmacies by the German paleontologist Von Koenigswald (1935). Since the first discovery of *G. blacki* from an *in situ* geological horizon in Guangxi Zhuang Autonomous Region (Guangxi ZAR) in the 1950s, there have been at least 16 sites found in southern China and northern Vietnam, all dating to early-middle Pleistocene (Woo, 1962; Huang and Fang, 1991; Ciochon et al., 1996; Zheng, 2004; Wang et al., 2005, 2007a, 2007b; Zhao et al., 2006, 2008, 2011; Wang, 2009; Jin et al., 2009, 2014; Zhao and Zhang, 2013; Zhang et al., 2014, 2015).

The initial *G. blacki* teeth were commonly found from the "Drugstore fauna" without stratigraphic control. Both Chow (1957) and Pei (1962) agreed that the fauna from Liucheng *Gigantopithecus* Cave was more primitive than the typical middle Pleistocene *Ailuropoda-Stegodon* fauna (*sensu stricto*) and was referred to as the *Gigantopithecus* fauna with an estimated age of Early Pleistocene. *Sinomastodon* (Proboscidea) was once prevalent, together with *Gigantopithecus*, during the Early Pleistocene and possibly became extinct at the end of the Early Pleistocene in southern China (Wang Y et al., 2012, 2014). The Early Pleistocene fauna from South China is suggested to be revised as the *Gigantopithecus-Sinomastodon* fauna (Wang Y et al., 2014).

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During the past decade, the most diverse and intriguing of *Gigantopithecus* fossils and other vertebrate remains have been discovered from a number of cave sites in the Chongzuo, Zuojiang River area of Guangxi ZAR, South China (Jin et al., 2009, 2014; Dong et al., 2010, 2014; Harrison et al., 2014; Takai et al., 2014; Wang Y et al., 2014 Yan et al., 2014; Zhang et al., 2014; Zhu et al., 2014, 2015). These newly discovered cave sites have estimated dates that span the early-middle Pleistocene, even possibly late Pleistocene (Sun et al., 2014; Zhang et al., 2014). For example, the early Early Pleistocene faunas from Baikong Cave of Liyu Mountain and Yanliang Cave of Gaoyan Mountain include some primitive species, such as *Sinomastodon jiangnanensis*, *Ailuropoda microta*, *Megantereon microta, Cervavitus ultimus*, and *Tapirus sanyuanensis* (Jin et al., 2014; Yan et al., 2014; Zhu et al., 2014, 2015). The middle Early Pleistocene faunas from Juyuan Cave in Boyue Mountain and Sanhe Cave in Wuming Mountain are characterized by the first appearance of *Sinomastodon yangziensis*, *Ailuropoda wulingshanensis* and *Tapirus sinensis* (Jin et al., 2009, 2014; Wang Y et al., 2014). The late Early Pleistocene fauna from Queque Cave of Wuming Mountain is characterized by the first appearance of *Stegodon orientalis* and *Bubalus brevicornis chowi* and the last appearance of *Sinomastodon* (Dong et al., 2014; Jin et al., 2014). The Middle Pleistocene fauna from Hejiang Cave of Mulan Mountain is characterized by the appearance of *Ailuropoda baconi* and *Stegodon orientalis* (Zhang et al., 2014). The fauna from Shuangtan Cave of Mulan Mountain also from Chongzuo including *Ailuropoda melanoleuca*, *Elephas maximus,* and *Megatapirus augustus*, possibly is late Pleistocene and awaits systematic research.

To date, the earliest record of *G. blacki* in Chongzuo area is from the early Early Pleistocene Baikong Cave of Liyu Mountain (2 Ma) (Jin et al., 2014; Sun et al., 2014), and the latest occurrence is from Hejiang Cave in Mulan Mountain (400–320 Ka) (Zhang et al., 2014). The geographic distribution of *G. blacki* is limited to the Oriental zoogeographic realm of southern China (south of the Yangtze River and Qinling Mountain) and northern Vietnam (Tham Khuyen Cave; Ciochon et al., 1996) associated with mesic tropical and subtropical climatic zones. In China, the northernmost limit is 30°51′N (Longgupo in Chongqing) (Huang and Fang, 1991; Wei et al., 2014) and the southern boundary is located at 22°16′N (Chongzuo cave sites, Guangxi) (Jin et al., 2014).

In 2004, Wenshi Pan discovered some large primate fossil teeth and other vertebrate remains from the cave sediments in Boyue Mountain in Chongzuo Ecological Park, Guangxi. The large primate fossil teeth were subsequently identified by Zhanxiang Qiu as *Gigantopithecus blacki*. It was the first discovery of *G. blacki* in Chongzuo area, so this site was called Juyuan Cave in Boyue Mountain ("Juyuan" in Chinese means "*Gigantopithecus*").

Since 2006, a research team co-organized by Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP, CAS) and Peking University has carried out the systematic excavations in Juyuan Cave and has unearthed a plethora of higher primate remains, including *G. blacki*, *Pongo,* and *Macaca,* as well as other abundant associated mammalian fossils.

Jin et al. (2014) has provided a preliminary account of the Juyuan fauna. This paper conducts a systematic study on the *Gigantopithecus-Sinomastodon* fauna from Juyuan Cave of Boyue Mountain based on new faunal data and previously published paleomagnetic data of Sun et al. (2014). The present study aims at providing important new evidence regarding the evolutionary trends, taxonomic composition, biochronological stages and paleoenviromental context of *Gigantopithecus-Sinomastodon* fauna.

2. Geographical and geological background

Chongzuo Ecological Park is about 16 km southeast of the Chongzuo urban district and 120 km northeast of the China-Vietnam border. Juyuan Cave (22°17′21.9″N, 107°30′40.1″E) is located on the eastern slope of Boyue Mountain which is near the entrance of Chongzuo Ecological Park (Figs. 1 and 2).

Chongzuo was a part of the Tethys during the late Paleozoic, and subsequent late Mesozoic tectonic movement led to the deposition of multiple sedimentary layers. As a consequence of the continuous uplift of the area since the Pliocene, multiple horizons of karst caves have formed at different elevations. These show a degree of regularity in the relationship between elevation and time of cave formation. Generally, the higher the elevation of the cave, the older the age of its formation within its deposits.

A total of six horizons of karst caves have been recognized in the Chongzuo area (Fig. 3). The elevation of the sixth, highest, horizon is about 270 m above sea level, and that of the first, lowest, horizon is about 150 m above sea level, which is situated only a few meters above the valley floor, with a likely age of the Holocene. The sediments of the karst caves of the fifth horizon with an elevation of about 200 m above sea level (e.g., Sanhe Cave and Yangliang Cave) yield the typical fossil members of the Early Pleistocene of southern China, such as *Gigantopithecus*, *Sinomastodon*, *Stegodon huananensis*, and *Cervavitus fenqii* (Jin et al., 2009, 2014; Yan et al., 2014).

The northern tropical karst in this area include peak valleys and peak depressions. The height of the mountains is generally about 300 m above sea level. Hejiang River between Boyue Mountain and Liyu Mountain flows from west to east, and the river valley floor is about 145 m above sea level (Fig. 3). On the steep faces of the karst slopes, numerous caves and fissures of various dimensions have been formed. These caves or fissures are normally filled with yellowish-brown or red–brown clay with breccia, most of which contain fossils.

Juyuan Cave is an elongated slit-like cave oriented southeast to northwest. The natural entrance of the cave faces east. The maximum width of the cave is 3.6 m (Fig. 4a). The elevation of the cave entrance is 206 m above sea level, and is situated more than 60 m above the valley floor. The sediments of the cave are approximately 5.5 m in thickness, which can be divided into six layers from top to bottom (Fig. 4b). The *G. blacki* and associated mammalian remains were recovered from the first and fifth layers. Layer 1: yellow–brown silty conglomerates with relatively hard nodules and limestone breccias of 3–4 cm, containing abundant fossils (110 cm). Layer 2: brown calcareous silts with relatively hard nodules (50 cm). Layer 3: dark-brown lutaceous silts (108 cm). Layer 4: gray–white calcareous floor with crystallized carbonate (12 cm). Layer 5: maroon argillaceous silts, relatively unconsolidated, with few large limestone breccias but well-developed calcite and iron-manganese nodules, yielding abundant fossils (130 cm). Layer 6: red clays (140 cm, bottom unseen).

3. Paleontology

The mammalian assemblage discovered from Juyuan Cave of Boyue Mountain contains 8 orders, 24 families, 36 genera and 45 species, including 20 species of large mammals and 25 species of small mammals (Tables 1 and 2).

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Table 1
Faunal list and specimens from Juyuan Cave, Boyue Mountain (large-mammals).

Genus/Species	IVPP no.	N	Details of specimens
Primates			
Gigantopithecus blacki	PA1603	7	P4 (01), two M1s (02, 03), two m1/m2s (04, 05), two m3s (06, 07)
Pongo weidenreichi	PA1604	13	C (01), M1 (02), two cs (03, 04), i1 (05), i2 (06), p3 (07), two p4s (08, 09), m1 (10), three m2s (11–13)
Nomascus sp.	V22671	1	P3 (01)
Macaca sp.	V22672	5	M1 (01), M2 (02), M3 (03), m2 (04), m3 (05)
Trachypithecus sp.	V22673	3	m1 (01), m2 (02), m3 (03)
Carnivora			
Ailuropoda wulingshanensis	V22674	5	M1 (01), M2 (02), p4 (03), m2 (04), m3 (05)
Arctonyx collaris	V22675	3	Left maxilla fragment with P4 and M1 (01), M1 (02), m1 (03)
Ursus thibetanus	V22676	6	Two M1s (01, 02), two M2s (03, 04), two m1s (05, 06)
Ursus sp.	V22676.07	1	M2
Panthera sp.	V22676.08	1	p4
Proboscidea			
Sinomastodon yangziensis	V22677.01	1	One molar fragment
Stegodon huananensis	V22677.02	1	One M3 fragment
Perissodactyla			
Tapirus sinensis	V22678	2	dp4 (01), m3 (02)
Rhinoceros fusuiensis	V22679	5	DP2 (01), DP3 (02), P3 (03), p2 (04), p3 (05)
Artiodactyla			
Hippopotamodon ultimus	V17751	5	M3 (01), p3 (02), m1 (03), m2 (04), m3 (05)
Sus xiaozhu	V17751.09	1	m3
Megalovis guangxiensis	V17753.06	1	m2
Muntiacus lacustris	V17752	5	M1 (01), M2 (02), M3 (03), two m3s (04, 05)
Caprinae	V17753	3	M2 (07), M3 (08), m3 (09)
Bos (*Bibos*) sp.	V17753	3	M2 (01), m1 (02), m3 (03)

Table 2
Faunal list and specimens from Juyuan Cave, Boyue Mountain (small-mammals).

Genus/Species	IVPP no.	N	Details of specimens
Insectivora			
Scaptochirus sp.	V22680	4	P4 (01), M1 (02), p3 (03), m3 (04)
Anourosorex quadratidens	V22681	1	One fragmentary mandible (01)
Crocidura sp.	V22682	2	M1 (01), M2 (02)
Blarinella wannanensis	V22683	2	One fragmentary mandible with m1–m3 (01), One maxilla fragment with P4, M1 (02)
Soriculus fanchangensis	V22684	1	One fragmentary mandible (01)
Chiroptera			
Rhinolophus Youngi	V22685.01	1	One fragmentary mandible with i1-p2 and m1–m3
Rhinolophus cf. *R. affinis*	V22685	2	Upper incisor (02), M1 (03)
Rhinolophus sp.	V22685.04	1	M1
Hipposideros pleistocaenicus	V22686.01	1	m1
Hipposideros pratti	V22686.02	1	One fragmentary mandible with m1–m3
Hipposideros sp.	V22686.03	1	m1
Rodentia			
Pteromys sp.	V22687.01	1	M1
Typhlomys intermedius	V22687	2	M1 (02), m1 (03)
Atherurus sp.	V22688.01	1	M1
Hystrix subcristata	V22688.02	1	p4
Hystrix magna	V22688.03	1	M1
Eothenomys sp.	V22689	2	Two M3s (01, 02)
Mus aff. M. pahari	V22690	3	Two M1s (01, 02), m1 (03)
Apodemus cf. *A. peninsulae*	V22691	2	Two m1s (01, 02)
Hapalomys augustidens	V22692	1	M1 (01)
Hapalomys gracilis	V22693	3	M1 (01), two M2s (02, 03)
Niviventer preconfucianus	V22694	1	One fragmentary maxilla with M1–M3 (01)
Niviventer andersoni	V22695	2	M1 (01), m1 (02)
Leopoldamys edwardsioides	V22696	1	One fragmentary mandible with m1 and m2 (01)
Rattus sp.	V22697	1	M1 (01)

Table 3
Comparison of *Gigantopithecus-Sinomastodon* fauna from Juyuan Cave, Chongzuo and other related Pleistocene faunas from southern China (Large-mammals).

Genus/Species	Sanhe[a]	Hejiang[b]	Mohui[c]	Chuifeng[d]	Liucheng[e]	Longgupo[f]
Primates						
Nomascus sp.	⊚	⊚			⊚	
Gigantopithecus blacki	⊚	⊚	⊚	⊚	⊚	⊚
Pongo weidenreichi	⊚	*P.* sp.	*P.* sp.	*P.* sp.	*P.* sp.	
Macaca sp.	⊚	⊚	⊚	⊚	⊚	⊚
Trachypithecus sp.	⊚	⊚	⊚			
Carnivora						
Ailuropoda wulingshanensis	⊚	*A. baconi*	*A. microta*	*A. microta*	*A. microta*	*A. microta*
Arctonyx collaris	⊚		⊚	⊚		*A.* cf. *minor*
Ursus thibetanus	*U.* cf. *thibetanus*		⊚	⊚	*U.* cf. *thibetanus*	*U.* cf. *thibetanus*
Ursus sp.		⊚				
Panthera sp.	⊚	⊚	⊚		⊚	⊚
Proboscidea						
Sinomastodon yangziensis	⊚		⊚	⊚		⊚
Stegodon huananensis	⊚	*S. orientalis*	⊚	⊚	⊚	⊚
Perissodactyla						
Tapirus sinensis	⊚	⊚	*T. sanyuanensis*	*T. sanyuanensis*	*T. peii*	*T. sanyuanensis*
Rhinoceros fusuiensis	*R. sinensis*	*R. sinensis*	⊚	⊚	⊚	⊚
Artiodactyla						
Hippopotamodon ultimus	⊚		⊚	⊚	⊚	⊚
Sus xiaozhu	⊚	⊚	⊚	⊚	⊚	⊚
Megalovis guangxiensis	⊚	⊚	⊚		⊚	
Muntiacus lacustris	⊚	*M.* sp.	*M.* sp.	*M.* sp.	⊚	⊚
Caprinae	⊚		*Capricornis* cf. *sumatraensis*		⊚	
Bos (*Bibos*) sp.	⊚	⊚	Bovinae	Bovinae	⊚	⊚

[a] Jin et al., 2009.
[b] Zhang et al., 2014.
[c] Wang W et al., 2005, 2007a, 2014.
[d] Wang, 2009.
[e] Pei, 1987; Han, 1987.
[f] Huang and Fang, 1991.

3.1. Large mammals

The large mammal remains from Juyuan Cave consist of Primates (pongid, hylobatid, colobid, and cercopithecid), Carnivora (giant panda, ursid, mustelid, and felid), Proboscidea (gomphotheriid and stegodontid), Perissodactyla (rhinocerotid and tapirid) and Artiodactyla (suid, cervid, and bovid) (Fig. 5 and Tables 1 and 3).

3.1.1. Primates

3.1.1.1. Gigantopithecus blacki. In this study, seven fossil teeth unearthed from Juyuan Cave are identified as *Gigantopithecus blacki* (Table 1). The measurements (mm) are listed as following-MD (mesiodistal length)/BL (buccolingual breadth): P4 (PA1603.01, 15.55/23.19), M1 (PA1603.02, 18.20/22.48; PA1603.03, 18.26/22.30), m1/m2s (PA1603.04, 23.76/19.66; PA1603.05, 21.90/18.92), m3s (PA1603.06, 22.53/19.46; PA1603.07, 21.60/18.33).

The upper fourth premolar (P4, Fig. 5A4) is well-preserved, but the roots are mostly missing. The occlusal outline is round-trapezoidal in shape. The median longitudinal groove is sinuous, separating the labial and lingual cusp at the median basin. The lingual slope of the paracone is much more receding than the buccal slope of the protocone. The mesial and distal marginal ridges are well developed. The anterior fovea is deeper than the posterior fovea.

The upper first molar (M1, Fig. 5A3) is moderately worn. The occlusal outline of the crown is somewhat rhomboidal in shape. The protocone, hypocone, paracone, and metacone are well developed. The protocone and paracone are slightly higher and larger than the distal cusps. The paracone and metacone rise steeply, while the protocone and hypocone are inclined buccally. The lingual and buccal cusps are clearly separated by a vertical furrow.

The lower first or second molar (m1/m2, Fig. 5A1) is well-preserved. The occlusal outline of these teeth is round-oblong and mesio-distally elongated. The five cusps are from largest to smallest: metaconid, protoconid, entoconid, hypoconid, and hypoconulid. These cusps are rounded and blunt, with a few narrow furrows. The buccal, lingual, and median longitudinal grooves are visible. The buccal and lingual grooves respectively separate the protoconid and hypoconid, and the metaconid and entoconid.

The lower third molar (m3, Fig. 5A2) is in good condition. The occlusal outline of these teeth is mesio-distally elongated. Five cusps are separated by a Y-shaped system of fissures. The metaconid is the largest cusp, followed by the protoconid, hypoconid, entoconid, and hypoconulid.

The fossil teeth are morphologically identical to those of *Gigantopithecus blacki*. The morphology and size of these *G. blacki* teeth tend to be a little larger than those from Longgupo (Chongqing), Liucheng *Gigantopithecus* Cave (Guangxi ZAR), and Chuifeng Cave (Guangxi ZAR) (Woo, 1962; Huang and Fang, 1991; Wang, 2009). However, the *G. blacki* teeth from Juyuan Cave differ from those of middle Pleistocene *Gigantopithecus* teeth which have larger dental dimensions and more complex crenulations from Hejiang Cave also in Guangxi and Tham Khuyen Cave in Vietnam (Ciochon et al., 1996; Zhang et al., 2014). In sum, the *G. blacki* teeth from Juyuan Cave are mostly similar to those from the Early Pleistocene Mohui Cave (Guangxi ZAR) (Wang et al., 2007b).

3.1.1.2. Pongo weidenreichi. Thirteen fossil teeth of *Pongo* from Juyuan Cave have been reported by Harrison et al. (2014), such as the lower fourth premolar (p4, MD/BL-13.6/13.9 in mm, Fig. 5B1)

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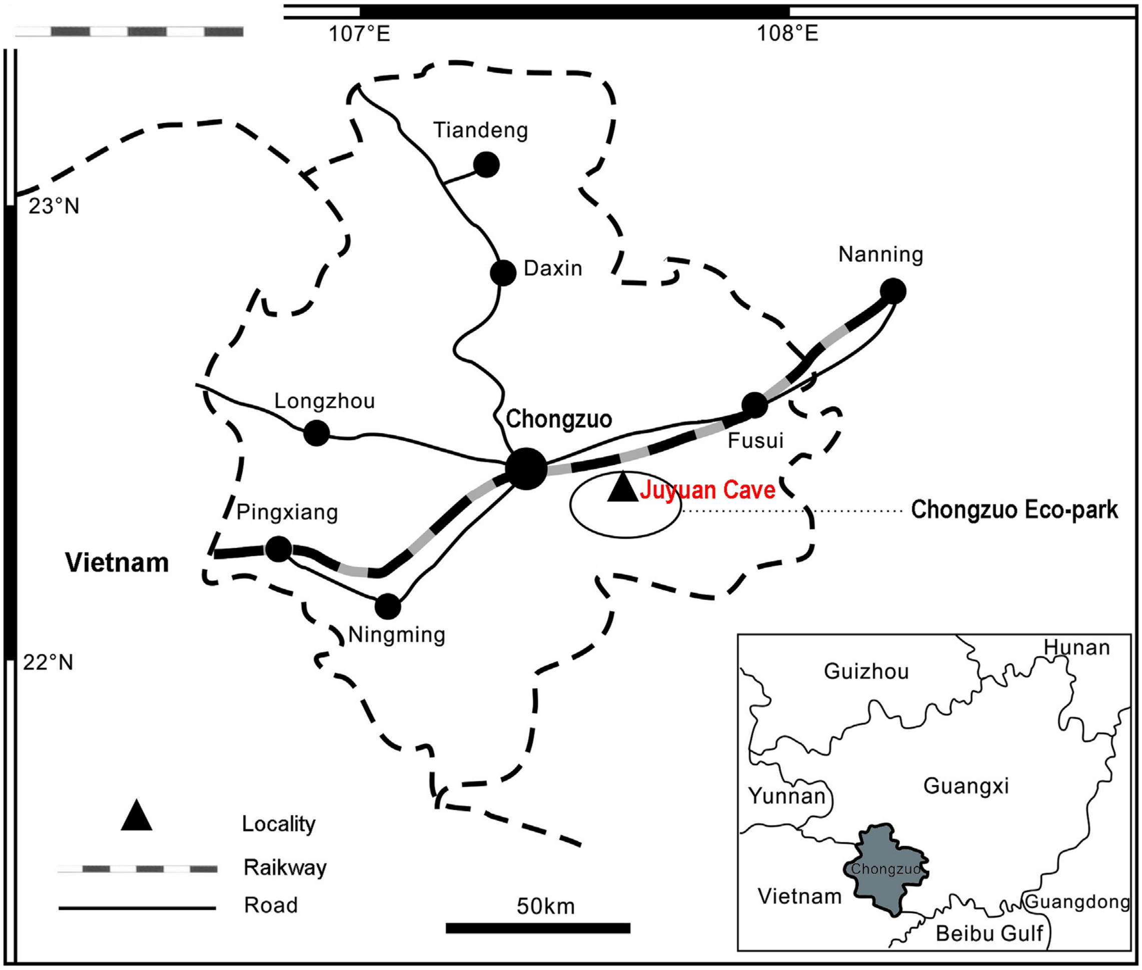

Fig. 1. Geographical location of Juyuan Cave of Boyue Mountain in Chongzuo Ecological Park, Guangxi ZAR, South China.

Fig. 2. Karst landscape of Chongzuo Ecological Park showing the locations of Boyue Mountain and Wuming Mountain in Guangxi ZAR, South China.

Fig. 3. Vertical distribution (elevation above sea level) of the karst caves in Chongzuo karst area, Guangxi ZAR, South China.

and lower first molar (m1, MD/BL-15.0/13.6 in mm, Fig. 5B2). These teeth are generally morphologically very similar to those of extant species of *Pongo*, but are much larger in size. All of the fossil specimens can be attributed to a single species, *Pongo weidenreichi*, which is a typical member of the Early and Middle Pleistocene fauna of southern China and Vietnam. *Pongo weidenreichi* is distinguished from extant taxa primarily by having considerably larger teeth on average, lower crowned canines, and relatively large second and third molars. The identification of more detailed species-specific characteristics of *P. weidenreichi* will require larger samples from sites in southern China (Wang CB et al., 2014).

3.1.1.3. Nomascus sp.. The gibbon is a rare species in the sample with only one worn upper third premolar (P3), which remains

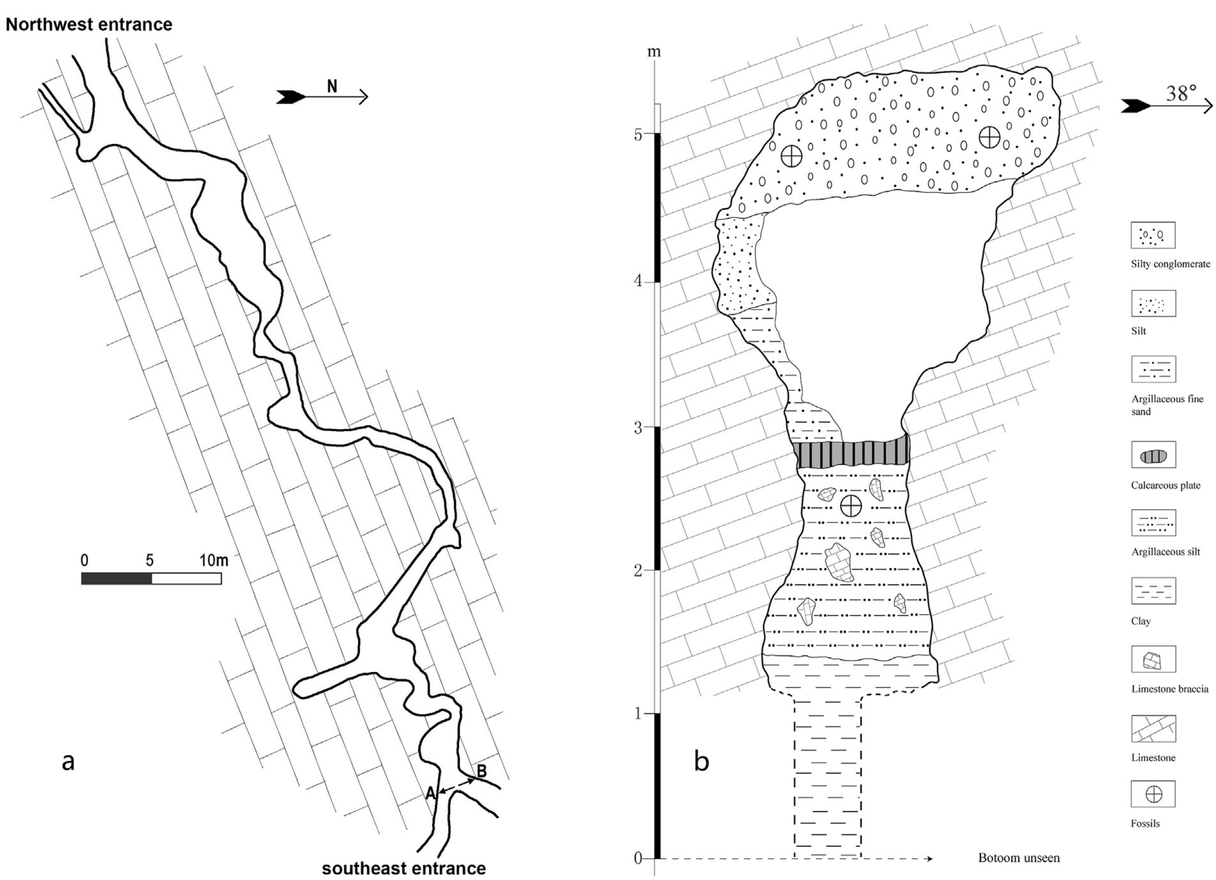

Fig. 4. Plan (4a) and geological section (4b) of the Juyuan Cave of Boyue Mountain.

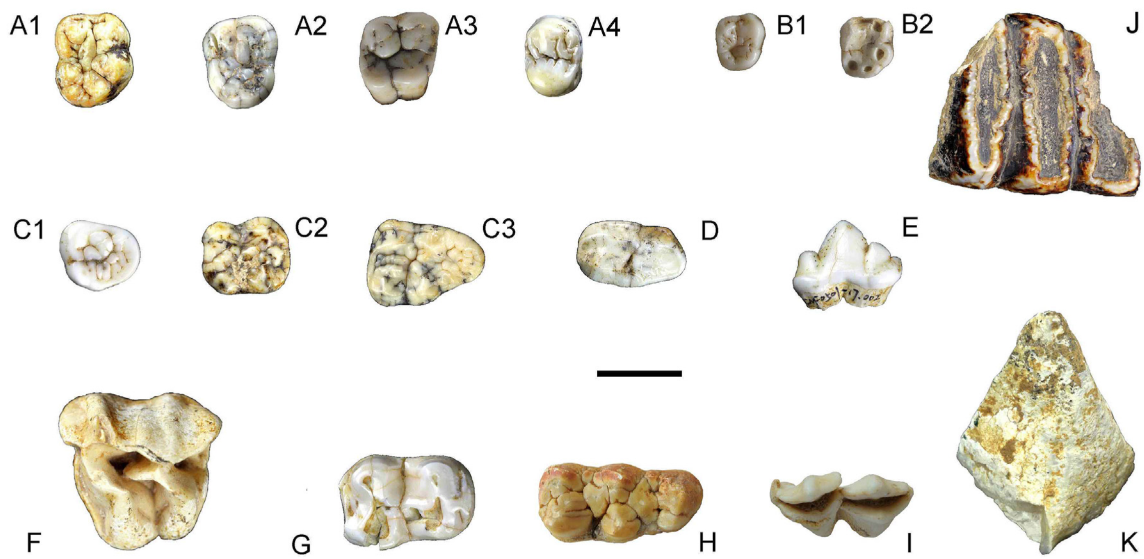

Fig. 5. The *Gigantopithecus blacki* and some of other large-mammalian fossils from Juyuan Cave. A1–A4, *Gigantopithecus blacki* (m1/m2-PA1603.04, m3-PA1603.06, M1-PA1603.02, P3-PA1603.02); B1–B2, *Pongo weidenreichi* (p4-PA1604.09, m1-PA1604.10); C1–C3, *Ailuropoda wulingshanensis* (m3-V22674.05, m2-V22674.04, M2-V22674.02); D, *Ursus thibetanus* (M2-V22676.04); E, *Panthera* sp. (p4-V22676.08); F, *Rhinoceros fusuiensis* (DP3-V22679.02); G, *Tapirus sinensis* (m3-V22678.02); H, *Hippopotamodon ultimus* (m3-V17751.05); I, *Megalovis guangxiensis* (m2-V17753.06); J, *Stegodon huananensis* (molar fragment-V22677.02); K, *Sinomastodon yangziensis* (molar fragment-V22677.01). A–D and F–J, occlusal view; E and K, labial view. Scale: 2 cm for A–I and K, 4 cm for J.

undetermined at the species level. The P3 (V22671.01, MD/BL-4.6/4.74 in mm) has a well-developed paracone, and an almost-absent protocone. The preprotocrista and postprotocrista are connected.

3.1.1.4. *Macaca sp.*. Among specimens, five cercopithecid teeth (3 upper and 2 lower) are attributed to an undetermined macaque (*Macaca* sp.), as the distinction between species is problematic, based on isolated teeth only.

The measurements (mm) are listed as following (MD/BL): M1 (V22672.01, 7.69/8.52), M2 (V22672.02, 10.23/9.26), M3 (V22672.03, 10.45/9.21), m2 (V22672.04, 9.58/7.38), and m3 (V22672.05, 10.31/6.68).

The protocone, hypocone, paracone, and metacone are well developed on upper molar. The lower molars are dilambdodont. The hypoconulid is visible on m3 besides the metaconid, protoconid, hypoconid and entoconid.

3.1.1.5. *Trachypithecus sp.*. At least three lower molars suggest that one colobid is present in Juyuan fauna. However, as the taxonomic attribution is limited to the genus level, the size comparison with the taxa from the other Pleistocene sites of southern China is not informative.

The measurements (mm) are listed as following (MD/BL): m1 (V22673.01, 6.25/4.83), m2 (V22673.02, 7.42/6.37), and m3 (V22673.03, 9.75/6.18).

The lower molars here are obviously smaller than those of macaque. The m1 and m2 are dilambdodont. The hypoconulid is present on m3.

3.1.2. *Carnivora*

3.1.2.1. *Ailuropoda wulingshanensis.* At least five fossil teeth from Juyuan Cave can be assigned to genus *Ailuropoda* (Table 1). The measurements are shown in Table 4 and Fig. 6.

Table 4
Dental dimensions of *Ailuropoda wulingshanensis* from Juan Cave and other species (mm).

	Juyuan cave	*Ailuropodami crota*[a)]	*Ailuropoda wulingshanensis*[b)]	*Ailuropoda baconi*[c)]	*Ailuropoda melanoleuca*[d)]
M1					
L	21.9	17.7–23	20–26.3	25.1–29	22.4–26.2
W	24.7	16.5–23.2	21.8–27.5	26–31.5	25.1–29.6
M2					
L	27.5	20–25	24.2–32.5	31–40.5	30.4–36.5
W	20.3	16–20	19–26	23.7–30.5	24–28.2
p4					
L	22.2	16.2–19.1	16.3–23.4	21.5–26.5	20.5–24.2
W	12.5	8.6–11	9–13.2	11.8–14.8	11.0–13.9
m2					
L	21.1	17–20.5	19–25.4	25–30	22.1–27.2
W	18.3	13.8–16.5	16–20.9	20–25.9	18.2–24.6
m3					
L	18.3	9.5–16.3	13–17	16.8–23.6	16.5–21.3
W	19.4	11.5–16.5	13.6–19.2	18.2–24.5	17.7–22

L: length; W: width. Data from: a) Jin et al., 2007; b) Zheng, 2004; c) Pei, 1963; Woodward, 1915; d) Colbert and Hooijer, 1953; Wan et al., 2005.

Table 5
Proportions of extinct genus and species of Juyuan fauna in Chongzuo and other related faunas (Large mammal).

Mammal faunas	Number of the extinct genus	The proportion of extinct genus	Number of extinct species	The proportion of extinct species
Boyue	6	33%	12	60%
Sanhe	9	32%	15	47%
Hejiang	3	15%	7	35%
Mohui	8	33%	15	58%
Chuifeng	6	35%	12	67%
Liucheng	12	44%	21	60%
Longgupo	17	50%	32	80%

The upper second molar (M2, Fig. 5C3) is moderately worn. The occlusal outline of the crown is almost triangular in shape. The crown can be divided into trigon (anterior part) and talon (posterior part). The trigon is composed of four main cusps and has distinct enamel wrinkles.

The occlusal outline of the lower second molar (m2, Fig. 5C2) is retangular in shape. The protoconid, metaconid, hypoconid and entoconid are well-developed. The metaconid has a relatively high position. The hypoconid and entoconid, with a relatively low position, are the same height as enamel wrinkles.

The development of enamel wrinkles on molars ensures the identification of genus *Ailuropoda*. Considering the size range (Table 4 and Fig. 6), these specimens should be assigned to *A. wulingshanensis,* which shows intermediate links between *A. microta* and *A. baconi*. *A. wulingshanensis* from Juyuan Cave is different from *A. microta* by its larger size and an accessory cusplet present at the lingual side of posterior cusp on the p4 (Jin et al., 2007). The *A. wulingshanensis* here differs from *A. baconi* in having a smaller size except the m3 and simpler enamel crenulations on molars.

3.1.2.2. Arctonyx collaris. Fossil badgers are common from the Pleistocene caves of southern China. The measurements (mm) of teeth from Juyuan Cave are (Length/Width, L/W): one fragment maxilla-P4 (10.1/7.6), M1 (13.9/10.6); M1 (17.3/13.5); m1 (18.6/7.6).

Fossil badgers differ from *Meles* by having a more posterior position of protocone on P4 and the M1 with a longer labial length and subsequently should be assigned to *Arctonyx collaris,* which has a larger size and cusps developed on inner cingulum (Pei, 1987).

3.1.2.3. Ursus thibetanus. At least six teeth of *Ursus thibetanus* are present in Juyuan fauna. The measurements (mm) are (L/W): M1s (19.5/14.7, 17.7/14.2), M2s (24.9/14.7, 25.9/16.1; Fig. 5D) and m1s (20.6/8.7, 18.8/8.2). These fossils are similar in dental size to those from Early Pleistocene sites from southern China, such as Liucheng *Gigantopithecus* Cave (Guangxi ZAR) and Renzidong Cave (Anhui) (Pei, 1987; Jin and Liu, 2009), but seem more derived based on dental morphology.

3.1.2.4. Ursus sp.. One upper second molar (M2, L/W, 20.9/12.7 in mm) indicates another type of *Ursus* with relatively smaller size, which is similar to *Ursus* sp.1 described by Pei (1987).

3.1.2.5. Panthera sp.. One lower fourth premolar (p4, L/W, 26.1/13.2 in mm; Fig. 5E) is preserved, with a larger size than *Panthera pardus*.

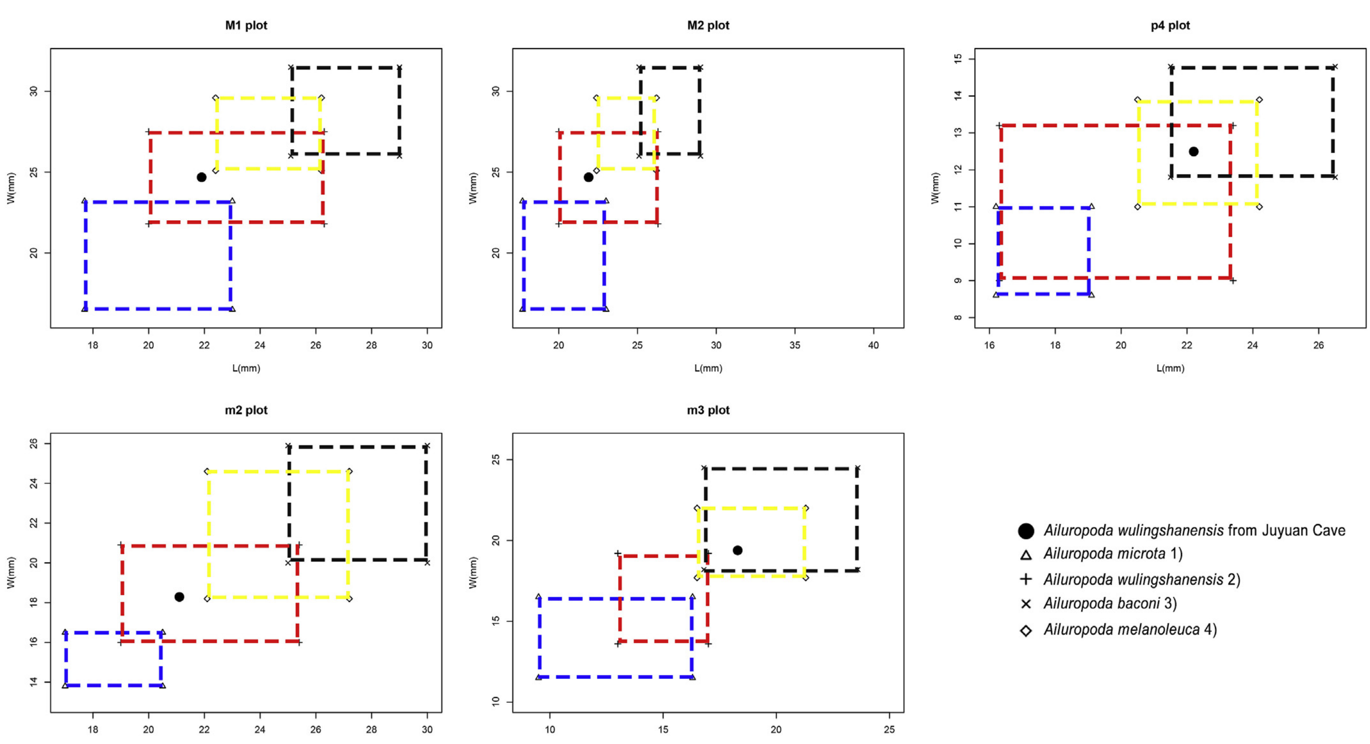

Fig. 6. Plot diagram of dental dimensions of *Ailuropoda wulingshanensis* from Juyuan Cave and other species. Data from: 1) Jin et al., 2007; 2) Zheng, 2004; 3) Pei, 1963; Woodward, 1915; 4) Colbert and Hooijer, 1953; Wan et al., 2005.

However, taxonomic attribution is limited to the genus level based only one isolated tooth.

3.1.3. Proboscidea

3.1.3.1. Sinomastodon yangziensis. One molar fragment (V22677.01, Fig. 5K) of a bunodont gomphothere, preserved from Juyuan Cave, is possibly part of the pretrite half-lophid with a height of 58 mm. Some cement and ectoflexi are present on the surface of the molar fragment.

The genus *Sinomastodon* is the only trilophodont gomphothere ever found in southern China during Pleistocene. Wang Y et al. (2014) has divided the temporal evolution of Pleistocene *Sinomastodon* in South China into three stages based on the molar morphology. The molar fragment from Juyuan Cave should belong to the early stage of *S. yangziensis,* as remains from Longgupo (Chongqing), Liucheng *Gigantopithecus* Cave (Guangxi ZAR), and Mohui Cave (Guangxi ZAR) (Pei, 1987; Huang and Fang, 1991; Wang W et al., 2014).

S. jiangnanensis and *S. yangziensis* are commonly discovered from the early cave sites from southern China (Wang et al., 2012), so the Early Pleistocene fauna from South China has been revised as the *Gigantopithecus-Sinomastodon* fauna (Wang Y et al., 2014), to distinguish it from the typical Middle Pleistocene *Ailuropoda-Stegodon* fauna (s. s.).

3.1.3.2. Stegodon huananensis. One fragment of upper third molar with three lophs (V22677.02, Fig. 5J) has been recovered with the characteristics of the genus *Stegodon*. The fragmentary lophs are ridge-shaped with low crown. The largest width of lophs is about 90 mm. The number of complete lophs is probably 8. Between two lophs, the valley has a “Y” shape. The dental morphology suggests it to be *Stegodon huananensis*.

The specimen is mostly similar with those of *Stegodon preorientalis* from Longgupo (Chongqing), Liucheng *Gigantopithecus* Cave (Guangxi ZAR), and Sanhe Cave (Guangxi ZAR) (Pei, 1987; Huang and Fang, 1991; Jin et al., 2009). Chen (2011) erected a new species *Stegodon huananensis* based on the *Stegodon* remains from the Early Pleistocene southern China, including the materials of *Stegodon preorientalis*.

3.1.4. Perissodactyla

3.1.4.1. Rhinoceros fusuiensis. Three rhino fossil teeth are measured (L/W, mm): DP3 (38/39), p2 (29/15), and p3 (31/21).

The mesocone rib is distinct in ectoloph on DP2, though the anterior part is broken. DP3 (V22679.02, Fig. 5F) is trapezoidal in occlusal outline, the parastyle and paracone rib are developed, the crochet is simple, and the anterior and posterior cingulua are absent. On p2, the paralophid and protolophid are almost fused with each other, and the hypolophid and entolophid are formed a closed shallow fossa after wear. The p3 is rectangular in occlusal outline and has thick enamel; the paralophid is weak, the trignoid is narrower than the talonid, and the trignoid basin is shallower than the talonid basin.

The dimensions of the rhino teeth from Juyuan Cave are distinctly smaller than those of extant *Rhinoceros* (i.e., *R. unicornis* and *R. sondaicus*), but larger than that of *Dicerorhinus sumatrensis* (Hooijer, 1946). The measurements of these teeth fall in the range of *R. fusuiensis*, a primitive species from the Early Pleistocene described by Yan et al. (2014).

3.1.4.2. Tapirus sinensis. The tapir fossil teeth are measured as following (L/W, mm): dp4 (30/19), m3 (33/23, V22678.02, Fig. 5G). The two specimens have relatively smaller sizes, lower crowns, and thinner enamel. The dental characteristics of these two teeth are similar to each other, with rectangular occlusal outlines and the well-developed two transverse crests. The anterior cingulum is less developed in m3 than that in dp4, but the posterior cingulum is stronger in the latter. There is a small gap between hypolophid and metalophid, and no enamel features in this gap.

Two genera of fossil tapir (*Tapirus* and *Megatapirus*) have been found in southern China in the Quaternary (Zheng, 2004; Tong, 2005), and the latter is much larger than the former. The dental dimension of tapir remains from Juyuan Cave fall into the range of *Tapirus sinensis* (Colbert and Hooijer, 1953).

The teeth measurements from Juyuan Cave are large than those of *T. sanyuanensis* from Yanliang Cave, an early Early Pleistocene site also in Chongzuo, but smaller than those of *T. sinensis* from Sanhe Cave, a late Early Pleistocene site also in Congzuo. In addition, the *T. sinensis* from Juyuan Cave is the earliest record of this species, indicating an important biological event from *T. sanyuanensis* to *T. sinensis*.

3.1.5. Artiodactyla

The artiodactyls associated with *Gigantopithecus* unearthed from Juyuan Cave have been systematically described by Dong et al. (2010) and Dong and Zhang (2014) (Table 1). The identified taxa include some Neogene relics or typical Early Pleistocene species, such as *Hippopotamodon ultimus* (m3, Fig. 5H), *Sus xiaozhu*, *Muntiacus lacustris*, and *Megalovis guangxiensis* (m2, Fig. 5I).

The large-sized suid fossils from Juyuan Cave were initially described as “*Dicoryphochoerus ultimus*” (Han, 1987) by Dong et al. (2010). The taxonomic position of the former “*Dicoryphochoerus ultimus*” associated with *G. blacki* fossils from Guangxi, Guizhou, and Chongqing has been revised from *Dicoryphochoerus* to *Hippopotamodon* based on systematic research on both new and old materials (Dong and Zhang, 2014). *H. ultimus* is a valid species of this genus and ranges only in southern China during the early to middle stages of the Early Pleistocene. It is an ultimate representative of the Neogene relic *Hippopotamodon*.

The artiodactyls from Juyuan Cave are mostly similar to those from Sanhe Cave, Chongzuo (Jin et al., 2009), and Liucheng *Gigantopithecus* Cave in Guangxi (Han, 1987), which indicate Early Pleistocene age and tropical bush and forest environments favorable for habitation of primates such as *Gigantopithecus*.

3.2. Small mammals

3.2.1. Insectivora

The insectivores from Juyuan Cave consist of *Scaptochirus* sp., *Crocidura* sp., *Anourosorex quadratidens, Blarinella wannanensis* and *Soriculus fanchangensis* (Table 2).

The short-faced mole fossils include several isolated teeth: one upper fourth premolar (P4), one upper first molar (M1), one lower third premolar (p3) and one lower third molar (m3). The P4 is massive; M1 is little degenerated and narrow and long, with strong protocone and weak hypocone. The p3 is large, with developed talonid; the m3 is slightly degenerated. The above morphology suggests them to be *Scaptochirus* sp.

The white-toothed shrew is represented by an incomplete maxilla. The separation of the hypocone and protocone and no pigmentation show that this specimen should belong to *Crocidura*. An indeterminate species is cited here tentatively.

The *Anourosorex* fossil includes one incomplete mandible. It is comparable with *A. quadratidens* in the anterior border of ascending ramus not hiding the m3 in labial view, and the articulate process far away from the mandible foramen.

The short-tailed shrew fossils are represented by an incomplete maxilla with P4, M1and an incomplete mandible with m1–m3 (Fig. 7A). P4 with protocone; M1 with small protocone, developed metaloph and long entoloph; talon of M1 clearly projecting medial;

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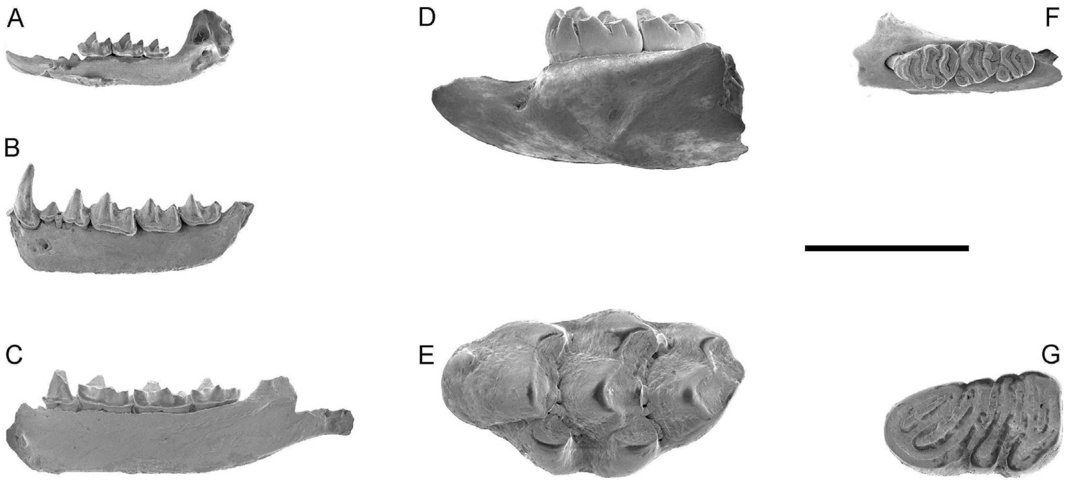

Fig. 7. The micro-mammalian fossils from Juyuan Cave. A, *Blarinella wannanensis* (one fragmentary mandible with m1–m3 – V22683.01); B, *Rhinolophus Youngi* (one fragmentary mandible – V22685.01); C, *Hipposideros pratti* (one fragmentary mandible with m1–m3 – V22686.02); D, *Leopoldamys edwardsioides* (One fragmentary mandible with m1 and m2 – V22696.01); E, *Rattus* sp. (M1 – V22697.01); F, *Niviventer preconfucianus* (One fragmentary maxilla with M1–M3 – V22694.01); G, *Typhlomys intermedius* (m1 – V22687.03). A–D, labial view; E–G, occlusal view. Scale: 8 mm for A–D and F, 2 mm for E and G.

m3 reduced; and presence of a horizontal crest within adductor fossa of mandible. Therefore, the specimens should be assigned to *Blarinella wannanensis* (Jin and Liu, 2009).

The *Soriculus* remains include one incomplete mandible. It is similar to *S. fanchangensis* by the lower cheek teeth laterally placed, with laterally compressed metaconid, lower entoconid and weak cigulun, and m3 having an entoconid (Jin and Liu, 2009).

The Insectivora assemblage from Juyuan fauna is mostly similar to that of Renzidong Cave, Anhui of the early Early Pleistocene (Jin and Liu, 2009).

3.2.2. Chiroptera

The bat remains from Juyuan Cave include three kinds of rhinolophids and three kinds of hipposiderids: the large rhinolophid (*Rhinolophus youngi*, Fig. 7B), the medium-sized rhinolophid (*Rhinolophus* cf. *R. affinis*), the large hipposiderid (*Hipposideros pratti*, Fig. 7C), and the medium-sized hipposiderid (*Hipposideros pleistocaenicus*).

3.2.3. Rodentia

The rodentia remains from Juyuan Cave are much more diversified than other micro-mammals, including petauristid, platacanthomyid, hystricid, arvicolid and murid.

The rodentia assemblage from Juyuan fauna consists of a few primitive species of Early Pleistocene, such as *Typhlomys intermedius* (Fig. 7G), *Hystrix magna, Hapalomys augustidens, Niviventer preconfucianus* (Fig. 7F), *Niviventer andersoni,* and *Leopoldamys edwardsioides* (Fig. 7D). The characteristics of this assemblage mostly resemble that of Longgupo (Chongqing) and Renzidong (Anhui) (Huang and Fang, 1991; Jin and Liu, 2009), and is more primitive than that of Sanhe Cave, Chongzuo (Jin et al., 2009).

4. Discussion

4.1. Characteristics and age of Juyuan fauna in Boyue Mountain

The mammalian assemblage discovered from Juyuan Cave of Boyue Mountain is composed of 20 species of large mammals and 25 species of small mammals. The abundance of *Gigantopithecus* specimens suggests that this giant ape was one of the most common taxa at that time or at least one of the most common to be deposited in the cave.

The large mammals of Juyuan fauna include a few Neogene relics, such as *Sinomastodon*, *Hippopotamodon*, and *Muntiacus lacustris*, and many Pleistocene extinct genera (e.g., *Gigantopithecus*, *Stegodon*, *Megalovis*, and *Bibos*). The small mammal fauna is characterized by common Early Pleistocene Oriental species, including *Anourosorex quadratidens*, *Soriculus fanchangensis*, *Typhlomys intermedius*, *Hapalomys augustidens*, *Niviventer preconfucianus*, and *Leopoldamys edwardioides*. Therefore, the Juyuan fauna has a notable Early Pleistocene character. The geographical distribution of *G. blacki* ranges from southern China to northern Vietnam (Tham Khuyen Cave). The representative faunas are from Sanhe Cave and Hejiang Cave in Chongzuo (Guangxi), Mohui Cave and Chuifeng Cave in Tiandong County (Guangxi), Liucheng *Gigantopithecus* Cave (Guangxi), Longgupo Cave in Wushan County (Chongqing), and Longgudong Cave in Jianshi County (Hubei). These faunas represent different ages of Pleistocene and all belong to the Oriental realm. Therefore, their geological sequence has a relatively high degree of comparability (Table 3).

The statistical study on the dental dimensions of *G. blacki* indicates that a certain consistency exists in terms of size variation and that there is a tendency for a gradual increase in the size of teeth (especially on premolar and molar) from the early to middle Pleistocene (Zhang, 1982; Zhang et al., 2015). Therefore, the dental dimensions of *G. blacki* have significance to judge the age of the site. The larger size of the *G. blacki* teeth, the more derived the associated fauna.

G. blacki from Juyuan Cave is different from its counterparts at the middle Pleistocene sites, such as Hejiang Cave also in Chongzuo and Tham Khuyen Cave in Vietnam (Ciochon et al., 1996; Zhang et al., 2014). The teeth of *G. blacki* in Hejiang and Tham Khuyen bear larger dimensions and more complex crenulations than those in Juyuan Cave. The middle Pleistocene faunas are also more derived than Juyuan fauna owing to disappearance of Neogene relic genera (such as *Sinomastodon* and *Hippopotamodon*), appearance of very limited Pleistocene extinct genera (only *Gigantopithecus, Stegodon* and *Megalovis*) and emergence of the progressive species, like *Ailuropoda baconi*. Therefore, the ages of Hejiang Cave and Tham Khuyen Cave are evidently younger than that of Juyuan Cave. *G. blacki* remains document the latest occurrence of *Gigantopithecus* (400–320 ka).

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The geological age of Sanhe Cave also in Chongzuo is estimated to be middle Early Pleistocene based on the faunal and paleomagnetic correlation (1.2–1.6 Ma) (Jin et al., 2009, 2014; Sun et al., 2014) or late Early Pleistocene by the coupled ESR/U-series method (890 ± 130 ka) (Shao et al., 2015). Both Sanhe and Juyuan faunas contain *Sinomastodon yangziensis*, *Stegodon huananensis*, *Ailuropoda wulingshanensis, Niviventer preconfucianus*, and *Leopoldamys edwardioides,* implying their contemporaneity. However, there are 9 extinct genera in Sanhe fauna which account for about 32% of the large mammals, and 25 extinct species which account for about 47% of total species of large mammals. These two proportions are both less than those of Juyuan fauna which are about 33% of extinct genera and 60% of extinct species (Table 4). Besides, Sanhe fauna includes a relatively derived type of rhino (*Rhinoceros sinensis*), while a primitive species of rhino (*R. fusuiensis*) exists in Juyuan fauna. In addition, the average sizes of the teeth of *G. blacki* and *Ailuropoda wulingshanensis* from Sanhe Cave are larger than those from Juan Cave. Accordingly, the age of Juyuan fauna is inferred to be a little earlier than that of Sanhe fauna.

In Mohui fauna, the extinct genera account for about 33% of the large mammals (also 33% in Juyuan fauna), and extinct species account for about 58% of total species of large mammals (60% in Juyuan fauna) (Table 4). The similar data on these two proportions indicate the close age of these two faunas, consistent with the paleomagnetic data. Moreover, the morphology and evolutionary level of the key taxa (*Ailuropoda*, *Tapirus* and *Rhinoceros*) from two faunas are similar to each other, also implying their contemporaneity. The age of Mohui Cave is estimated to be Early Pleistocene by the coupled ESR/U-series method (1.69 ± 0.22 Ma) (Shao et al., 2015).

According to the biochronological characteristics of the fauna, the mammalian assemblage from Longgupo (Chongqing), Liucheng *Gigantopithecus* Cave (Guangxi ZAR), and Chuifeng Cave (Guangxi ZAR) is relatively primitive, with small-sized teeth in *G. blacki* and a higher proportion of extinct genera and species. For example, the proportions of extinct species of large mammals from Longgupo, Liucheng, and Chuifeng faunas are respectively 80%, 60%, and 67% (Table 4). The faunas at the above sites have yielded primitive species, such as *Ailuropoda microta* and *Tapirs sanyuanensis*; while Juyuan fauna contains relatively advanced species, such as *Ailuropoda wulingshanensis* and *Tapirus sinensis*. The new combined chronologies (ESR, U-series and paleomagnetic dating) establish an Olduvai subchron (1.95–1.78 Ma) for the lowermost Chuifeng Cave sediments (Shao et al., 2014). Moreover, the proportion of extant species in Juyuan fauna is higher than those of the above early Early Pleistocene faunas. Therefore, the age of the Juyuan fauna is inferred to be younger than the above three faunas. From Table 4, the largest proportions of extinct genera and species of large mammals in Longgupo fauna indicate its earliest age while the smallest proportions in Hejiang fauna demonstrate that it is the youngest site.

Combined with the proportion of extinct genera and species and the dental dimensions of *Gigantopithecus* and *Ailuropoda*, the Juyuan fauna is slightly earlier than the middle Pleistocene Sanhe fauna, but later than the early Early Pleistocene Longguppo, Chuifeng and Liucheng faunas. The paleomagnetic data show that the fossil-bearing sediments in Juyuan Cave are of normal polarity (Sun et al., 2014). According to the biochronological evidence, the Juyuan sediments should be earlier than the Gilsa normal subchron and can be best correlated with the Olduvai normal subchron, giving an estimated age of 1.8 Ma (Fig. 8). In summary, the chronological sequence of *Gigantopithecus-Sinomastodon* faunas in southern China from Early to Middle Pleistocene is Longgupo-Liucheng-Chuifeng-Mohui and Juyaun-Sanhe-Hejiang.

4.2. *Paleoecology of Juyuan fauna in Boyue Mountain*

The composition of Juyuan fauna is distinctive. Statistics on family-level taxa in the fauna show that 46% of the total classes occur in the Oriental realm or tropical to subtropical. These include Rhinolophidae, Hipposideridae, Platacanthomyidae, Rhizomyidae, Hystricidae, Ailuridae, Gomphotheridae, Stegodontidae, Hylobatidae, Cercopithecidae, and Pongidae. Statistics at the genus-level shows that 33 genera, more than 90% of the total genera, belongs to the Oriental realm. These include *Rhinopithecus*, *Hipposideros*, *Rhizomys*, *Atheruru*, *Typhlomys*, *Eothenomys*, *Leopoldamys*, *Ailuropoda*, *Sinomastodon*, *Tapirus*, *Rhinoceros*, *Muntiacus*, *Gigantopithecus*, *Pongo*, *Nomascus*, *Macaca*, and so on. Comparison at the species-level shows that except for widespread taxa, the typical Palaearctic species are missing. Apparently, this fauna is a typical Oriental tropical fauna.

The Juyuan fauna is quite different from other *Gigantopithecus-Sinomastodon* faunas in southern China. As one of the northernmost sites yielding *Gigantopithecus blacki*, the Longgupo fauna contains both Palaearctic (such as Cricetidae, *Mimomys* and Hyaenidae) and Oriental elements, indicating its transitional characteristics (Huang and Fang, 1991). The proximity of Liucheng *Gigantopithecus* Cave and Juyuan Cave results in the occurrence of similar general features in the two faunas. However, the former includes some Palaearctic taxa (such as Hyaenidae, *Felis teilhardi,* and Equidae), suggesting that zoogeographic connections between south and north China still existed during the early Early Pleistocene (Pei, 1987). Given the combination of mammals in the assemblage, the Juyuan fauna can be characterized as an Oriental tropical fauna.

Among the Juyuan fauna, tropical mammals are dominant, indicating a hot tropical climate. There are some Oriental forest mammals of the Hengduanshan Mountains in this fauna, such as *Anourosorex quadratidens*, *Blarinella* and *Soriculus,* which now mainly live in montane seasonal rainforest around 1000 m above sea level. However, Juanyuan Cave is only 206 m above sea level and the highest peak in Chongzuo area is just about 600 m, indicating that topographic relief was more pronounced during the Early Pleistocene. The arboreal Chiroptera and Rodentia fossils are common in Juyuan fauna, such as *Rhinolophus youngi, Niviventer preconfucianus* and *Leopoldamys edwardsioides*. In addition, there are also many primate taxa preferring forests. Consequently, the paleoecological setting at Juyuan Cave can be reconstructed as tropical forest and shrub.

5. Conclusions

The Juyuan fauna in Boyue Mountain, Guangxi ZAR consists of 45 large and small mammalian species and is characterized by the combination of *G. blacki*, *Sinomastodon yangziensis*, *Ailuropoda wulingshanensis*, *Stegodon huananensis*, and *Rhinoceros fusuiensis,* showing the features of a typical Early Pleistocene *Gigantopithecus-Sinomastodon* fauna of southern China. The Juyuan fauna is mostly similar to Mohui fauna, in addition to an estimated age of 1.8 Ma by paleomagnetic analyses. There have been abundant remains of *G. blacki* and associated mammals recovered from a number of important cave sites spanning different periods of Pleistocene from southern China, as well as considerable progress in research on chronology using various methods, such as paleomagnetism, ESR and U-series dating.

Jin et al. (2009) considered that the faunas including *G. blacki* fossils in southeast Asia can be divided into three temporal stages: the early stage (2.58–1.8 Ma), middle stage (1.77–1.07 Ma) and late stage (1.07–0.42 Ma). Afterwards, the Early Pleistocene *Gigantopithecus* fauna from Chongzuo area, which has been revised as *Gigantopithecus-Sinomastodon* fauna by Wang Y et al. (2014), has

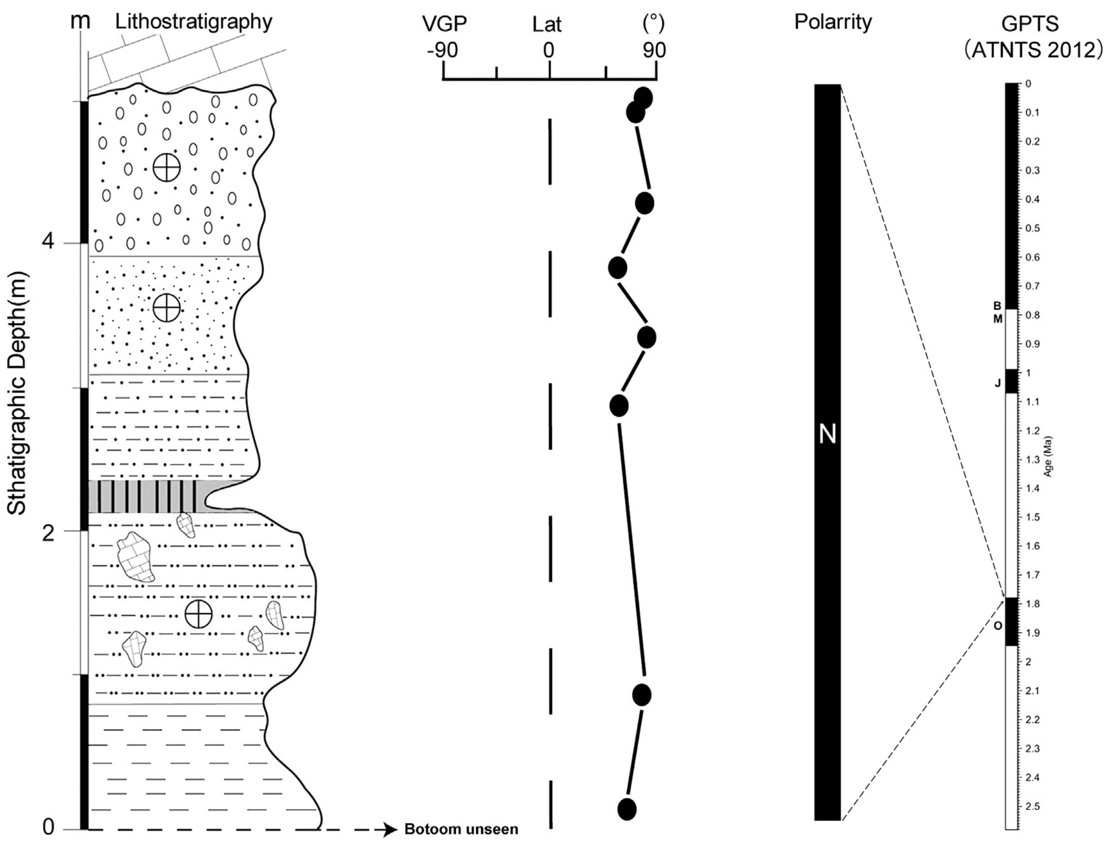

Fig. 8. Stratigraphic sections and magnetostratigraphy of the Juyuan Cave of Boyue Mountain, and its correlation with the geomagnetic polarity time scale (GPTS).

also been divided into three temporal stages: the early stage (2.6–1.8 Ma), middle stage (1.8–1.2 Ma) and late stage (1.2–0.8 Ma) (Jin et al., 2014). The present comprehensive study, based on the updated information, re-divides the faunas including *G. blacki* fossils in East Asia into four chronological stages.

The stage of the early Early Pleistocene (between the Gauss-Matuyama boundary and the bottom of Olduvai normal subchron, 2.58–1.95 Ma) is represented by the Longgupo fauna (Chongqing), Chuifeng fauna (Guangxi) and Liucheng fauna (Guangxi), which include *G. blacki* with relatively small teeth, some Neogene relics (e.g., *Sinomastodon*, *Hesperotherium* and *Hippopotamodon*), and taxa that make their first appearance during the Pleistocene (e.g., *Sinomastodon jiangnaensis, Ailuropoda microta, Megantereon microta, Sinicuon dubius*, and *Tapirus sanyuanensis*).

The stage of the middle Early Pleistocene (between the Olduvai subchron and Cobb Mountain subchron, 1.95–1.24 Ma) is represented by the Mohui fauna from Tiandong, Juyuan fauna and Sanhe fauna from Chongzuo. This stage is characterized by the increased body size of *G. blacki, Ailuropoda and Tapirus* (compared to the previous stage), the disappearance of primitive species, such as *Ailuropoda microta*, *Cuon dubius,* and *Tapirus sanyuanensis,* and the first appearance of *Ailuropoda wulingshanensis*, *Cuon antiquus*, *Sinomastodon yangziensis* and *Tapirus sinensis*. The faunas of this stage possess transitional features.

The stage of the late Early Pleistocene (between the Cobb Mountain subchron and Matuyama-Brunhes boundary, 1.24–0.78 Ma) is represented by the Queque fauna from Chongzuo. This stage is characterized by the distinctly increased dental dimensions of *G. blacki, Ailuropoda and Tapirus*, the last appearance of *Sinomastodon yangziensis*, and the first appearance of *Ailuropoda baconi*, *Stegodon orientalis* and *Bubalus brevicornis chowi* (Dong et al., 2014; Jin et al., 2014).

The stage of the middle Pleistocene (between the Matuyama-Brunhes boundary and the middle Brunhes chron, 0.78–0.32 Ma) is represented by the Hejiang fauna (Guangxi) and Tham Khuyen fauna (Vietnam). This stage is characterized by a higher proportion of extant species and the disappearance of Early Pleistocene taxa, such as *Sinomastodon yangziensis, Stegodon huananensis* and *Ailuropoda wulingshanensis* which are replaced by the typical middle Pleistocene taxa (*Stegodon orientalis* and *Ailuropoda baconi*).

Based on comparisons among the *Gigantopithecus* fossils from Pleistocene sites in southern China and Vietnam, the *Gigantopithecus* teeth show an evolutionary tendency to increase in size from early to middle Pleistocene. The first increase of dental dimensions of *G. blacki* from Juyuan Cave implied favourable conditions for this great ape at that time.

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