Quaternary International 563 (2020) 29–37

Contents lists available at ScienceDirect

Quaternary International

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

A late Middle Pleistocene mammalian fauna recovered in northeast Guangxi, southern China: Implications for regional biogeography

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ARTICLE INFO

Keywords:
Pongo
Quaternary
Nanling mountains
Diaozhongyan cave
South China

ABSTRACT

In Guangxi Zhuang Autonomous Region, southern China, Quaternary mammalian assemblages, commonly known as "*Stegodon-Ailuropoda* fauna", are well documented in the central and southwest parts of the region. Unfortunately, our knowledge of Quaternary biogeographic variation in other areas of Guangxi is poor due to limited systematic investigations. Here, we report the faunal remains from the newly discovered Diaozhongyan ("DZY") cave site in northeast Guangxi. Our initial excavation in autumn 2016 resulted in the removal of 10 square meters of sediment and the discovery of 304 pieces of large mammal teeth. Biostratigraphic correlations indicate a late Middle Pleistocene age and *in situ* fossil teeth and calcites were Uranium-series dated to ~210 ka. The DZY faunal assemblage consists of many typical components of the traditional "*Ailuropoda-Stegodon*" fauna representative of southern China. Interestingly, giant pandas, identified as *Ailuropoda melanoleuca baconi*, are one of the dominant components of the DZY fauna (15% of the entire assemblage). However, giant pandas rarely dominate Quaternary faunal assemblages in southern China. In addition, fossil orangutan (*Pongo weidenreichi*), one of the most common species in central and south Guangxi during the Middle Pleistocene, is absent in DZY in northeast Guangxi. Further, fossil orangutans have not been reported from other sites in Hunan or Hubei province. We hypothesize that the Nanling Mountains served as a geographic barrier for this species. Fossil orangutans are present southwest of this biogeographic line, but are absent northeast of the line. This biogeographic boundary needs to be further evaluated with additional studies.

1. Introduction

Systematic survey of Pleistocene cave deposits in Guangxi, southern China began in the 1950s. As a result, many important Quaternary fossil localities were discovered. For instance, the *Gigantopithecus* sites, Liucheng (Pei, 1957b) and Daxin (Pei and Woo, 1956), were identified in central and southwest Guangxi, as well as modern human fossils found in Liujiang (Woo, 1959) and Laibin (Jia and Woo, 1959) in central Guangxi. The *Gigantopithecus* site in Daxin is the first locality to yield *in situ Gigantopithecus* fossils in southwest Guangxi (Pei and Woo, 1956). Further, the discovery of the jaw bone in Liucheng *Gigantopithecus* cave brought to an end the controversy over the purported "giant ape" or "giant man" of southern China (Pei, 1957b). The excavation of Liucheng *Gigantopithecus* cave from 1957 to 1963 revealed the largest sample of *Gigantopithecus* (three mandibles and 1006 teeth) and an abundant fossil mammalian assemblage representing the Early Pleistocene in south China (Woo, 1962; Han, 1987; Pei, 1987). The human skeleton from Tongtianyan, Liujiang represents one of the few well-preserved modern *Homo sapiens* fossils in Pleistocene East Asia (Woo, 1959; Bae et al., 2017).

Since 2000, Quaternary cave sequences from the Bubing and Chongzuo regions in southwest Guangxi have been systematically surveyed, excavated, and studied by the Guangxi Natural History Museum, the Anthropology Museum of Guangxi, and the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. As a result of these large scale interdisciplinary studies a number of new sites were discovered (Fig. 1) and the sequence of Quaternary mammalian fossils, including hominins, are much better understood (Wang et al., 2005, 2007; Liu et al., 2010; Bae et al., 2014, 2018; Jin et al., 2014). Although Bubing and Chongzuo are geographically not far from each other, the variation in coeval Pleistocene faunas suggests different ecological habitats. For example, *Pongo* appears commonly in both

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https://doi.org/10.1016/j.quaint.2019.12.013
Received 23 May 2019; Received in revised form 18 November 2019; Accepted 12 December 2019
Available online 14 December 2019
1040-6182/

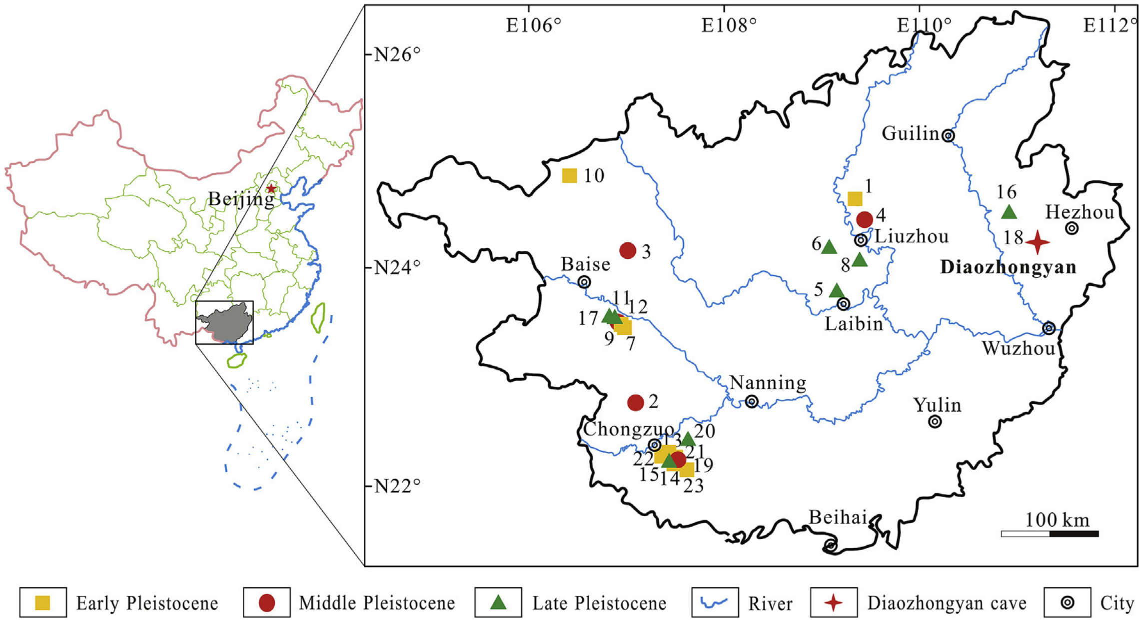

Fig. 1. Fossil localities in Guangxi during the Pleistocene and the geographical position of DZY Cave. 1, Liucheng (*Gigantopithecus* cave) (Pei, 1957b); 2, Daxin cave (Heidong) (Pei and Woo, 1956); 3, Bama cave (Zhang et al., 1975); 4, Bijiashan cave (Han et al., 1975); 5, Qilinshan cave (Jia and Woo, 1959); 6, Ganqian cave (Tubo) (Li et al., 1984); 7, Chuifeng cave (Wang, 2009); 8, Liujiang cave (Tongtianyan) (Woo, 1959); 9, Mohui cave (Wang et al., 2005); 10, Jinyin cave (Jin et al., 2007); 11, Dingmo cave (Li et al., 1985); 12, Wuyun cave (Chen et al., 2002); 13, Sanhe cave (Jin et al., 2008); 14, Queque cave (Jin et al., 2014); 15, Zhiren cave (Jin et al., 2009a); 16, Jimuyan cave (Wang et al., 2011); 17, Luna cave (Bae et al., 2014); 18, DZY cave; 19, Hejiang cave (Zhang et al., 2014); 20, Nanshan cave (Wang and Mo, 2004); 21, Juyuan cave (Dong et al., 2010); 22, Baikong cave (Jin et al., 2014); 23, Yanliang cave (Zhang et al., 2016).

regions from the Early to Middle Pleistocene. *Gigantopithecus* disappears in the Bubing Basin after the end of the Early Pleistocene, but continues to persist in Chongzuo up through the late Middle Pleistocene (Jin et al., 2014; Wang et al., 2014b; Zhang et al., 2014).

As a result of these extensive research programs, Quaternary mammalian faunas are abundant and well documented in southwest Guangxi. However, our knowledge of vertebrate faunas in north and northeast Guangxi is poor. In order to rectify this problem beginning in 2016 the Anthropology Museum of Guangxi began to conduct a systematic cave investigation in northwest Guangxi. To date, dozens of caves have been surveyed, though the majority of them lack fossiliferous deposits. Fortunately, a rich mammal fossil assemblage was discovered and excavated in Diaozhongyan ("DZY") cave, northeast Guangxi. Here, we present the preliminary assessment of the DZY cave faunal remains in its broader biogeographic context.

2. Geological background and context setting

Diaozhongyan (24°14′34.5″ N, 111°12′6.8″ E) is located in Chunfu Village, Zhaoping County in Hezhou City, northeast Guangxi (Fig. 1). The cave was originally discovered by a research team from the Anthropology Museum of Guangxi when they were on a field survey expedition to northeast Guangxi in 2016. This cave formed in a limestone hill that is surrounded by a shallow karst erosion valley. The cave entrance faces north and is 6 m wide and 12 m in height. The entrance sits approximately 60 m above the valley floor (Fig. 2). The entrance leads into a narrow chamber that is only 1 m wide and 3 m in height. Further into the cave it branches into two smaller chambers. The sediment is well-preserved and concentrated in the corridor and terminal chamber. The latter room is about 6 m in length, 2 m in height, and 1–3 m in breadth.

Three test pits (A, B, C) were set up in the cave. Pit A (1 × 2 m) and Pit B (1.2 × 2.6 m) were set in the corridor and Pit C in the terminal chamber. Because this back room is irregular in shape, Pit C was 4 m in length but varied from 1.2 to 3 m in breadth (Fig. 3). Pit A and Pit C were selected for systematic excavation, while Pit B was preserved intact for future fieldwork. Pit A was excavated down to the limestone bedrock to a depth of 60 cm and Pit C was excavated down to a depth of 1.7 m. Both pits were dug down at 10 cm arbitrary increments. Because the sediment was highly compacted, hammers and chisels were used to remove large blocks of sediment. Medium and large sized mammalian fossils could still be identified during the initial excavation process this way. Smaller fossils were collected by dry-sieving through 4 mm mesh screens which was performed at the entrance of the cave.

The basic stratigraphic profile of the cave is from Pit C because it is the deepest test pit and the fossil density was the highest. The stratigraphy is divided into four layers (from top to bottom) (Fig. 4):

I, Brown sandy clay (20–40 cm), contains a few mammal fossils and cave pearls;
II, Light brown sandy clay with a few limestone breccias (20–45 cm), contains some mammal fossils and cave pearls;
III, Brown sandy clay with limestone breccias (70–130 cm), contains abundant mammal fossils;
IV, Brown silt (15 cm in minimum), fossil sterile layer.

3. Faunal assemblage

In general, the vertebrate fossils are in good condition. However, most of the teeth are rootless, almost surely due to porcupine gnawing. To date, a total of 304 isolated mammal teeth were recovered during the excavation. These fossils belong to 6 orders: Artiodactyla; Perissodactyla; Proboscidea; Carnivora; Rodentia; Primates (Figs. 5 and 6). The fossils were further identified to genus and when possible species levels (Table 1). In general, the DZY assemblage can be considered a typical "*Stegodon-Ailuropoda* fauna" that is widely abundant in the Middle Pleistocene in southern China (Pei, 1957a; Han and Xu, 1985; Wang et al., 2007; Norton et al., 2010).

The DZY collection includes four extinct species: *Ailuropoda melanoleuca baconi*, *Stegodon* sp., *Tapirus sinensis* and *Rhinoceros sinensis*, but lack any evidence of Early Pleistocene taxa. The characteristics of this assemblage resembles that of Wuyun cave (Chen et al., 2002) in the

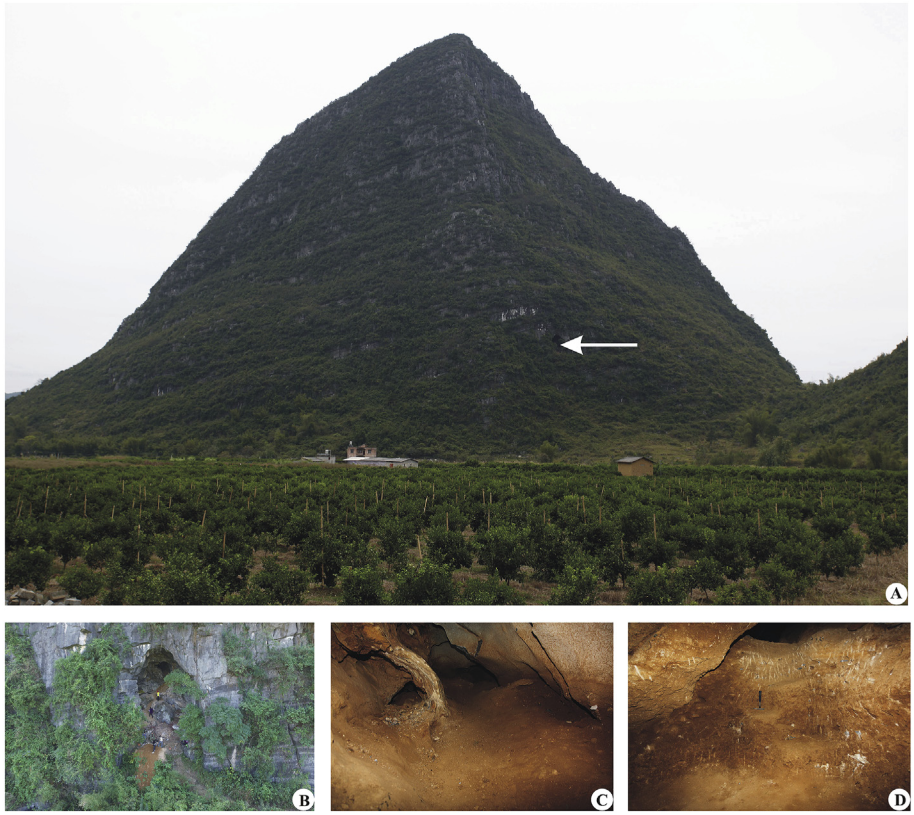

Fig. 2. Map showing basic situation of the DZY Cave Site. (A) Landscape around the DZY Cave (from northeast), the arrow points to the cave entrance; (B) the aerial figure of the cave entrance; (C) interior corridor before excavation; (D) stratigraphic profile of the C after excavation.

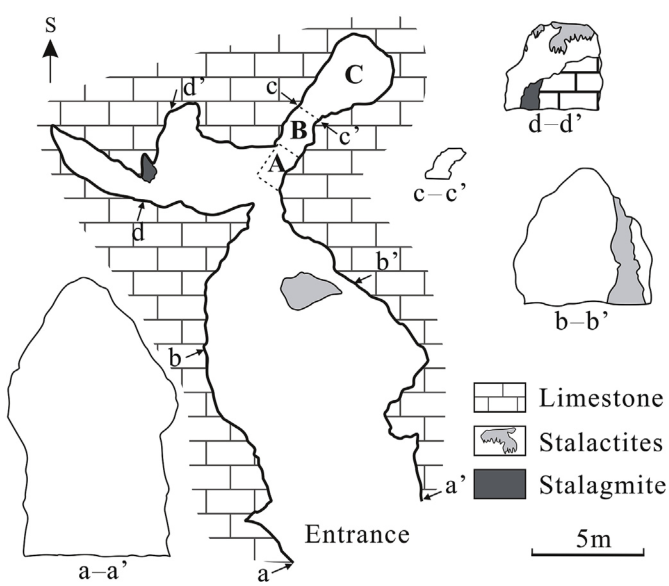

Fig. 3. Plan and sections of the DZY Cave.

Bubing Basin that was chronometrically dated to the late Middle Pleistocene around 200 ka (Rink et al., 2008).

Based on Number of Identifiable Specimen (NISP) counts on the teeth, Artiodactyls, accounting for 46.7% of the total, represent the most abundant taxa, followed by Carnivores (19.4%), Rodents (15.1%), Perissodactyls (7.9%), Proboscideans (6.9%), and Primates (3.9%). Based on NISP counts of the identified genera, *Cervus*, *Sus*, *Ailuropoda* and *Hystrix* are the most common. A Minimum Number of Individuals (MNI) analyses that at least 39 individuals. By MNI, the fossils of species at DZY are: *Cervus* (17.9%), *Sus* (15.4%), *Hystrix* (15.4%), *Ailuropoda* (10.3%), *Macaca* (7.7%), *Arctonyx* (7.7%), *Muntiacus* (2.6%), Bovinae (2.6%), Caprinae (2.6%), *Tapirus* (2.6%), *Stegodon* (2.6%), *Ursus* (2.6%), *Trachypithecus* (2.6%) and *Hylobates* (2.6%) in descending order of abundance. The MNIs of the DZY fauna also indicate *Cervus*, *Sus*, *Hystrix* and *Ailuropoda* are dominate taxa (Table 1).

Table 2 lists the presence/absence of macromammals from DZY and other regional faunal collections from the Middle Pleistocene to Late Pleistocene in southern China, specifically Wuyun, Luna, Zhiren, Jimuyan, Fuyan and Yangjiawan cave 1 (Table 2).

Wuyun cave, located in Bubing Basin, southwest of Guangxi, was excavated in 1999. *In situ* travertine and associated mammal fossils have been dated to 200 to 300 ka by U-series and Electron Spin Resonance (ESR) analyses (Wang et al., 2007; Rink et al., 2008). A number of extinct species appear in Wuyun, such as *Ailuropoda melanoleuca baconi*, *Stegodon orientalis*, *Pongo pygmaeus*, *Tapirus sinensis*, *Megatapirus augustus*, *Rhinoceros sinensis* and *Elephas maximus* (Chen et al., 2002).

Luna cave, located in Tiandong in the Bubing basin, dates to 70–120 ka by MC-ICP-MS analyses. The associated mammalian assemblage contains two extinct species, including *Ailuropoda melanoleuca baconi* and *Stegodon orientalis*. The cave is best known for the presence of two teeth assigned to modern *Homo sapiens* (Bae et al., 2014).

Zhiren cave is located in Chongzuo, which is approximately 150 km south of the Bubing basin. The Zhiren fauna is characterized by hominin fossils thought to represent mid-Pleistocene *Homo* or early modern *H. sapiens* (Jin et al., 2009a; Liu et al., 2010). Interestingly, due to the absence of *Ailuropoda melanoleuca* and *Stegodon orientalis*, the Zhiren fauna differs from the typical "*Ailuropoda-Stegodon*" faunal complex of the Middle Pleistocene. Based on a combination of biostratigraphy and U-series dating the Zhiren cave deposits date to ~110 ka (Liu et al., 2010). A more recent dating program that relied on a combination of paleomagnetic, stratigraphic, and optically stimulated luminescence

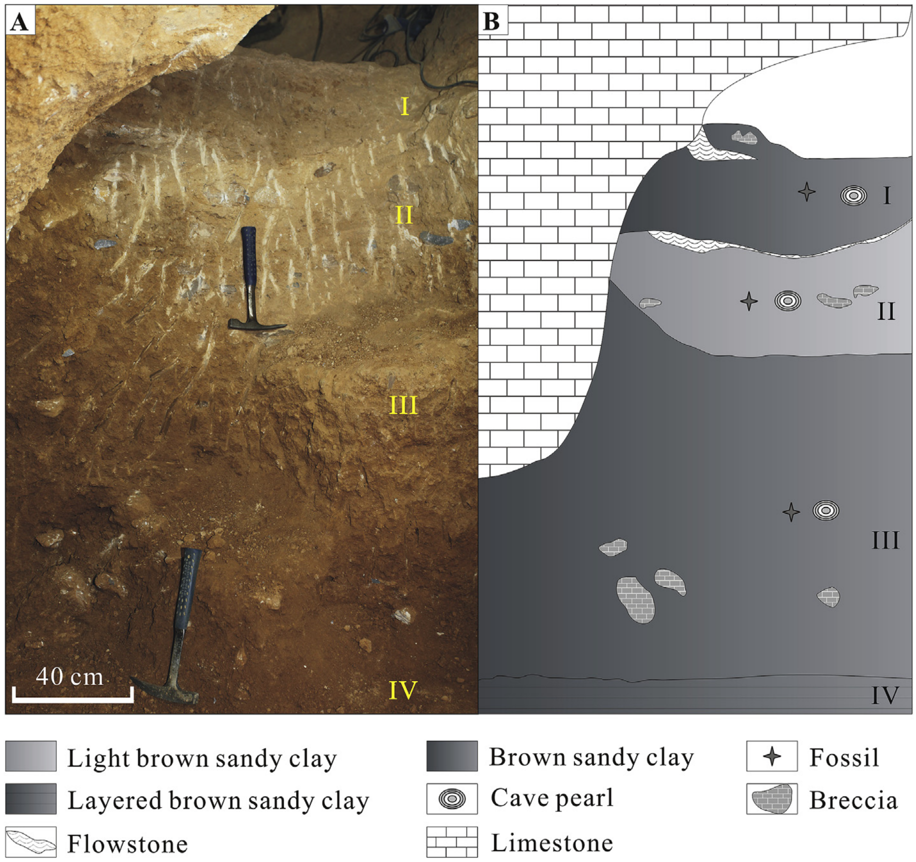

Fig. 4. Stratigraphic profile at Pit C of the DZY Cave.

dating more confidently bracketed the fossil assemblage to 116–106 ka (Cai et al., 2017).

Jimuyan cave is located in Pingle County, northeast Guangxi. It is best known for the presence of modern human fossils. The associated mammalian assemblage contains four species that are either extinct or at least no longer present in this region, including *Pongo pygmaeus weidenreichi*, *Ailuropoda melanoleuca baconi*, *Stegodon orientalis* and *Tapirus sinensis*. The faunal assemblage is similar to Zhiren cave except that *Tapirus sinensis* is absent and *Megatapirus augustus* is present (Wang et al., 2011). A phylogenetic line can be tentatively proposed: *Tapirus sanyuanensis* - *Tapirus sinensis* - *Megatapirus augustus* (Tong and Xu, 2001). However, *Tapirus sinensis* and *Megatapirus augustus* appeared simultaneously in Wuyun cave, a cave that only dates to 200–300 ka (Rink et al., 2008). Based on faunal correlations with Zhiren cave and Wuyun cave then, the age of the Jimuyan cave fauna should be a little earlier or equivalent to the Wuyun cave fauna. Thus, the Jimuyan cave fauna should be assigned to the late Middle Pleistocene.

Fuyan cave is located in Hunan Province and considered to be the southern margin of the North Subtropical Zone. The cave has been systematically excavated from 2011 to 2013 and yielded forty seven modern human teeth and an abundant fossil mammalian assemblage. The mammalian fossil assemblage is composed of thirty eight species. A few of the taxa are currently extinct, including *Ailuropoda melanoleuca baconi*, *Stegodon orientalis*, *Megatapirus augustus* and *Crocuta ultima*. The dates for Fuyan cave are tentatively bracketed between 80 and 120 ka based on biostratigraphy and a stalagmite that formed in the area of the human fossils (Liu et al., 2015; but see Michel et al., 2016).

The mammal assemblage from Yangjiawan cave 1 is similar to Fuyan Cave, except no hominin fossils were discovered. Extinct taxa include *Ailuropoda melanoleuca baconi*, *Stegodon orientalis*, *Crocuta ultima*, *Felis teilhardi* and *Megatapirus augustus* (Zou et al., 2016).

Compared with the above-mentioned regional fauna, the DZY fauna may be considered a representative of the typical "*Ailuropoda-Stegodon*" faunal complex. The presence of *Ailuropoda melanoleuca baconi*, *Stegodon* sp., *Rhinoceros sinensis*, and *Tapirus sinensis* distinguishes DZY from the Early Pleistocene Gigantopithecus-Sinomastodon fauna. Other Late Pleistocene dominant taxa (e.g., *Elephas maximus*) are absent. Interestingly, orangutan (*Pongo weidenreichi*), one of the most common species in central and south Guangxi during the Middle Pleistocene does not appear in the cave. Based on biochronology the age of DZY can be confidently assigned to the late Middle Pleistocene.

4. Discussion

Extensive research over the past several decades in Bubing and Chongzuo has contributed to a deeper understanding of Quaternary mammal evolution in southwest Guangxi (Wang et al., 2007; Jin et al., 2009a). As a result of these interdisciplinary studies, it is now realized that South China was not a stagnant environment, but rather a dynamic one where various faunas appeared and disappeared over time. The Pleistocene faunal complex of southern China is divided into three stages: Early Pleistocene Gigantopithecus-Sinomastodon fauna; Middle Pleistocene Ailuropoda- Stegodon fauna; Late Pleistocene Asian elephant fauna (Jin et al., 2007, 2009a; 2009b; Rink et al., 2008; Wang et al., 2007, 2014b; 2014c; Zou et al., 2016). Except for the Jimuyan Cave faunal assemblage, which displays similar characteristics of the southern Guangxi Zhiren Cave, northeast Guangxi is poorly known. The DZY fauna is very similar to other Middle Pleistocene collections in south China, except for two noticeable differences. First, *Ailuropoda melanoleuca baconi* is a dominant taxon in DZY (15% of the entire faunal assemblage). Second, there is a complete absence of *Pongo*, which is a very common species during the Middle Pleistocene in central and south Guangxi.

Currently, more than 30 sites, that altogether span the Pleistocene,

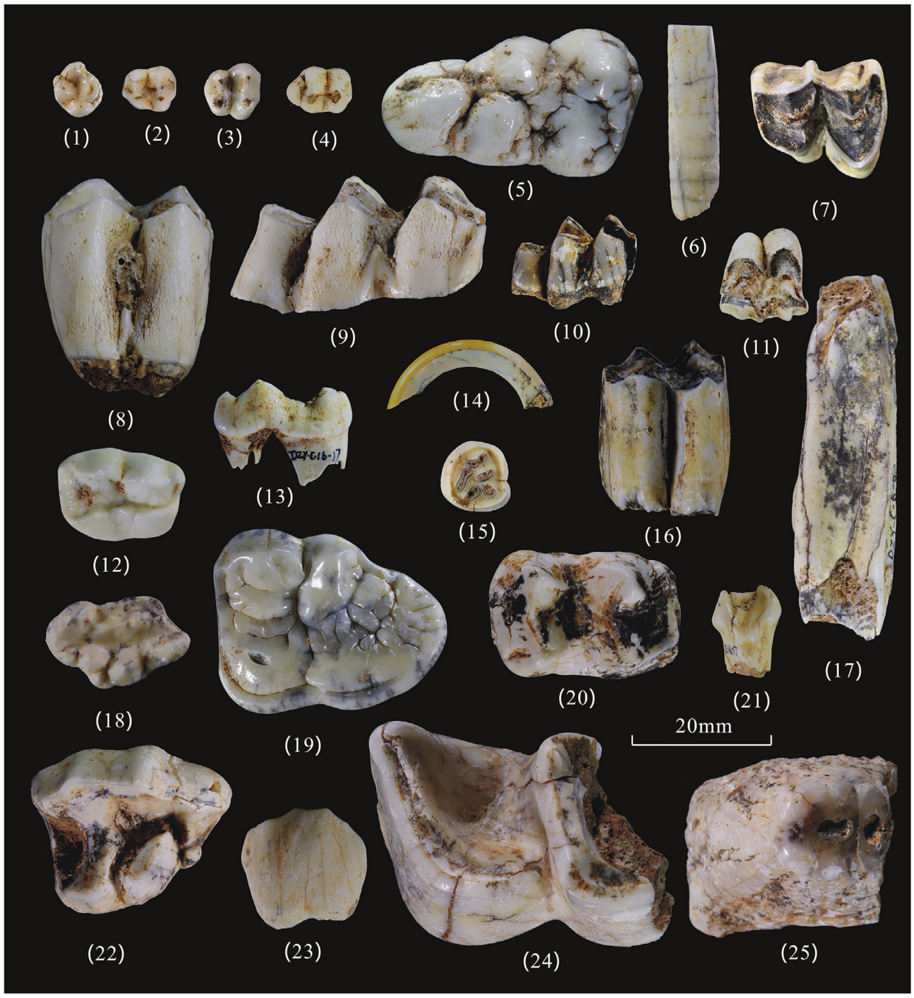

Fig. 5. Mammal fauna from the DZY Cave. (1) *Hylobates* sp.; (2) *Macaca* sp.; (3–4) *Trachypithecus* sp.; (5–6) *Sus scrofa*; (7–9) *Cervus* sp.; (10–11) *Muntiacus* sp.; (12–13) *Ursus thibetanus*; (14–15) *Hystrix subcristata*; (16) Caprinae; (17) Bovinae gen. et sp. indet.; (18) *Arctonyx collaris*; (19) *Ailuropoda melanoleuca baconi*; (20–21) *Tapirus sinensis*; (22–24) *Rhinoceros sinensis*; (25) *Stegodon* sp.

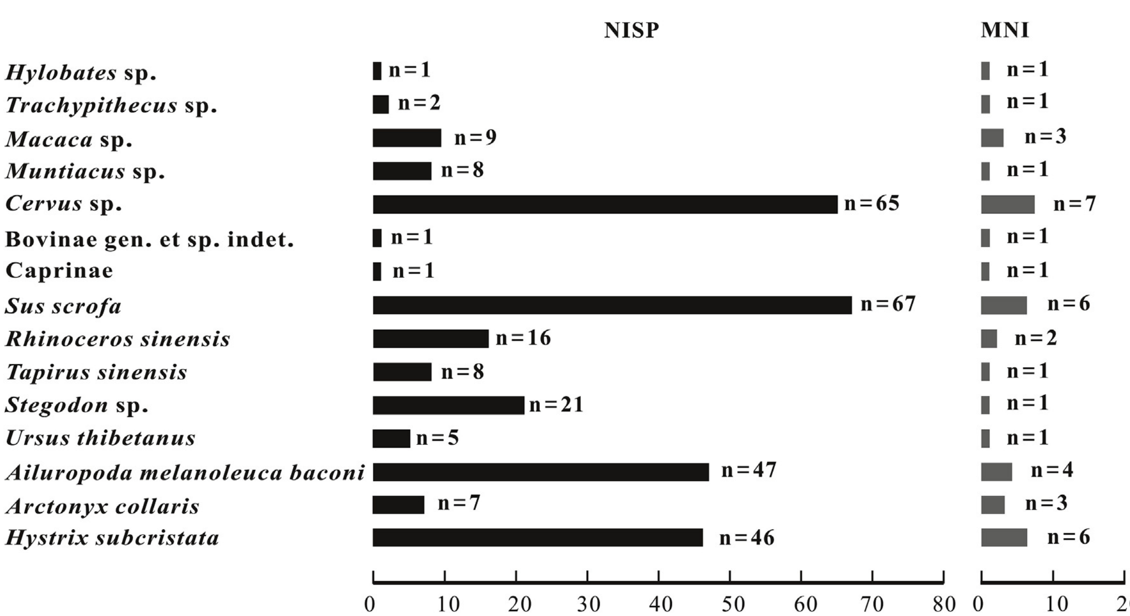

Fig. 6. NISP and MNI counts based on teeth of mammalian taxa from DZY Cave.

Table 1
Detailed mammalian faunal lists of DZY (both fragmented and complete teeth).

Species	N	%N	MNI	%MNI	Teeth
Artiodactyla Owen, 1848	142	46.7	16	41.0	
Muntiacus sp.	8	2.6	1	2.6	1R M1/2, 1L M3, 1L i1, 1R p2, 1R m1, 1R m2, 1L m3 and 1R M3
Cervus sp.	65	21.4	7	17.9	1R di2, 1L dm1, 2R I1, 5R P2, 1R P3, 1L P4, 4R P4, 2R M1, 1L M2, 2L M3, 2R M3 1L i1, 2L i2, 2R i2, 1L p2, 2R p2, 1L p3, 2R p3, 2L p4, 2R p4, 7L m1, 2R m1, 2R m2, 4L m3, 2R m3 and 11 incomplete teeth
Bovinae gen. et sp. indet.	1	0.3	1	2.6	Just half tooth
Caprinae	1	0.3	1	2.6	1R M1/2
Sus scrofa	67	22.0	6	15.4	1L DP3, 1L dp4, 1R dp4, 1L I2, 1R I2, 4C, 1L P1, 1L P3, 1R P3, 1L P4, 2R P4, 2L M1, 2R M1, 2L M2, 1R M2, 2L M3, 6R M3 1R i1, 1L i2, 1L i3, 1L p1, 1L p2, 2R p2, 3L p3, 1L p4, 5R p4, 1R m1, 5L m2, 2R m2, 2L m3, 2R m3 and 9 pieces
Perissodactyla Owen, 1848	24	7.9	3	7.7	
Rhinoceros sinensis	16	5.3	2	5.1	1R dp1, 1L DP1, 2R DP1, half R m3 and 11 pieces
Tapirus sinensis	8	2.6	1	2.6	1L I2, 1R I2, 1R p4 and 5 half teeth
Proboscidea Illiger, 1811	21	6.9	1	2.6	
Stegodon sp.	21	6.9	1	2.6	21 pieces
Carnivora Bodwich, 1821	59	19.4	8	20.5	
Ailuropoda melanoleuca baconi	47	15.5	4	10.3	2L P2, 2R P2, 1L P3, 1L P4, 1R P4, 1L M1, 1R M1, 1L M2, 1R M2, 1L p2, 2R p2, 3R p3, 1L p4, 2R p4, 3L m2, 4R m2, 1L m3, 1R m3, and 18 incomplete teeth
Ursus thibetanus	5	1.6	1	2.6	1L P4, 1R M1, 1R m1, half R m1 and half L M3
Arctonyx collaris	7	2.3	3	7.7	2L M1, 3R M1, 1L m1 and 1R m1
Rodentia Bowdich, 1821	46	15.1	6	15.4	
Hystrix subcristata	46	15.1	6	15.4	4L C, 4R C, 1L P4, 5R P4, 1L M1, 6R M1, 4R M2, 2L M3, 1R M3, 2l c, 2L p4, 3L m1, 3L m2, 4L m3 and 4R m3
Primates Linnaeus, 1758	12	3.9	5	12.8	
Macaca sp.	9	3.0	3	7.7	1L P4, 3R M2, 2L M3, 1L i1, 1R p4 and 1L m1
Trachypithecus sp.	2	0.7	1	2.6	1L M2 and 1R m3
Hylobates sp.	1	0.3	1	2.6	1R M2
Total	**304**	**100.0**	**39**	**100.0**	

have reports of orangutan fossils in southern China, distributed in Guangxi, Guangdong, Yunnan, Guizhou and Hainan (Wang et al., 2009, 2014a; Harrison et al., 2014). In south Guangxi, *Pongo* is considered a common species during the Middle Pleistocene, with Wuyun from Bubing Basin a representative example (Zhao et al., 2009). To date, there are also some Pleistocene mammalian fossil sites where *Pongo* is absent. These sites have been found in northeastern Guangxi and further north, such as Daoxian in Hunan Province and Yangjiawan in Jiangxi Province. Fossil orangutans (*Pongo weidenreichi*) do not appear in DZY, nor in any other sites in Hunan or Hubei province. Interestingly, fossils orangutans were discovered at Jimuyan, a cave only 100 km away from DZY. Although DZY and Jimuyan are not geographically too far apart from each other, the variation in the presence/absence of *Pongo* suggests different ecological habitations. This evidence suggests that a physical boundary between northeast Guangxi and central China existed for *Pongo*. Based on the distribution of fossil orangutan sites and the range of the Nanling Mountains, a biogeographic boundary can be clearly delineated (Fig. 7).

The Nanling Mountain area is a clear regional demarcation line. This was confirmed by researchers from Sun Yat-Sen University through the use of Geodetector, a new spatial analysis model that, based on variables such as temperature, precipitation, vegetation type and soil type, can quantitatively identify ecological zones (Wang and Dong, 2018). Based on the planting system and the accumulation of daily temperature, the sub-tropical belt is divided into three sub-belts: the south, the middle and the north sub-tropics (Qiu, 1984). As an important natural dividing line between the south-subtropical and mid-subtropical regions in China, the Nanling Mountain area is comprised of a series of five connected mountains ranges: Yuechengling, Dupangling, Mengzhuling, Qitianling and Dayuling Mountains (Huang, 1959; Editorial board of encyclopedia of China, 1992). The region forms an important ecological barrier in southern China that marks the difference between precipitation and temperature on the northern and southern sides of the Nanling Mountain Range (Zhou et al., 2018). The Nanling Mountain Range has a typical subtropical flora, which is characteristic of the floristic transition from tropical to temperate elements (Chen and Zhang, 1994). Ecologically, evergreen broad-leaved forests is the natural vegetation of subtropical regions (Corlett, 2013). Comparing with other areas at the same latitudes, the Nanling Mountains is considered to be representative of one of these subtropical evergreen broad-leaved forest regions (Zhou et al., 2018). The common species of the “Ailuropoda-Stegodon” faunal complex are primarily distributed in the subtropical zone, but some tropical species mainly live in the tropical and south-subtropical zone. Examples of such taxa are *Hylobates*, *Pongo*, *Rhinoceros sinensis*, *Megatapirus augustus* and *Elephas maximus* which indicate a forest environment with features of the south of mid-subtropical climate (Li et al., 2015).

Extent *Pongo* (*Pongo pygmaeus*, *Pongo abelii* and *Pongo tapanuliensis*) are representative members of evergreen tropical rain forest communities (MacKinnon, 1974; Davies, 1986; Payne and Prudente, 2008; Nater et al., 2017). As such, the presence of *Pongo* in fossil assemblages has often been used as an indicator of a heavily forested habitat (Van den Bergh et al., 2001; Storm et al., 2005; Tougard and Montuire, 2006; Cranbrook and Piper, 2007). This is consistent with the $\delta^{13}C$ results of several cave sites, such as Yanliang, Liucheng, Mohui, Sanhe, Tantang, Baxian and Quzai Caves in southern China (Wang et al., 2007; Nelson, 2014; Qu et al., 2014; Li et al., 2017; Ma et al., 2017, 2019; Stacklyn et al., 2017). All these $\delta^{13}C$ results indicate a heavily forested environment for *Pongo* in southern China. The region was dominated by C_3 vegetation throughout the Pleistocene, which was confirmed by an extensive comparison and evaluation of the $\delta^{13}C$ data from fossil mammals in mainland Southeast Asia during the Early to Late Pleistocene. Southern China experienced relatively stable environments during the Pleistocene due to a largely mountainous region that offered protection (Ma et al., 2019). The Pleistocene environment of southwest Guangxi is a subtropical-tropical forest with pockets of open ground and water readily available, an environment clearly conducive to the flourishing of *Pongo* in the region (Chen et al., 2002; Jin et al., 2008;

Table 2
Comparisons of macromammal assemblages in various regions.

Location	Wuyun	Luna	Zhiren	Jimuyan	Fuyan	Yangjiawan cave 1	Diaozhongyan
(Genus/Species)	(200–300 ka)	(70–120 ka)	(110 ka)	(late Pleistocene)	(80–120 ka)	(late Pleistocene)	(~210 ka)
Macaca sp.	+	+	+	+	+	+	+
Trachypithecus sp.	+		+		+	+	+
Hylobates sp.		+	+		+	+	+
Pongo pygmaeus weidenreichi	+		+	+			
Pongo sp.		+					
Homo sapiens		+	+	+	+		
Hystrix subcristata	+		+	+	+		+
Hystrix magna			+				
Hystrix sp.		+					
Cuon sp.						+	
Cuon javanicus					+		
Cuon cf. C. javanicus antiquus	+						
Vulpes sp.						+	
Arctonyx collaris	+		+		+	+	+
Ursus thibetanus	+		+	+	+	+	+
Helarctos sp.						+	
Ailuropoda melanoleuca baconi	+	+		+	+	+	+
Crocuta crocuta ultima					+	+	
Martes sp.						+	
Paguma larvata						+	
Paguma sp.			+				
Panthera tigris	+				+	+	
Panthera pardus	+		+		+	+	
Prionailurus bengalensis					+		
Felis chaus						+	
Felis teilhardi	+					+	
Felis sp.			+			+	
Paradoxurus sp.	+						
Viverricula sp.					+	+	
Viverra sp.			+		+	+	
Neofelis sp.						+	
Stegodon orientalis	+	+		+	+	+	
Stegodon sp.							+
Elephas kiangnanensis			+				
Elephas maximus	+		+		+	+	
Tapirus sinensis	+			+			+
Megatapirus augustus	+		+		+	+	
Rhinoceros sinensis	+		+			+	+
Dicerorhinus sumatrensis					+		
Sus scrofa	+	+	+	+	+	+	+
Sus cf. S. xiaozhu			+				
Moschus sp.					+		
Muntiacus muntjak					+		
Muntiacus sp.	+	+	+	+		+	+
Cervus nippon					+		
Cervus unicolor			+		+	+	
Cervus sp.	+	+		+	+		+
Capricornis sumatraensis	+				+	+	
Bovinae gen. et sp. indet.	+	+		+			+
Bos (Bibos) gaurus					+		
Bubalus bubalus			+				
Bubalus sp.						+	
Megalovis guangxiensis			+				
Caprinae							+

Zhao et al., 2011; Zhao and Zhang, 2013; Qu et al., 2014; Shao et al., 2014; Li et al., 2017). The Pleistocene environment of northwest Guangxi appears to be more variable, perhaps due to the local geology.

The local geology as an influencing factor on the climate in Guangxi is an important consideration. For instance, a main pathway is invaded by cold air from the Xianggui Corridor through the gap in the Mengzhuling Mountains in northeast Guangxi (Fig. 7). In western Guangxi this invasion of cold air significantly weakens because of the presence of the Yunnan-Guizhou Plateau range. This results in the same temperature given similarities in latitude, with it being much higher in the west than in the east. DZY is located in a gap in the Mengzhuling Mountains. This results in a lower average temperature in the DZY region vis-à-vis other regions of Guangxi (Editorial board of forestry of Guangxi, 2001). Further, the DZY mammal assemblage dates to Marine Isotope Stage 7, which is a relatively warm period (Liao et al., In Press). Thus, variation in the local geology likely contributed to the absence of *Pongo* in DZY, but yet, contributed to orangutans' appearance at nearby Jimuyan.

5. Conclusion

The DZY mammal fossil assemblage represents 6 orders, 12 families, 15 genera and 15 species, and includes most of the representative taxa from the traditional "*Ailuropoda-Stegodon*" faunal complex in southern China. Given the variation in the assemblage, including extinct taxa like *Ailuropoda melanoleuca baconi*, *Stegodon* sp., *Tapirus sinensis* and *Rhinoceros sinensis*, the deposits likely date to the late Middle Pleistocene. *In situ* fossil teeth and calcites were dated to ~210 ka using

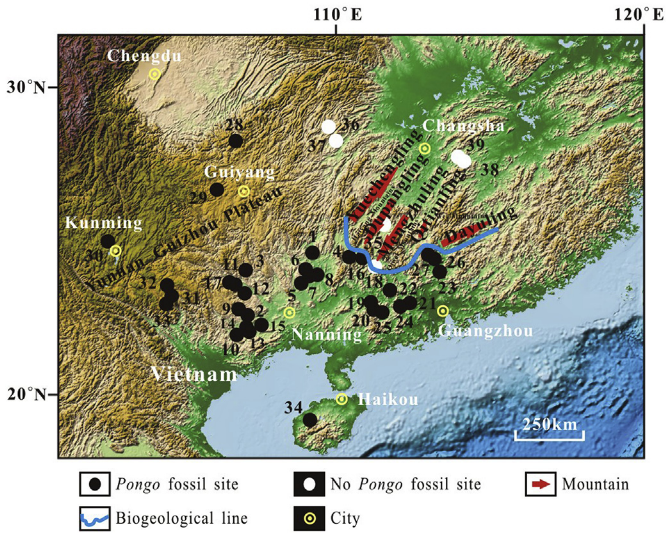

Fig. 7. Distribution of the Pleistocene fossil sites in south China and biogeological line for *Pongo* species. (Modified after Wang et al., 2009). **Distribution of fossil localities in Guangxi**: 1, Liucheng (*Gigantopithecus* cave) (Pei, 1957b); 2, Daxin cave (Heidong) (Pei and Woo, 1956); 3, Bama cave (Zhang et al., 1975); 4, Fufengyan cave (Wu et al., 1962); 5, Tongshan cave ; 6, Ganqian cave (Tubo) (Li et al., 1984); 7, Baipeng cave (Gu et al., 1986); 8, Liujiang cave (Tongtianyan) (Woo, 1959); 9, Mengkuang cave (Gu et al., 1987); 10, Pingxiang cave (Gu et al., 1986); 11, Dingmo cave (Li et al., 1985); 12, Wuyun cave (Chen et al., 2002); 13, Sanhe cave (Jin et al., 2008); 14, Queque cave (Jin et al., 2014); 15, Zhiren cave (Jin et al., 2009a); 16, Jimuyan cave (Wang et al., 2011); 17, Luna cave; 18, DZY cave. **Distribution of fossil localities in Guangdong**: 19, Xiashan cave (Huang et al., 1988); 20, Shanbeiyan cave (Gu et al., 1987); 21, Qixingyan cave (Zhang, 1959); 22, Huangyan cave (Song et al., 1981); 23, Shuangyan cave; 24, Feishu cave; 25, Guantang cave (Gu et al., 1987); 26, Luokeng cave (Gu et al., 1987); 27, Maba cave (Gu et al., 1987). **Distribution of fossil localities in Guizhou**: 28, Huiyan cave (Wu et al., 1975); 29, Guanyin cave (Pei et al., 1965). **Distribution of fossil localities in Yunnan**: 30, Heshang cave (Young, 1932); 31, Xianren cave (Xichou) (Chen and Qi, 1978); 32, Jiulong cave (Wang et al., 2009); 33, Xianren cave (Maguan) (Wang et al., 2009). **Distribution of fossil localities in Hainan**: 34, Honglin quarry (Wang et al., 2009). **Distribution of fossil localities in Hunan** (No *Pongo*): 35, Fuyan cave (Li et al., 2013); 36, Dongpao cave (Wang et al., 1982); 37, Luosixuanshan cave (Wang et al., 1982). **Distribution of fossil localities in Jiangxi** (No *Pongo*): 38, Zhushanyuan cave (Li et al., 1992); 39, Yangjiawan cave (1st) (Zou et al., 2016). s.

U-series, supporting the biostratigraphy (Liao et al., In Press).

Two key observations of the DZY faunal assemblage are the over-abundance of *Ailuropoda melanoleuca baconi* (15% of the entire faunal assemblage) and the absence of *Pongo*. Orangutans are generally a common species in central and south Guangxi during the Middle Pleistocene. At least in part, due to the influence of the Nanling Mountains and the Yunnan-Guizhou Plateau, the mammalian assemblage in north Guangxi is different from central and southwest Guangxi. A boundary for *Pongo* has been tentatively drawn along the southern edge of the Nanling Mountains. Fossil orangutans are present southwest of this biogeographic line, but are absent northeast of the line.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank L. Yang, J.P. Li, G.J. Xu from Anthropology Museum of Guangxi, J.J. Guo, X. Mo, B.S. Liang from Institute of Culture Relics Management of Hezhou City, Guangxi, Q. Chen from Sun Yat-sen University for their participation in the investigation and excavation. This research has been supported by funds from the National Natural Science Foundation of China grant 41572023, and the Bagui Scholar grant of Guangxi Zhuang Autonomous Region. We thank Fabrice Demeter for comments on an early manuscript, and two anonymous reviewers who helped make significant improvements to the paper.

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