




Taphonomy and biochronology of the Late Pleistocene mammalian fauna at Baolai cave, in Bubing Basin, southern China

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ABSTRACT

This paper reports a mammalian fauna collected from the excavation of Baolai cave, southeast of Bubing Basin, in 2004. The fauna mainly consists of extant species and only a few typical members of ‘*Ailuropoda-Stegodon* fauna’ (*Stegodon*, *Ailuropoda* and *Rhinoceros*). According to results of the U-series dating from flowstones overlying and below the fossil beds (54–24 Ka), the Baolai fauna represents the mammalian assemblage in the Late Pleistocene. Compared with the faunas of Middle and Late Pleistocene in southern China and Southeast Asia, extant species dominate the Baolai fauna, mostly consistent with modern fauna of southern China during the Holocene. Modern fauna emerged later in southern China than in Southeast Asia, presenting successive characteristics. Significant bias for small or tiny fossils in Baolai cave reveals a special taphonomic process. Baolai cave is located at the same horizontal level as Upper Wuyun cave and Ganxian cave which yield Middle Pleistocene deposits with mammalian fossils. However, the Baolai fauna is much younger. Based on the gnawing marks on tooth roots, rodents may be the main taphonomic agent, or the fossils were brought in by flow-water through the karstic system above.

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Introduction

Fossil-bearing cave deposits are common in southern China and Southeast Asia. These fossil assemblages, referred to as ‘*Ailuropoda-Stegodon*’ faunas (Colbert and Hooijer 1953; Pei 1957; Kahlke and Hu 1961), have existed throughout the Pleistocene, being characteristic of the Indochinese subregion fauna, especially in the Middle Pleistocene (Corbet and Hill 1992). In southern China, scholars have been investigating these cave deposits for a long time (Teilhard de Chardin et al. 1935) and discussed the chronological sequence by using biostratigraphy (Matthew and Granger 1923; Bien and Chia 1938; Pei 1957, 1962, 1965; Zhou 1957). Recently, with the progress of research on the sedimentary process, cave stratigraphy and dating methods (e.g. Shen et al. 2002, 2007, 2014; Westaway et al. 2007; Rink et al. 2008; Shao et al. 2014, 2015; Sun et al. 2017, 2021a), it has been proposed that the cave at higher elevations generally formed earlier with older deposits (Stock et al. 2005; Wang et al. 2007; Rink et al. 2008). This assumption is especially evident in Bubing Basin: the highest Mohui cave containing fossil remains similar to the Late Pliocene and Early Pleistocene fauna, a late Middle Pleistocene fauna recovering from Wuyun cave which is ~50 m lower in elevation than Mohui cave and the mammalian faunas of lowest Lower Pubu cave and Cunkong cave assigned to the Late Pleistocene and Holocene respectively (Wang et al. 2007).

The taphonomic process of Southeast Asia karstic caves has obtained a better understanding (Bacon et al. 2008; Durringer et al. 2012). To explore the extinction and evolution process of quaternary mammal fauna, scholars attempted to provide chronological frameworks for areas with numerous fossil sites, such as the Chongzuo region and Bubing Basin in Guangxi (Wang et al. 2007; Rink et al. 2008; Jin et al. 2014; Deng et al. 2019).

Since *Gigantopithecus blacki* was named by von Koenigswald (1935), the appearance and extinction of this ‘giant ape’ of

Hominoidea have attracted increased attention (Pei and Woo 1956; Pei 1957; Wang et al. 2014; Zhang et al. 2014). A chronological sequence for mammalian assemblages containing *Gigantopithecus* in the Early Pleistocene has been built with reliable dating (Jin et al. 2008, 2014; Sun et al. 2013). The Late Pleistocene fauna was often found with another hotspot, *Homo sapiens* (Jin et al., 2009; Bae et al. 2014). Thus, the age frame of contemporaneous mammalian fauna is the key to promoting the understanding of modern human origins, as well as the extinction of ancient species. Despite progress in dating technology, determining the age of cave faunas is difficult because of the complex taphonomic process in the karstic context. To date, the secure and successive chronological sequence is still incomplete, not only because of the lack of reliable dated sites but also due to debates on the age of some key sites, such as Zhiren cave and Fuyan cave (Ge et al. 2020; Martín-Torres et al. 2021; Sun et al. 2021a). The Late Pleistocene mammalian assemblages with accurate age in southern China have been found in Luna cave (70.2 ± 1.4 ka to 126.9 ± 1.5 ka), Mocun cave (66–101 ka) and Yanlidong cave (30–65 ka) (Bae et al. 2014; Yao et al. 2020; Fan et al. 2022) according to recent reports.

Despite the scarcity of fossil records in the Early Pleistocene (Colbert 1943; Bocherens et al. 2017), the *Ailuropoda-Stegodon* fauna was widespread in Southeast Asia since the Middle Pleistocene, showing a connection between two regions (Southeast Asia and southern China) (Tougaard 2001; van den Bergh et al. 2001). Although the integrated regional biochronological sequence is deficient, numerous fossil sites in Thailand, Vietnam, Laos and Cambodia were reported with accurate dating data (e.g. Esposito et al. 2002; Bacon et al. 2008, 2011, 2018; Duval et al. 2019), providing a basic frame to understand the migration and evolution of Middle to Late Pleistocene faunas. The earliest modern fauna in Southeast Asia is reported in northern Vietnam,

from Duoi U’Oi cave at 60–70 ka (Bacon et al. 2008). In the same period, more extinct or ancient species survived in southern China (Fan et al. 2022), suggesting multiple modes in the transition of fossil fauna to extant fauna. Because of scarce fossil records during the Late Pleistocene, it is hard to discuss the evolutionary events. The emergence of modern fauna in southern China remains less known than that in Southeast Asia.

In the past years, a series of cave sites at different elevations have been recovered in Bubing Basin (Li et al. 1985; Chen et al. 2002; Wang et al. 2005; Wang 2009; Bae et al. 2014). Here, we report a new fossil site, Baolai cave in Bubing Basin, to supplement the biochronological frame of this region and provide a case of cave deposition. Considering its thick and complete sedimentary profile, Baolai cave has been analysed using magnetostratigraphic dating with a series of caves in Bubing Basin and given a result of 0.99–0.78 Ma for the age of the lower unit (Sun et al. 2017). Since the upper sediment of Baolai cave, which contains mammalian fossils, has so far been ignored, we now describe the Baolai fauna and re-estimate its age.

Description of Baolai cave

Geological setting

The Baolai cave (106° 59′ 52.8″ E, 23° 36′ 3.8″ N), located in northeast Bubing village, Tiandong, Guangxi, was formed as part of a karst system of Bubing Basin in the eastern margin (Figure 1). On the basis of clues provided by local villagers, the Natural History Museum of Guangxi organised the excavation in 2004.

Bubing Basin is a smaller basin in the southwest of Bose Basin separated by a watershed. According to previous investigations, the karst system in this area was produced on the Carboniferous and

Permian limestone formed during carboniferous transgression (Wang 2005). The rivers in Bubing Basin appeared after the ‘Youjiang erosion period’ (~0.5 Ma), connected to the surrounding karstic underground channels. More than 50 cave sites with quaternary deposits have been found so far, preserved at different elevations (Wang et al. 2007). It is generally believed that, based on river cutting and uplift of the basin, the higher caves represent older age, while the newly formed caves are at a relatively lower altitude (Sasowsky et al. 1995; Stock et al. 2005; Düringer et al. 2012). The Baolai cave is adjacent to Ganxian cave, Wuyun cave, Chuifeng cave and Mohui cave, lying in southeastern Bubing Basin. The entrance of Baolai cave is 191 m above sea level, which is horizontally the same as Ganxian cave and Wuyun cave in the Middle Pleistocene (Figure 1).

Stratigraphy

The entrance of Baolai cave facing southeast is hidden in a forest with a 15 m narrower passageway that leads into a first chamber. At the right of the first chamber, a V-shaped branch is formed. Another passageway and two 6–7 m width chambers are found after travelling through two sections of corridors separated by huge limestones, opening out to the terminal chamber. The total length of the cave is about 65 m, and the width is about 5 m at the terminal chamber (Figure 2). The second branch is connected to the terminal chamber by a narrow corridor at the right. The excavation of Baolai cave is executed on the deposits in the terminal chamber and the second branch. Cemented breccia was excavated by hammers and chisels to collect visible fossils. The entrance and the terminal of Baolai cave share the same set of sediments: silty clay with breccia for the upper unit and pure clay for the lower unit. Single-layer

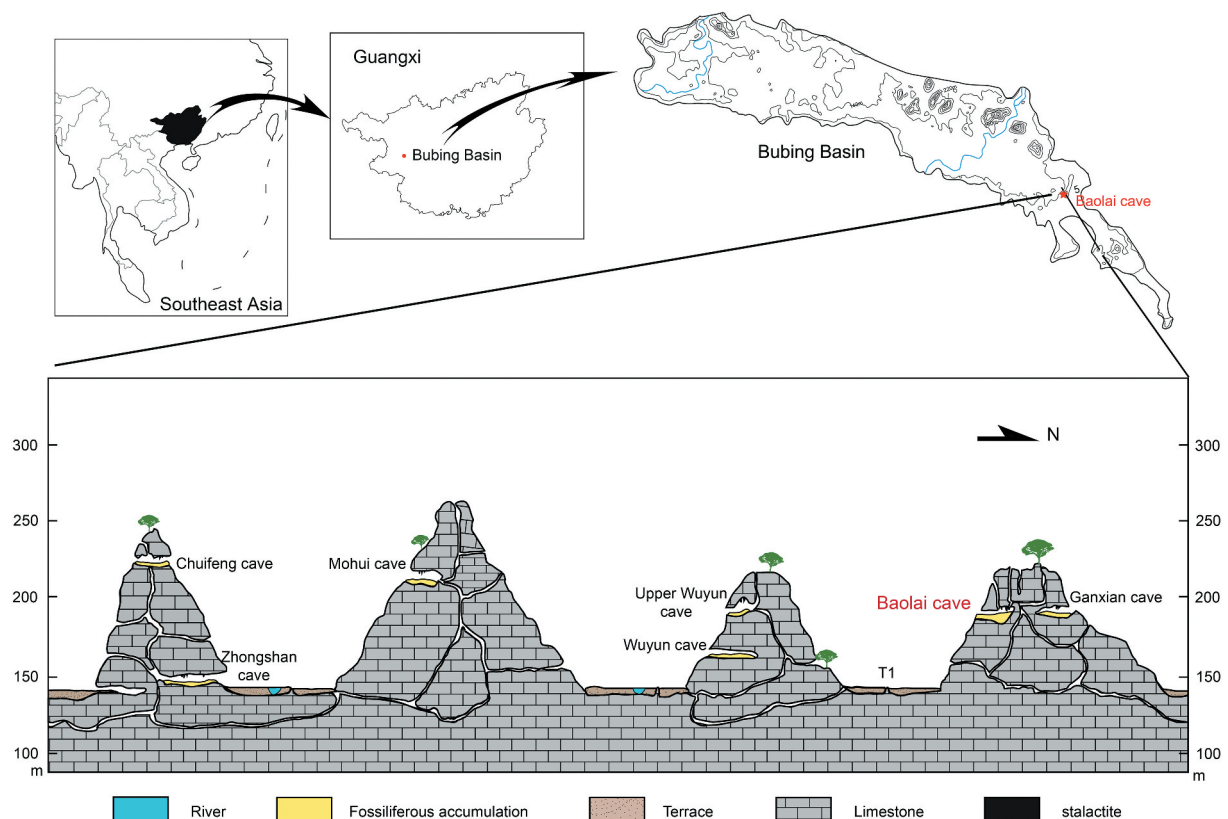


Figure 1. Location and elevation of Baolai Cave.

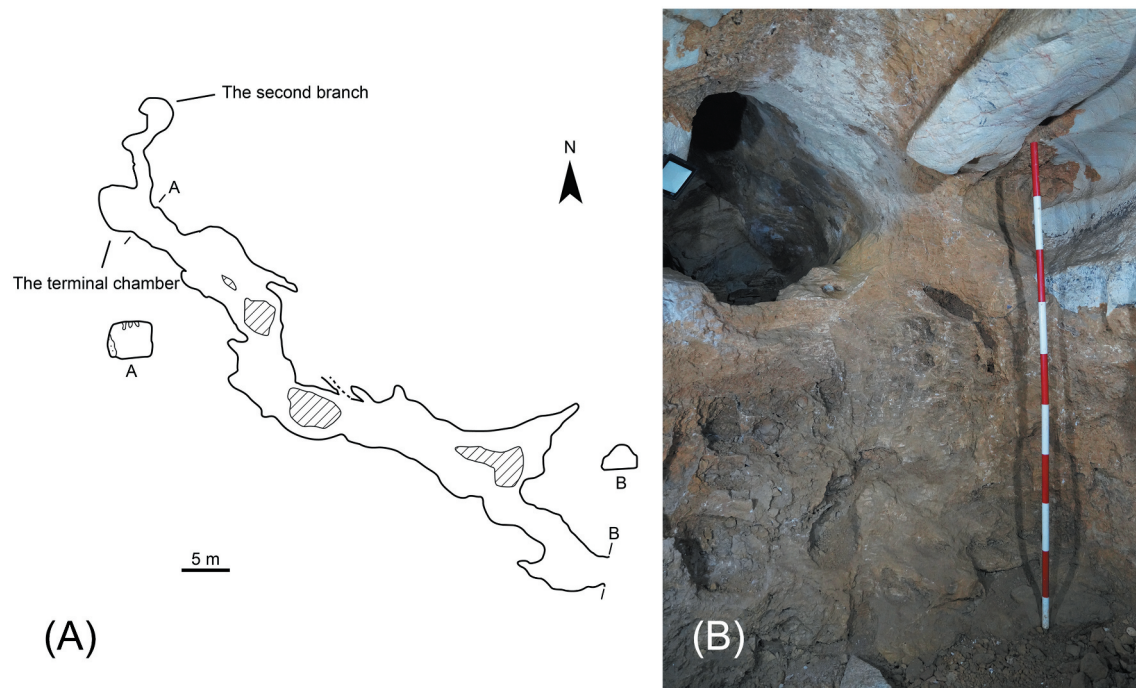


Figure 2. Plan of Baolai cave and photo of the second branch, (a) plan of Baolai cave, (b) the second branch.

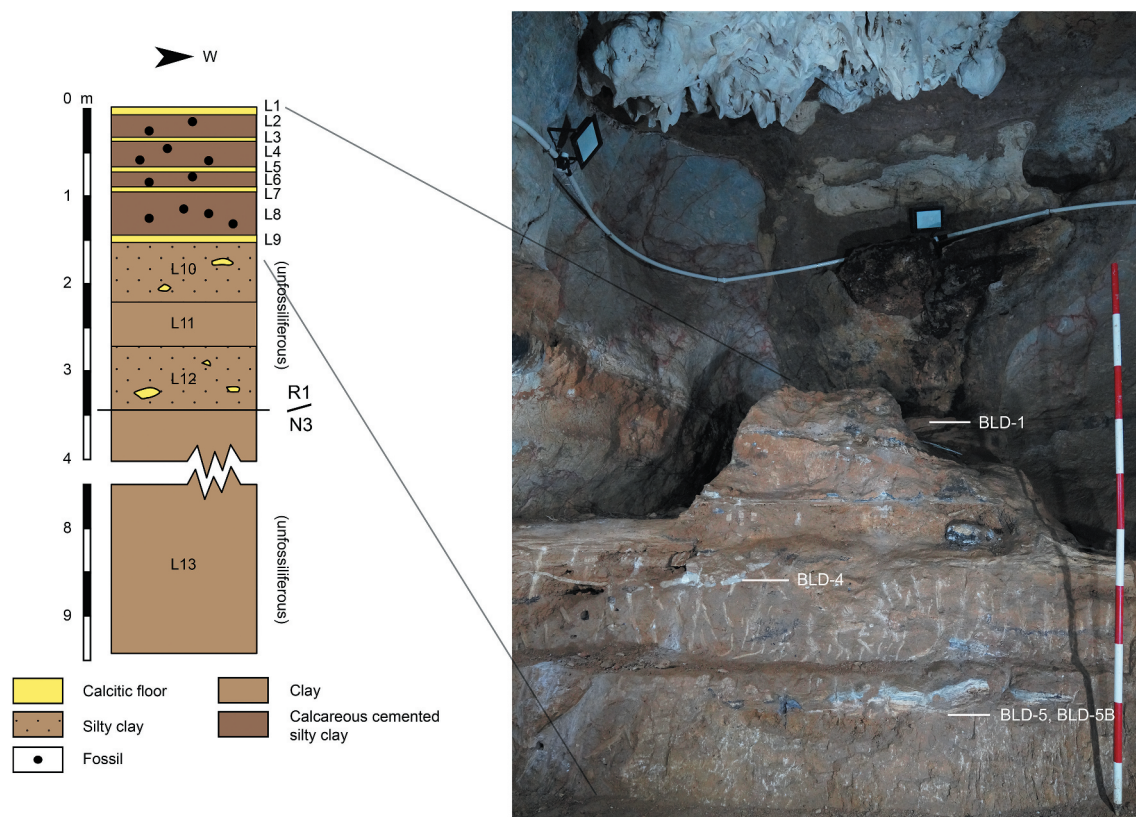


Figure 3. Stratigraphy of the terminal chamber sediments in Baolai cave (left) and photo of excavation profile (right). The normal/revised polarity interval transition is marked in the sedimentary column (left), and sampling locations are displayed in the profile (right).

deposits accumulate in the second branch, whereas the sediments at the terminal chamber are extremely thick. Despite being eroded by the karst fissure water from the cave ceiling, the strata of sediments remain distinct. The total thickness of deposits on the excavation is

9.5 m. The upper unit (from 0–1.5 m) that contains five flowstone layers yields mammalian fossils in silty clay cement. Fossils were located and recorded in layers. The sediments were sieved by a 5 mm mesh to collect fossils of small-sized mammals.

From the top to bottom, thirteen stratigraphic layers have been identified (Figure 3), with fossils yielded from L2, L4, L6 and L8:

- L1 Milk-white flowstone, 1–5 cm
- L2 Light brown calcareous cemented silty clay, 30 cm
- L3 Grey-white flowstone, 3–5 cm
- L4 Light brown calcareous cemented silty clay with limestone breccia, 20 cm
- L5 Milk-white calcitic floor, 2–5 cm
- L6 Light brown calcareous cemented silty clay, 20 cm
- L7 White-dark thick interlayered flowstone, 2–15 cm
- L8 Light brown calcareous cemented silty clay, 50 cm
- L9 Grey impure flowstone, 9 cm
- L10 Light brown silty clay with flowstone breccias, 50 cm
- L11 Light brown clay, 55 cm
- L12 Light brown silty clay, 85 cm
- L13 Light brown clay, unfossiliferous, more than 600 cm

Methodology

Taxonomy

All mammalian fossils collected from Baolai cave are stored in the Natural History Museum of Guangxi. Without large bones, the fragmentary bone pieces rarely present identifiable characteristics for taxonomy. Therefore, the taxonomic analysis concentrates on fossil teeth. Specimens are coded as 'BL' (Baolai) with a depth of 1–14 (1 = 10 cm). Fossil teeth were measured at the base of the crown for all groups to 0.01 mm by a digital caliper. We recorded the maximum length (L), which was taken along the mesial to distal margins and the maximum width (W) from the buccal to lingual sides. Based on the morphology and dimensions of specimens, taxa have been identified to the lowest level possible. The teeth are distinguished by minuscule letters for lower teeth and majuscules for upper ones (I/C/P/M/i/c/p/m).

The taphonomic process is discussed by observation of remaining marks on fossils and the quantitative results of the number of identified specimens (NISP). The Baolai cave produced both teeth and bones, with crushed or cracked marks, abrasion and gnawing marks. However, bones that appeared rarely were broken into small pieces, which are mostly long bone fragments less than 3 cm, lacking articular ends for taxonomic analysis and identification of skeletal elements. The marks on bones are consistent with those of tooth roots (gnawing and abrasion marks), proving the similar taphonomic agents of the two. However, these findings contribute little to a further understanding of taphonomic process, which is why we excluded these bone fragments in our statistics. NISP is applied to estimate the faunal composition of different loci in Baolai cave, and the frequency of each tooth to analyse the differential preservation. The Chi-square test of NISP was run in R statistical software version 4.0.5 with a significance level of 5%.

U-series dating

Most of the mammalian fossils were recovered from silty clays between L1 and L9. During the excavation, purer parts of calcitic floors from L1 (BLD-1), L7 (BLD-4), upper L9 (BLD-5) and lower L9 (BLD-5B) were collected. These carbonate samples were subjected to the $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ disequilibria dating method. The age of L1 is later than that of the underlying deposits, implying the youngest age of Baolai fauna; and L9 appeared earlier than the sediments above, therefore, it represents the maximum age of the fauna.

The samples with no evidence of secondary carbonate deposit or recrystallisation were cleaned by the ultrasonic cleaner and then

hand-picked to extract the purest possible carbonate specimens. More details of chemical pre-treatment procedures were described by Zhou et al. (2011). U-Th dating was executed by a Nu Plasma HR multi-collector inductively-coupled plasma mass spectrometers (MC-ICP-MS) at the School of Earth and Environmental Sciences, The University of Queensland. After measurements, the U-Th ages were calculated by the Isoplot/EX 3.0 program (Ludwig 2003).

Results

Taxonomic identification

In the Baolai assemblage, a total of 325 identifiable fossil teeth were recovered (226 from the terminal chamber and 99 from the second branch). These fossils represent 7 orders, 16 families and 25 species (including sp.) (Table 1), containing small- to large-sized mammals. The mammalian assemblage is dominated by modern Artiodactyla and Rodentia in southern China, including *Sus scrofa*, *Cervus (Rusa) unicolor*, *Elaphodus cephalophus*, *Muntiacus reevesi*, *Capricornis sumatraensis*, *Hystrix subcristata*, *Atherurus macrourus*, *Rhizomys* sp., *Niviventer* sp. In addition, the typical extinct taxa of 'Ailuropoda-Stegodon fauna', *Ailuropoda* and *Stegodon* also exist in Baolai cave (Figure 4).

Primates

Cercopithecidae are the only member of primates in Baolai cave. Twelve teeth belong to *Macaca* sp. with dimensions fall within those of modern species (Takai et al. 2014). Only one identified colobine specimen was recovered. Compared with macaques, this specimen presents a smaller size and sharper cusps. The outline of crown is approximately square. Based on dimensions, colobinae are divided into *Rhinopithecus*, *Pygathrix* and *Trachypithecus* in the Chongzuo region (Takai et al. 2014). The dimension of the Baolai specimen is close to that of *Pygathrix* sp. from Yixiantian cave (Pan 2021).

Proboscidea

Generally, the identification of Proboscidea is on the basis of morphological characteristics and dimension data, such as the number of lamellae and hypsodonty index (Maglio 1973). Several fragments of loph were collected from Baolai cave, representing a low crown of 24.54–29.08 mm. More enamel loops present with accessory styles splitting. The enamel is relatively thick. These specimens conform to *Stegodon* sp.

Carnivora

Carnivores from Baolai cave are mainly attributed to large-sized felids or ursids. Three specimens share the same dental pattern and similar size range with upper P4 and M1 of *Arctonyx collaris*. One fragmentary upper premolar (identified to P3) and a fragment of lower molar belong to *Ailuropoda* sp. Four premolars of felids belong to three species, *Panthera tigris*, *Panthera pardus* and *Neofelis nebulosa*, from large to smaller size. Given the difficulty of identifying at a species level, 15 incisors and canines are assigned to Carnivora indet.

Artiodactyla

Artiodactyla is dominated by suids and cervids. Suids are represented by 53 teeth with a majority of *Sus scrofa* (NISP = 44).

Table 1. Baolai faunal complex and the list of fossil teeth.

Order	Family	Taxon	The terminal chamber	The second branch
Primates	Cercopithecidae	<i>Macaca</i> sp.	1M1, 1P3, 1i2, 1m1, 1m3	1i1, 1P2, 2M1s, 1M2, 1i1, 1m2
		<i>Pygathrix</i> sp.	1M1	/
Rodentia	Hystriidae	<i>Hystrix subcristata</i>	1DP4, 1P4, 2M1s, 5M2s, 3M3s, 1i1, 3p4s, 2m2s, 3m3s	/
		<i>Atherurus macrourus</i>	2DP4s, 12i1s, 2P4s, 18M1/2s, 6M3s, 6dp4s, 7i1s, 9p4s, 18m1/2s, 2m3s	1DP4, 1M1/2, 2i1s, 2m1/2s
	Rhizomyidae	<i>Rhizomys</i> sp.	2i1s, 2P4s, 3M1/2s, 3M3s, 2i1s, 1p4, 4m1/2s, 1m3	1i1, 2i1s
	Muridae	<i>Niviventer</i> sp.	3i1s, 2i1s, 2m1s, 1m2	/
Chiroptera	Hipposideridae	<i>Hipposideros armiger</i>	/	2 incomplete mandibles
	Rhinolophidae	<i>Rhinolophus</i> sp.	/	1 incomplete mandible
Proboscidae	Stegodontidae	<i>Stegodon</i> sp.	3?	1?
Carnivora	Mustelidae	<i>Arctonyx collaris</i>	1P4, 1M1	1P4
	Ailuropodidae	<i>Ailuropoda</i> sp.	1P3	1m?
	Felidae	<i>Panthera tigris</i>	/	1p4
		<i>Panthera pardus</i>	/	1P3
		<i>Neofelis nebulosa</i>	/	2P3s
	Canidae	<i>Cuon</i> sp.	/	2i3s
	Ursidae	<i>Ursus thibetanus</i>	/	1M1, 1M2, 1m2, 1m3
		Carnivora indet.	5?	10?
Perissodactyla	Rhinocerotidae	<i>Rhinoceros</i> sp.	8?, 1m2	/
Artiodactyla	Suidae	<i>Sus scrofa</i>	2i2s, 2P4s, 2M1s, 2M2s, 1M3, 1i2, 1c1, 1p2, 1p3, 1p4, 5m1s, 2m2s, 1dp4	3i1/2s, 2i3s, 4P2s, 2P3s, 1P4, 1M1, 2p2s, 1p3, 2p4s, 3m2s, 1m3
		<i>Sus xiaozhu</i>	1i1, 1i2, 1P3, 1M1, 2m1s, 1m3	2P2s
	Cervidae	<i>Muntiacus reevesi</i>	1P2, 1P4, 2p4s	3M1s, 1i2, 1p4, 1m3
		<i>Elaphodus cephalophus</i>	1P2, 3P3s, 2P4s, 3M1/2s, 1p2, 1p3, 1p4, 1?	1P3, 2P4s, 1M1/2, 1p2, 1p4, 2m1s, 1m3
		<i>Cervus (Rusa) unicolour</i>	1P2, 1P3, 2P4s, 2M1s, 1M2, 4p2s, 1p4, 3m1s, 3m2s	1P4, 2M3s, 1i3, 2p3s, 2p4s, 2m1s, 2m2s, 2m3s
	Bovidae	<i>Capricornis sumatraensis</i>	1M1, 1p?, 1m1, 2m2s, 1m3	1p3, 1m1, 1m2
		Bovinae gen. et sp. indet.	1p?	1p4

The morphology and size of Pleistocene *Sus* overlap among species in southern China. According to morphological features of the male lower canine, the Baolai specimen is attributed to 'scrofic type' (Fujita et al. 2000; Sun et al. 2021b). Besides, nine small-sized teeth (Table 2) of *Sus* show a simple dental pattern with few accessory cuspids or styles on molars. These specimens conform to *Sus xiaozhu*.

Three members of different body sizes in cervids are identified (Table 2). The teeth of *Cervus (Rusa) unicolour* are relatively large and robust. The enamel is thick with sculptured surface. Upper molars develop a robust entostyle, tapered in shape. The paracoid of lower p4 is fused with the metaconid, presenting a closed trigonid basin. No *Palaeomeryx* fold appears on lower molars. The medium-sized teeth of *Elaphodus cephalophus* developed a thick enamel and faintly sculptured crown surface. Entoflexus is absent on the lingual side of upper premolars. The metacone rib is also weakly developed on molars. The trigonid basin on lower p4s is closed. The smallest specimens are assigned to *Muntiacus reevesi*. These teeth present a smooth enamel surface and a simple occlusal pattern. The upper molars develop a weak entostyle. The third lobe of lower m3 exhibits a loop by closed entoconulid and hypoconulid.

Only two premolars are attributed to Bovinae gen. et sp. indet. The remaining specimens that are reduced in size (Table 2) with a simple crown surface (1 upper molar, 8 lower premolars and molars) belong to *Capricornis sumatraensis*. The four main cusps on molars are advanced without distinct styles or ribs. The mesostyle is well-developed on upper molars.

U-series dating analysis

Sun et al. (2017) conducted palaeomagnetic dating of the silty clay and clay from 2–8.4 m of the terminal chamber in Baolai cave. The result shows that unlike Ganxian cave and upper

Wuyun cave at the same level, the Baolai cave has an obvious reversed polarity interval (R1) above a long normal polarity interval (N3). Without a long reversed polarity interval during the Brunhes Chron, it indicates that the Baolai section correlates with the Jaramillo normal subchron and post-Jaramillo Matuyama reversed Chron. Close to the fossil-bearing deposits, the reversed polarity interval R1 approaches the termination of the Matuyama Chron (0.99–0.78 Ma). The result falls in the range of the late Early Pleistocene, however, the identified specimens of Baolai cave show a larger proportion of modern species. The composition of Baolai fauna suggests a relatively late age to the Late Pleistocene.

However, from ^{238}U – ^{234}U and ^{230}Th – ^{234}U disequilibria in the calcitic floor sample, an age of 23.49 ± 0.36 Ka is given for L1. The underlying capping flowstone (L7) formed about 10 Ka earlier than L1. The age of L9 produced a maximum age for the deposits of 54.67 ± 0.27 Ka (Table 3). Combining all the U-series data, the dating from the terminal chamber of Baolai cave shows an estimation of 54–24 Ka, indicating a Late Pleistocene mammalian fauna.

The result represents the age range of deposits between L1 and L9 of the terminal chamber. Fossiliferous sediments are divided into closed layers by five thin capping flowstones (Figure 3). The descending data of samples from bottom to top suggest a successive accumulation process. Around 30 specimens were collected from the surface of damaged deposits. For the layers underlying L9 yield no fossils, the ground specimens are supposed to be derived from the layers between L1 to L9. Without accurate dating, the fauna in the second branch presents a consistent modern composition with the terminal chamber. Despite more carnivores in the second branch, the whole assemblage appears a young age that similar to that of the terminal chamber. Therefore, the Baolai fauna is suggested to be the Late Pleistocene complex.

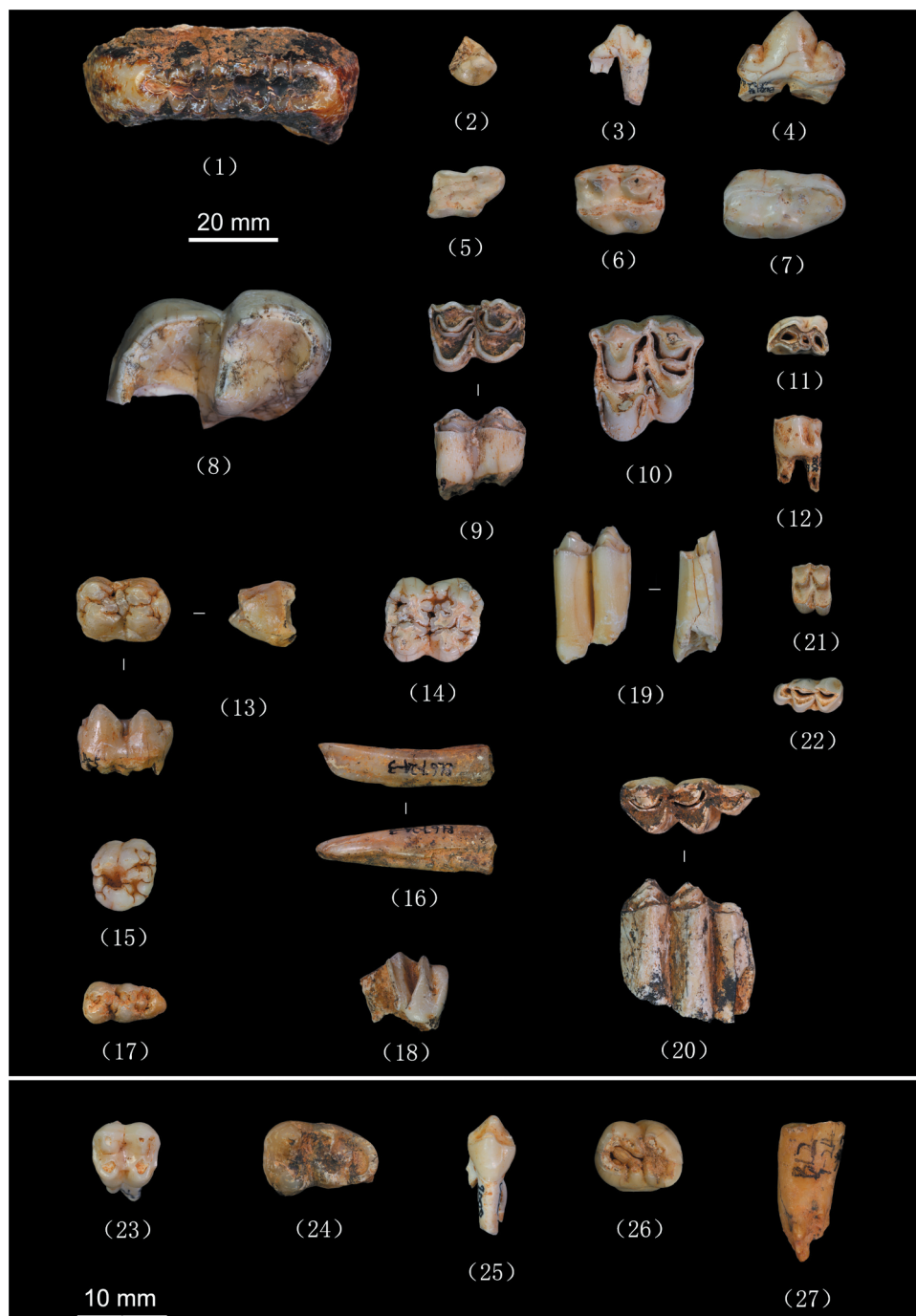


Figure 4. Mammalian fossils of Baolai cave. *Stegodon* sp.: (1) lamellae fragment, in occlusal view. *Ailuropoda* sp.: (2) tooth fragment, in occlusal view. *Neofelis nebulosa*: (3) right P3, in lingual view. *Panthera Tigris*: (4) left p4, in buccal view. *Arctonyx collaris*: (5) right M1, in occlusal view. *Ursus thibetanus*: (6) right M1, in occlusal view; (7) right M2, in occlusal view. *Rhinoceros* sp.: (8) left m2, in occlusal view. *Cervus (Rusa) unicolour*: (9) right m2, in occlusal and buccal view; (10) left M3, in occlusal view. *Elaphodus cephalophus*: (11) right p4, in occlusal view. (12) left p4, in buccal view. *Sus scrofa*: (13) right m2, in occlusal, lingual and distal view; (14) right M1, in occlusal view. (15) right P4, in occlusal view; (16) left I2, in lingual and distal view. *Sus xiaozhu*: (17) left m3, in occlusal view. Bovinae gen. et sp. indet. (18) left lower premolar, in lingual view. *Capricornis sumatraensis*: (19) right m1, in buccal and mesial view; (20) left m3, in occlusal and buccal view. *Muntiacus reevesi*: (21) right M1, in occlusal view; (22) right m3, in occlusal view. *Macaca* sp.: (23) right M2, in occlusal view; (24) left m3, in occlusal view; (25) right P2, in lingual view. *Hystrix subcristata*: (26) left M2, in occlusal view; (27) left m2, in lingual view.

Taphonomy

In Baolai cave, the second branch deposited only one layer of accumulation, whereas the terminal chamber shows more abundant and various sediments. The fossil quantity of the terminal chamber is also larger than that of the second branch. Fourteen taxa are

shared between the two loci: *Macaca*, *Atherurus macrourus*, *Rhizomys*, *stegodon*, *Arctonyx collaris*, *Ailuropoda*, Carnivora indet., *Sus scrofa*, *Sus xiaozhu*, *Muntiacus reevesi*, *Elaphodus cephalophus*, *Cervus (Rusa) unicolour*, *Capricornis sumatraensis* and Bovinae gen. et sp. indet. More carnivores (felids, ursids and canids) and Chiroptera exclusively appear in the second branch. *Pygathrix*,

Table 2. Dimensions (mm) of measurable Artiodactyla teeth of Baolai cave.

Teeth	N	Length (mm)	x	Width (mm)	x
<i>Sus scrofa</i>					
dp4	1	19.81		10.22	
p2	3	11.02–12.76	11.95	3.88–6.62	5.51
p3	2	13.63–13.87	13.75	7.11–7.22	7.17
p4	3	13.32–17.32	15.59	7.62–10.58	9.04
m1	5	16.91–23.46	20.92	13.34–17.45	15.94
m2	5	17.58–24.32	20.77	13.68–16.75	15.39
m3	1	44.13		19.79	
P2	2	12.32–12.44	12.38	6.78–7.05	6.92
P3	2	13.91–14.09	14	8.85–12.05	10.45
P4	3	12.73–15.11	13.82	12.86–15.12	14.18
M1	3	16.48–19.62	18.05	13.22–18.24	16.02
M2	1	19.53		15.75	
<i>Sus xiaozhu</i>					
m1	1	12.18		9.21	
m3	1	18.19		9.28	
P2	2	7.03–8.07	7.55	3.45–3.87	3.66
P3	1	9.65		7.78	
M1	1	11.39		9.89	
<i>Cervus (Rusa) unicolor</i>					
p2	4	10.29–13.56	12.25	6.44–8.57	7.72
p3	2	15.21–18.41	16.81	9.05–10.25	9.65
p4	3	16.96–20.99	19.62	9.05–12.91	11.07
m1	5	16.08–20.18	18.49	11.02–14.06	12.38
m2	5	20.62–28.65	24.43	13.47–18.44	15.9
m3	2	30.13–34.89	32.51	15.46–17.01	16.24
P3	1	14.63		17.15	
P4	1	17.88		16.68	
M1	2	17.33–19.73	18.53	18.12–21.9	20.01
M2	1	24.38		23.97	
M3	2	22.64–23.57	23.11	23.11–25.74	24.43
<i>Elaphodus cephalophus</i>					
p2	2	9.24–10.32	9.78	4.91–5.56	5.24
p3	1	9.37		5.65	
p4	1	10.98		7.12	
m1	2	15.62–15.98	15.8	9.61–9.79	9.7
m3	1	19.51		10.4	
P3	4	7.71–10.91	8.97	9.44–11.19	10.32
P4	4	7.56–10.22	8.55	10.53–13.01	12.07
M1	2	10.15–11.28	10.72	12.83–13.93	13.38
M2	1	14.01		14.99	
<i>Muntiacus reevesi</i>					
p4	3	8.51–9.96	9.43	5.01–7.59	6.45
m3	1	14.53		7.34	
P2	1	8.49		6.91	
P4	1	7.55		9.63	
M1	3	9.04–10.23	9.67	11.28–12.65	11.83
<i>Capricornis sumatraensis</i>					
p3	1	16.81		12.01	
m1	2	15.36–18.11	16.74	10.19–11.5	10.85
m2	3	17.77–19.54	18.38	10.62–13.96	11.82
m3	1	28.57		12.59	
M1	1	18.42		15.44	

Table 3. U-series data of capping flowstone in Baolai cave.

Sample Name	U (ppm)	(²³⁰ Th/ ²³² Th)	(²³⁰ Th/ ²³⁸ U)	(²³⁴ U/ ²³⁸ U) s	Uncorr. Age (ka)	corr. Age (ka)
BLD-1	0.03414 ± 0.00004	27.33 ± 0.19	0.2782 ± 0.0018	1.3897 ± 0.0049	24.135 ± 0.201	23.49 ± 0.36
BLD-4	0.04789 ± 0.00003	80.20 ± 0.59	0.3613 ± 0.0026	1.3887 ± 0.0030	32.431 ± 0.276	32.15 ± 0.30
BLD-5	0.03177 ± 0.00003	80.16 ± 0.37	0.6545 ± 0.0029	1.3842 ± 0.0040	67.528 ± 0.485	67.03 ± 0.52
BLD-5B	0.05481 ± 0.00003	129.87 ± 0.44	0.7069 ± 0.0020	1.7333 ± 0.0037	54.933 ± 0.251	54.67 ± 0.27

Hystrix subcristata, *Niviventer* and *Rhinoceros* are recovered in the terminal chamber only.

The assemblage list of each locus is provided in Table 1 and the NISP is presented in Table 4. In the terminal chamber, the largest group is Rodentia (57.1% NISP), followed by Artiodactyla (31.4% NISP), Perissodactyla (4.0% NISP),

Carnivora (3.5% NISP), Primates (2.7% NISP) and Proboscidae (1.3% NISP). In the assemblage of the second branch, the most abundant group is Artiodactyla (54.8% NISP), followed by carnivora (21.2% NISP), Rodentia (8.7% NISP), Chiroptera (7.7% NISP), Primates (6.7% NISP) and Proboscidae (1% NISP).

Table 4. Number of identified specimens in Baolai cave according to taxon and tooth types (the number of tooth type according to the quantity of mandibles for Chiroptera).

	The terminal chamber					The second branch					Total NISP
	Deciduous teeth NISP	Molars NISP	Premolars NISP	Incisors/Canine NISP	Dental fragments NISP	Deciduous teeth NISP	Molars NISP	Premolars NISP	Incisors/Canine NISP	Dental fragments NISP	
Artiodactyla	1	33	30	6	1	0	23	27	7	0	128
Primates	0	4	1	1	0	0	4	1	2	0	13
Rodentia	9	73	18	29	0	1	3	0	5	0	138
Chiroptera	0	0	0	0	0	0	3	3	2	0	8
Proboscidae	0	0	0	0	3	0	0	0	0	1	4
Carnivora	0	1	2	0	5	0	5	5	2	10	30
Perissodactyla	0	1	0	0	8	0	0	0	0	0	9
Total NISP	10	112	51	36	17	1	38	36	18	11	330

Except for rodents, milk teeth are absent in most taxa, implying a strong destructive effect before deposition. Molars, premolars and incisors/canines of all taxa respectively make up 50.0%, 22.6% and 15.9% of all the identifiable teeth in the terminal chamber, and 36.5%, 34.6%, and 17.3% for the second branch.

A significant overlap in taxa is presented in two loci, and species found independently also indicate a modern assemblage, supporting an interpretation of similar age. However, the compositions of each taxon are significantly different in the two loci ($X^2 = 98.904$, $df = 6$, $p\text{-value} < 2.2e-16$), and a statistical difference in tooth types between two sediments presents ($X^2 = 10.007$, $df = 4$, $p\text{-value} = 0.04031$), thereby suggesting a possibly distinct deposition process.

Discussion

Taphonomic process

The agent of water flows dominates the formation of karstic systems in tropical and subtropical areas of Southeast Asia. The complex underground drainages contribute to the expansion of the channel or cave network, which are then lifted by tectonic movements. Hence, alluvial terraces and caves/passageways at the same elevation are generally considered to have formed simultaneously (Düringer et al. 2012). Nevertheless, the inner sedimentary filling experiences complicated infilling/removing phases caused by changes in climate, tectonic or water circulation. Using geochemical provenance analysis, Liao et al. (unpublished) obtained non-matched results of cave sediments and local river terraces in Bubing Basin which suggests a more complicated process of cave deposition occurred. The elevation of Baolai cave is lower than that of the Early Pleistocene Chuiheng cave and Mohui cave, and higher than that of the Late Pleistocene Dingmo cave in Bubing Basin. The thickness of deposits in the terminal chamber is over 9.5 m. According to magnetostratigraphy work and U-series dating, the age of the terminal chamber accumulation below 2 m is 0.99–0.78 Ma of the late Early Pleistocene (Sun et al. 2017), and the age of sections above 1.5 m (L9) is 54–24 Ka, which is during the middle- to late-Late Pleistocene. It indicates that the cave has retained at least two stages of deposits with an extremely long interval. When the fossil-bearing layers were accumulated, the Baolai cave had been higher than the terrace, indicating that the source of the fossils may be different from the other caves in Bubing Basin.

Small-sized artiodactyls and rodents dominate the Baolai fauna, whereas larger ungulates and proboscids are not so frequent and generally fragmentary. Most of the tooth roots and bone fragments (64.1%, rodents excluded) remained visible gnawing marks (2.59–8.48 mm in width, from small to large rodents). Rodents play an important role in collecting fossils in Baolai cave. Furthermore, the

cave is conjoint with other parts of the karstic network (fissures and drainages) inside the mountain. Jagged and transverse fracture patterns are found on most bone fragments and tooth roots (56.4%), which suggests that more dry breakage occurred on Baolai specimens. Meanwhile, relatively heavy weathering happened on the surface of fossils and less on fracture surface. As indicated by the abrasion and weathering of fossils, these mammalian remains were subjected to a long period of exposure, and during the water circulation, silty clays carried teeth and bones from the mountain surface were possibly transported into caves. It also explains the absence of pebbles from fluvial deposits and large-sized fossils. The absence of milk teeth implies a relatively strong destructive process before sedimentation and not *in situ* burial. The two loci of Baolai cave, however, have a recorded diverse deposition process, according to the quantitative statistical analysis. The mammalian assemblage from the terminal chamber, yielded over half portion of rodent teeth and deciduous teeth, was most likely an occupied nest by rodents. Fewer fossils were recovered from thinner and simple sediments in the second branch than from the terminal chamber. With more Artiodactyla and Carnivora, the fossils in the second branch were possibly carried by a different agent, flowing-water.

Pei (1965) suggested the age of deposit is related to the elevation of quaternary caves in Guangxi. The study of karst cave accumulation process and a large amount of dating data also support the relationship between the elevation and age of cave deposits (Wang et al. 2007; Rink et al. 2008; Düringer et al. 2012). The elevation of Baolai cave is comparable to those of the Middle Pleistocene caves, however, its sediment is from the late Pleistocene. It proves that the relative age of the cave cannot be absolutely estimated by its elevation. The sedimentary process of karst cave is complicated. Different sedimentary and taphonomic ways will retain fossils of different ages in caves, thus, further analysis and verification are needed.

Biochronological implication

In Baolai faunal assemblage, typical species of the *Ailuropoda-Stegodon* fauna in southern China still appear. However, compared with the late-Middle Pleistocene Ganxian cave, Wuyun cave fauna and the early-Late Pleistocene fauna of Mocun cave, the Baolai assemblage is dominated by modern species, showing a distinctly late faunal complex (Table 5). A larger portion of global or local extinct medium- to large-sized mammal species (43.5% for Wuyun cave, 53.6% for Ganxian cave and 38.5% for Mocun cave) is shown in earlier sites, but reduced to 31.6% in Baolai cave (tigers and rhinoceros survived in southern China until recent century). It indicates the elimination of archaic elements and the extant ones flourishing in local biocenosis.

Table 5. Composition of the Baolai mammal faunal list compared with that of some late Middle Pleistocene to Late Pleistocene sites in southern China and Southeast Asia: Wuyun cave (Chen et al. 2002), Ganxian cave (Liang et al. 2022), Mocun cave (Fan et al. 2022), Nam Lot and Duoi U'Oi (Bacon et al. 2015). Names in bold indicate global extinction; The asterisk (*) indicates local extinction.

	Wuyun cave	Ganxian cave	Mocun cave	Baolai cave	Nam Lot	Duoi U'Oi
<i>Rusa(Cervus) unicolour/sp.</i>	√	√	√	√	√	√
<i>Muntiacus reevesi</i>		√	√	√		
<i>Muntiacus muntjak/sp.</i>	√	√	√		√	√
<i>Elaphodus cephalophus</i>				√		
<i>Megalovis guangxiensis</i>		√				
<i>Bubalus bubalis/B. arnee</i>		√			√	
<i>Bos (Bibos) sp.</i>		√	√		√	√
*<i>Capricornis sumatraensis/Capricornis sp.</i>	√	√		√	√	√
Caprinae gen. et sp. indet.			√			
Bovinae gen. et sp. indet.	√			√		
<i>Sus xiaozhu</i>		√	√	√		
<i>Sus scrofa</i>	√	√	√	√	√	√
*<i>Sus barbatus</i>						√
<i>Megatapirus augustus</i>	√	√	√			
<i>Tapirus sinensis</i>	√	√	√			
*<i>Tapirus indicus/Tapirus sp.</i>					√	√
<i>Rhinoceros sinensis</i>	√					
*<i>Rhinoceros unicornis</i>					√	√
*<i>Rhinoceros sondaicus</i>		√			√	√
*<i>Rhinoceros sp.</i>		√	√	√	√	√
*<i>Dicerorhinus sumatrensis</i>		√				√
<i>Stegodon orientalis/sp.</i>	√	√	√	√	√	
<i>Elephas kiangnanensis</i>						
*<i>Elephas maximus/Elephas sp.</i>	√	√	√		√	√
*<i>Cuon alpinus/C. alpinus antiquus</i>	√	√			√	√
<i>Cuon sp.</i>			√	√		
<i>Arctonyx collaris (rostratus)</i>	√	√	√	√		√
<i>Paradoxurus hermaphroditus/sp.</i>	√		√			
<i>Viverra megaspila</i>						√
<i>Viverra sp.</i>			√		√	√
*<i>Felis(Panthera) tigris</i>	√	√		√		√
<i>Felis(Panthera) teihardi/sp.</i>	√					
<i>Neofelis nebulosa</i>		√	√	√		√
<i>Panthera pardus</i>	√			√		√
<i>Crocota ultima</i>		√	√		√	
<i>Ailuropoda melanoleuca baconi</i>	√	√			√	
*<i>Ailuropoda sp.</i>			√	√		
*<i>Helarctos malayanus</i>						√
<i>Ursus thibetanus</i>	√	√	√	√	√	√
*<i>Pongo pygmaeus/P. p. weidenreichi</i>	√	√			√	√
*<i>Pongo sp.</i>			√			
<i>Nomascus/Hylobates sp.</i>		√	√			√
<i>Macaca sp.</i>	√	√	√	√		√
<i>Pygathrix sp.</i>				√		
<i>Trachypithecus sp./Presbytis sp.</i>	√	√	√			
<i>Hystrix magna</i>			√			
<i>Hystrix kiangsenensis</i>						
<i>Hystrix subcristata</i>	√	√	√	√		
<i>Hystrix brachyura/Hystrix sp.</i>					√	√
<i>Atherurus macrourus</i>	√			√		

Given the unconformity strata, Baolai cave is proven to experience two phases of deposition. The sediments of early phase (0.99–0.78 Ma) are lacking in fossils, whereas all fossil remains are recovered from the deposits covered and restrained by later calcitic floors. Besides, from the taxonomical analysis, a lack of archaic species in the Early Pleistocene also exhibits in the Baolai fauna. Therefore, it is reasonable to exclude the mixture of two chronologically distinct assemblages. The U-series dating results of calcitic floors from the terminal chamber provide a secure age range for Baolai fauna (54–24 Ka), which is during the last glacial period. It fills in the blank of the chronological sequence of Late Pleistocene *Ailuropoda-Stegodon* fauna in southern China. Interestingly, *Elephas maximus* is missing in the Baolai fauna, but an ancient genus of *stegodon* presents. *Elephas maximus* has been found in adjacent Wuyun cave and Ganxian cave, indicating its existence in this area. The lack of *Elephas* can probably be attribute to the small sample size or bias of taphonomic process. The emergence of modern fauna in

the Late Pleistocene represents the replacement and disappearance of ancient genera. The change of Ganxian and Wuyun to Baolai assemblage also represents the evolution and alteration of fauna in Buning Basin. Until the last glacial period, represented by the Baolai fauna, the extant species gradually occupied the dominant position in the biomes, with the ancient species fading away, which built the basic frame of modern fauna in southern China.

Within the distribution range of the *Ailuropoda-Stegodon* fauna, Southeast Asia was proven to change into modern fauna earlier than southern China (Duoi U'Oi, Bacon et al. 2008). The overlap of Baolai assemblage with those of Wuyun, Ganxian and Mocun is 52% (13 taxa), 40% for that of Duoi U'Oi (10 taxa), and 24% for that of Nam Lot (6 taxa) (Table 5). Three ancient taxa survived in southern China at least to the late Late Pleistocene, thus indicating a different evolution rate among areas and species. For modern faunas, regional characteristics are still obvious among these two areas. Some species (e.g. *Sus barbatus*, *Dicerorhinus sumatrensis*)

appear in Southeast Asia only, partly due to the taxonomic method and possibly caused by various evolution and migration of different areas. With more sites filled in, the details of how modern fauna replaced *Ailuropoda-Stegodon* fauna in southern China and Southeast Asia will be revealed.

Conclusion

The faunal assemblage of Baolai cave still retains the typical species of the *Ailuropoda-Stegodon* fauna (panda and stegodon), but on the whole, it has been consistent with the current fauna of southern China since the Holocene. It reflects the replacement of extant species with extinct ones during the last glacial period (54–24 Ka). The Baolai fauna fills in the blank of biochronological sequence in the Late Pleistocene. In addition, it also shows a special case of cave deposition, which does not conform to the elevation. Therefore, the cave is of great significance for the study of biochronology, mammal evolution and cave deposition.

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