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Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China

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Abstract

A Plio-Pleistocene to Holocene faunal sequence has been recovered from four carefully excavated caves in the Bubing Basin, adjacent to the larger Bose Basin of South China. The caves vary in elevation; we suggest that the higher caves were formed and filled with sediments prior to the lower caves. The highest deposits, which are from Mohui Cave, contain hominoid teeth and other fossilized remains of mammalian taxa most similar to late Pliocene and early Pleistocene faunas. Wuyun Cave (~50 m lower in elevation than Mohui) contains a late middle Pleistocene fauna, which is supported by U-series age constraints from 350 to 200 ka. Lower Pubu Cave (~23 m below Wuyun) is assigned to the late Pleistocene, while the Cunkong Cave (the lowest, ~2 m lower elevation than Lower Pubu) preserves a Holocene fauna.

The four faunal assemblages indicate species-level changes in *Ailuropoda*, *Stegodon*, and *Sus*, the appearance of *Elephas*, the local disappearance of *Stegodon*, and the migration of *Equus hemionus* to South China. These initial results of our work call into question the continued value of the *Stegodon/Ailuropoda* Fauna, a category long used to characterize the Pleistocene faunas of South China. Excavation of karstic caves of varying elevation within the basins of South China holds promise for defining local sequences of mammalian fossils that can be used to investigate faunal variations related to climate change, biogeographic events, and evolutionary change over the past two million years.

Stable isotopic analysis of a small sample of mammalian teeth from Bubing Basin caves is consistent with 100% C₃ vegetation in the Bubing/Bose region, with certain δ¹³C values consistent with a canopied woodland or forest. A preliminary assessment of the hominoid teeth indicates the presence of diverse molar and premolar morphologies including dental remains of *Gigantopithecus blacki* and a sample with similarities to the teeth reported from Longgupo.

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Keywords: Bose; Fauna; *Gigantopithecus*; Mohui; Stable isotopes; *Stegodon/Ailuropoda* Fauna; U-series dating

Introduction

Although Quaternary fossil remains have long been known from the limestone caves of South China, systematic recovery of them has been rare, and the difficulty of determining age estimates for caves has meant that a sequential ordering of faunas has not yet been possible. As a result, Quaternary faunas of South China have been placed into the general

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category of “*Stegodon/Ailuropoda* Fauna” (Pei and Wu, 1956; Han and Xu, 1985), a term currently associated with faunas spanning most of the Pleistocene, and thus, potentially masking important temporal and spatial faunal variations.

We report here an initial assessment of faunas obtained by excavation from late Pliocene to Holocene caves of the Bubing Basin in western Guangxi Zhuang Autonomous Region, South China. This basin, located on the southeastern side of the Bose Basin (Huang et al., 1990; Yuan et al., 1999; Hou et al., 2000; Potts et al., 2000), is oriented northwest to southeast and is approximately 16 km long by 2 km wide (Fig. 1A, B). The caves are situated in late Paleozoic limestone hills on the margins of the basin. More than 50 caves containing sediments at varying elevations (140 to 215 m above sea level) have been found, representing a notable concentration for such a small basin, and four of these were excavated during three field seasons (December 1999 to January 2000, October to November 2002, and November 2003).

Thousands of mammalian fossil teeth and a few stone artifacts were recovered *in situ* in Mohui Cave, Wuyun Cave, Lower Pubu Cave, and Cunkong Cave. In addition to the faunal lists, which provide the first temporal sequence of Quaternary mammalian faunas known from South China, we report here preliminary dating of one of the caves and stable carbon isotopic analyses for a small sample of herbivore teeth from the caves, which provide initial evidence of herbivore diets and paleoenvironments during the Quaternary of South China.

Geological and archaeological background

The Bubing Basin caves have been studied in connection with our ongoing archaeological and geological research in the Bose Basin, which contains Quaternary sediments exposed in a series of terraces of the Youjiang River. Both of these basins are southeast of the Yuannan-Guizhou Plateau, which has experienced intermittent uplift with the Qinghai-Tibetan Plateau since the Miocene. The Bose investigations have yielded a lithic technology characterized by unifacial and bifacial large cutting tools, bold flaking of stone, and patterns of artifact shaping and flaking intensity similar to the African Acheulean of equivalent age (Hou et al., 2000). Extensive excavations show that the Bose (or Baise) industry occurs *in situ* within a narrow stratigraphic interval of the only river terrace characterized by strongly laterized sediment. The stone artifacts are directly and uniquely associated throughout the basin with *in situ* tektites dated to ~803 ka, which are also restricted to the same terrace (Hou et al., 2000; Potts et al., 2000).

The Bubing Basin is separated from the Bose Basin by small watersheds formed by Eocene fluvial and lacustrine sediments that overlap isolated late Paleozoic limestone hills (Fig. 1A). As in the Bose Basin, multiple terraces can be seen in Bubing. The highest terrace in the Bubing area is distributed on the southeastern side of the watersheds, and consists of an upper lateritized unit and a lower thick conglomerate. This strongly-weathered laterite has yielded stone artifacts associated with tektites. The tektite terraces in the

Bubing and Bose basins are thus very similar lithologically and archaeologically.

Surrounding the fluvial sediments and terraces of the Bubing Basin are karstic limestone highlands of late Paleozoic age, in which caves occur at varying elevations (Fig. 1B). On the southwestern margin of the basin, the peaks of the limestone hills vary from 260 to 900 m above sea level, and isolated hills within the basin and on the northeastern margin vary in elevation from about 200 to 250 m.

The elevation of caves in these limestone hills varies considerably. Dissolution of the limestone was controlled in the past by water that reached relatively stable levels at various points in time. Based on well-established ideas about karstic cave formation (e.g., Palmer, 1991; Stock et al., 2005), we hypothesize that over a long period of uplift and river downcutting, limestone was dissolved and caves were formed along paths of groundwater discharge at different elevations. During the end of each phase of cave development, sediments were introduced into the cavities through floodplain runoff and downward movement through openings in the limestone. According to this standard interpretation, the caves themselves were not uplifted but, rather, basin groundwater descended to lower levels, and the dissolution and sedimentary infilling of the caves followed as the river cut downward. Caves at progressively higher elevations, therefore, reflect progressively older periods of cave formation and infilling, and preserve fossil assemblages of increasing age (Stock et al., 2005).

To date, we have counted at least six significantly different cave elevations in the Bubing Basin highlands. The fossils recovered from these caves offer a way of developing a temporal sequence of mammalian fossils. Of the four caves reported here, Cunkong Cave (23°36′18″N, 106°58′26″E) is the lowest (140 m above sea level) and thus the youngest cave, while Mohui (23°34′54″N, 107°00′8″E) is the highest (215 m) and oldest. Wuyun Cave (23°25′9″N, 107°00′00″E) is situated at 165 m, and Lower Pubu Cave (23°35′53″N, 106°59′10″E) is at 142 m.

Methods

Excavations

Excavations were focused on the southeastern margin of the Bubing Basin where the caves are concentrated. Mohui, Wuyun, Lower Pubu, and Cunkong caves were selected for excavation due to their distinctly varying elevations and the presence of surface fossils in each cave. Sediments were excavated down to bedrock in either 5 or 10 cm intervals, depending on the density of fossil material. Visible fossils and stone artifacts were mapped, recorded, and collected, and the sediment sieved (0.5 mm mesh) by water to gather microfossils. In the course of excavation, flowstones, charcoal, spore, and sediment grain-size samples were collected. The fossils were easily separated from the sediment during excavation and preparation, and were then assessed taxonomically using comparative collections.

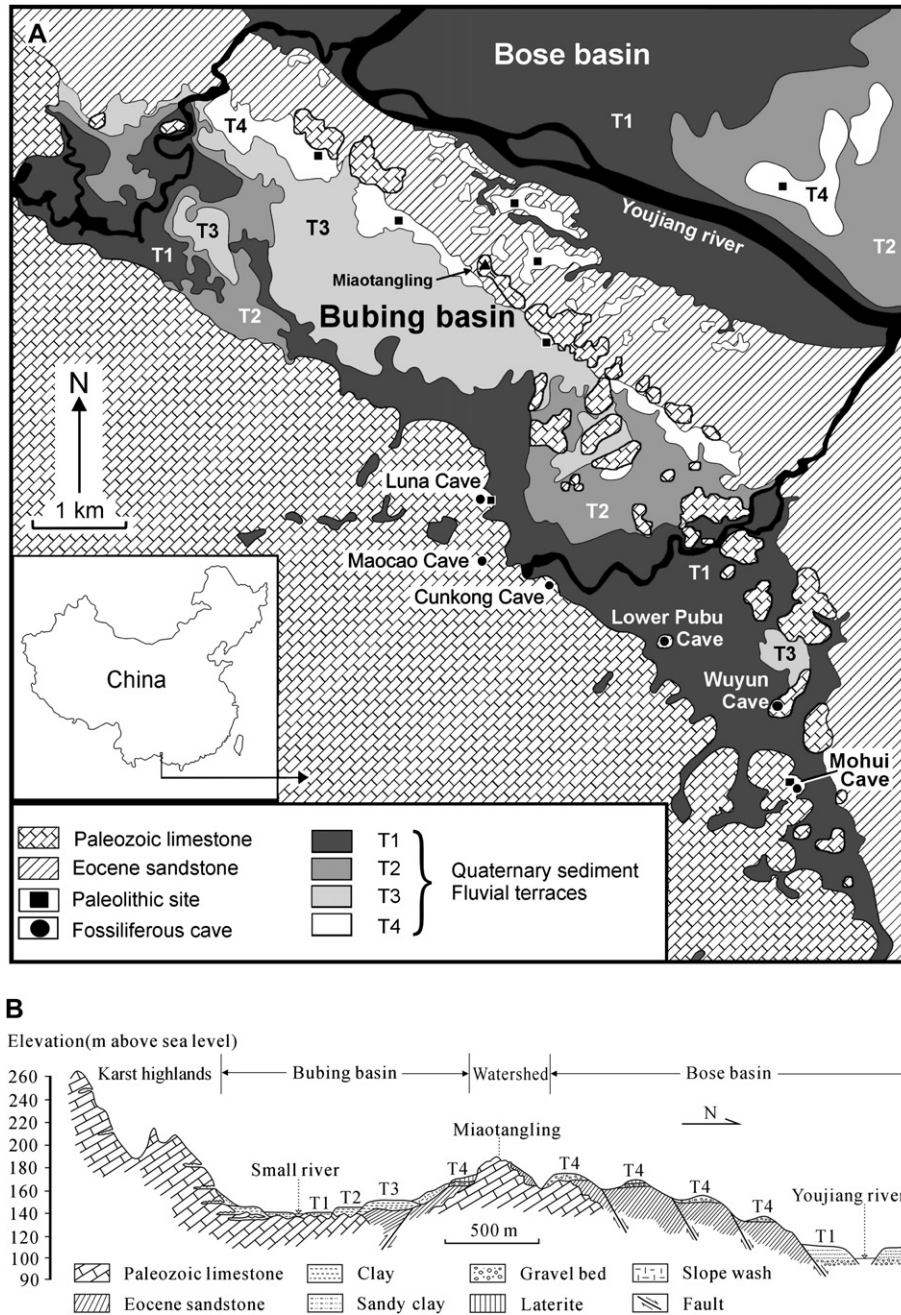


Fig. 1. Location of the Bubing Basin caves. A: Map of the Bubing Basin's relationship to the larger Bose Basin, and the location of the caves in the karstic limestone bordering the Bubing Basin. Many Paleolithic sites occur in the Quaternary river terraces of the Bose Basin, and several have also been discovered in the terraces of the Bubing area. B: Section across the Bubing Basin and southern half of the Bose Basin across the divide at Miaotangling (see Fig. 1A). Fossiliferous caves occur at varying elevations in the karstic highlands along the southern margin of the Bubing Basin.

Our excavations have focused on Mohui Cave, which is located in the southeastern corner of the basin in the middle of a marginal hill at ~215 m above sea level and 65 m above local ground level (Fig. 2). Mohui Cave is ~50 m long and extends in an eastward direction with an average width of ~5 m. The cave infilling is divided into three major units: an upper cave breccia with few fossils, a middle poorly-cemented fossiliferous unit consisting mainly of sandy clay, and a lower fine-clay deposit containing sparse fossilized teeth of large mammals and many teeth and bones of micromammals. *In*

situ fossils were recovered in six areas (Fig. 3) that were excavated to the limestone bedrock.

Wuyun Cave is ~60 m long, 4 m wide, and 5 m high. Deposits in this cave were mainly sandy-clay interstratified with a few layers of flowstone. Wuyun was excavated in four squares (2 × 2 m) to an average depth of 2.5 m. Mammalian teeth were very densely concentrated in the upper part of the excavation. Lower Pubu Cave is ~60 m long and varies 1–4 m in width and 1–5 m in height. Sandy-clay sediments in Lower Pubu were excavated in two squares

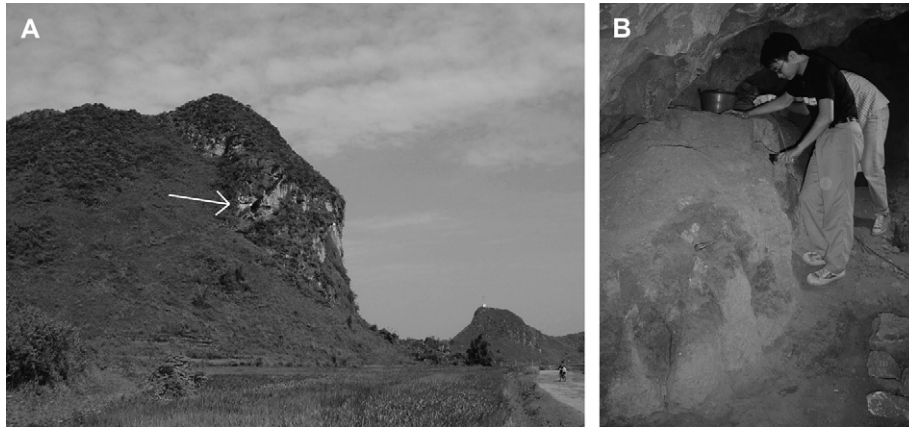


Fig. 2. Mohui Cave. A: View of the cave opening (arrow) from the floor of the Bubing Basin. B: Excavation in progress in the middle stratigraphic unit (Photographs: Wang Wei).

(2 × 2 m) to a depth of 2.5 m. Cunkong Cave is ~10 m long, 2 m wide, and 1–3 m high. Sandy-clay deposits in this cave were excavated in three squares (2 × 2 m) to a depth of ~1.2 m.

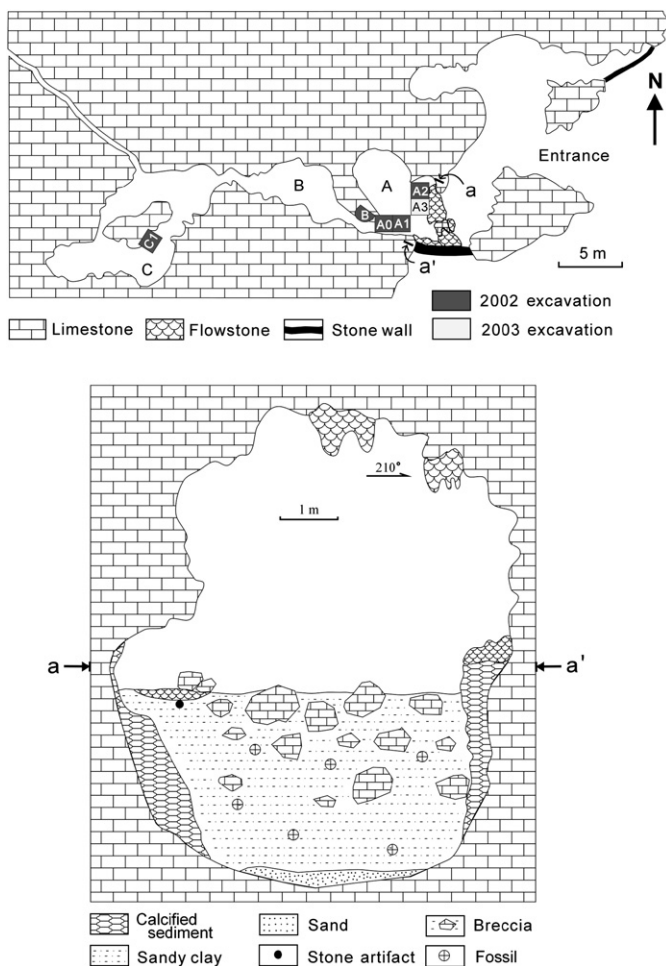


Fig. 3. Upper: Plan view of Mohui Cave, indicating three main sections of the cave (A–C) and the location of excavation squares. Lower: Stratigraphic profile through excavation squares A0–A2, defined by points a and a' in the upper figure. Fossils were distributed throughout the deposit and concentrated especially in the middle and lower two-thirds of this profile. Vertical and horizontal scales are equal. A stone artifact was found at the top of the deposit.

U-series dating

To assess the potential for estimating the age of sediments in the caves, we obtained flowstone samples for U-series dating from the sequence in Wuyun Cave. The validity of U-series dating of carefully-selected, pure, compact and well-crystallized cave calcites has previously been demonstrated (Ludwig et al., 1992; Schwarcz, 1992). In southern China, U-series dating of cave flowstones of late middle Pleistocene to late Pleistocene age has been effective (Shen et al., 2002b). In Wuyun Cave, samples were collected from an upper flowstone (sample No. 3), a middle flowstone (No. 4, 45 cm below the first flowstone), and a lower flowstone (No. 5, 180 cm below the first flowstone). All fossils recovered *in situ* are between the upper and lower flowstones. The middle flowstone occurs in the upper half of the fossil bed excavated in Wuyun Cave.

U-series analyses were carried out by Cheng and Edwards at the University of Minnesota. Hand specimens of each flowstone were chiseled into pieces a few millimeters in diameter. A few hundred milligrams of the cleanest of these pieces were separated under a binocular microscope for each analysis. For flowstone No. 5, two groups of pieces were separated for replicate analysis (No. 5a and 5b). Samples were dissolved, spiked, and separated into uranium and thorium fractions using modifications (Cheng et al., 2000) of techniques originally described by Edwards et al. (1987). Uranium and thorium isotopic measurements were performed by magnetic sector inductively-coupled plasma mass spectroscopy on a Finnigan Element (Shen et al., 2002a).

Stable isotopes

As part of a wider investigation into the paleoenvironments of the Bose and Bubing basins, we conducted a preliminary study of the carbon and oxygen stable isotopic composition of a limited subset of the Bubing fossil fauna. Stable isotopic analysis of tooth enamel can provide useful information about terrestrial paleoenvironments, particularly with regard to the representation of C₃ and C₄ vegetation in an ecosystem (Kingston et al.,

1994; Cerling et al., 1997) and the degree of canopy closure/openness in wooded habitats (Cerling et al., 2004).

The feasibility of stable isotopic study of mammalian teeth was tested on a sample of 11 specimens representing a variety of herbivore taxa. Six teeth excavated *in situ* from Mohui Cave were from *Sus peii*, *Sus xiaozhu*, *Stegodon* sp., *Rhinoceros* sp., Cervidae (gen. et sp. indet.), and Bovidae (gen. et sp. indet.). Two *in situ* teeth were sampled from Lower Pubu Cave, representing *Elephas* sp. and *Ailuropoda melanoleuca baconi*. In addition, three surface-collected teeth were made available from inside Upper Pubu Cave, which has an equivalent elevation and a similar fauna to that of Wuyun Cave; these specimens were from *Elephas* sp. and *Stegodon* sp. ($n = 2$).

Samples for isotopic analysis, ~ 100 micrograms each, were extracted with a low-speed, high-torque, 0.5-mm-diameter diamond drill. Powders were then treated with 3% sodium hypochlorate solution at 25 °C for three hours to remove any organic contamination. All samples were run on a “VG-Prism” mass spectrometer fitted with an “Isocarb” common acid bath preparation line. Reaction of samples with the 100% phosphoric acid was conducted at 90 °C. Evolved CO₂ was preconcentrated using a cold finger prior to insertion into the mass spectrometer. All of the isotopic analyses were conducted by Ditchfield at the University of Oxford.

Results

Dating

U-series analytical results are shown in Table 1. All errors are reported at the 2σ level of uncertainty. The ages of the three flowstones are nominally in stratigraphic order, consistent with age accuracy. The two youngest flowstones have ages that are clearly resolved when errors are considered, whereas the two oldest flowstones have ages that are not resolved at the 2σ level of uncertainty. Reproducibility is demonstrated by the two replicate ages on the oldest flowstone. The main age uncertainties are associated with the corrections for initial ^{230}Th . To make this correction, we have used an initial $^{230}\text{Th}/^{232}\text{Th}$ value of 4.4×10^{-6} , with an assigned error of 50%. The correction is minor for the middle flowstone as its measured $^{230}\text{Th}/^{232}\text{Th}$ value is much higher than 4.4×10^{-6} . Thus, the age estimate for this flowstone, 242 ± 21 ka, is robust. The measured $^{230}\text{Th}/^{232}\text{Th}$ values of the two other flowstones

are lower and the corrections larger. As initial $^{230}\text{Th}/^{232}\text{Th}$ values cannot be negative, the uncorrected ages for each of these flowstones are robust maximum ages. Thus, the upper flowstone is younger than 21 ka, the middle flowstone 242 ± 21 ka, and the lower flowstone younger than 350 ka. These age constraints suggest that the majority, if not all of the fossil sample excavated from Wuyun Cave, can be assigned to the late middle Pleistocene, probably 350 to 200 ka.

In addition, sediment samples were obtained from Mohui Cave for preliminary paleomagnetic analysis that was conducted by Prof. Zhu Rixiang in the Paleomagnetism and Geochronology Lab, Institute of Geology and Geophysics, Beijing. Of 18 samples from the upper 3 m of the sequence, two samples at consecutive stratigraphic levels, 10 cm apart, were magnetically reverse. Although consistent with the idea that the fossiliferous deposit was formed prior to the Brunhes, that initial study did not yield a coherent magnetostratigraphy relatable to the geomagnetic polarity time scale (Zhu Rixiang, pers. comm.).

Excavated faunal remains

Almost all of the excavated materials from the four caves comprise isolated teeth that retain tooth marks consistent with rodent gnawing and possibly carnivore activity, which occurred before burial of the teeth. Fauna from the caves are listed in Table 2.

Although the volume of sediment excavated was roughly similar in all the caves, differences in fossil sample sizes are apparent and probably result from varied rates of bone accumulation and attrition due to animal gnawing in the four caves. Cunkong Cave yielded an extant fauna associated with Holocene archaeological remains. The fauna from Lower Pubu Cave exhibits an overall similarity to the fauna from the late Pleistocene Nanshan Cave (Wang and Mo, 2004). The Wuyun Cave fauna is most similar to that from the middle Pleistocene to early late Pleistocene on the basis of faunal comparisons presented by Chen et al. (2001). This age assignment is supported by the U-series analyses reported here.

Fauna and hominoid teeth from Mohui Cave

Twenty-eight distinct mammalian taxa have been identified in the fauna obtained from Mohui Cave, the highest cave

Table 1

U-series dating results of travertine in Wuyun Cave. All data were measured on an inductively-coupled plasma mass spectrometer with a sector magnet for sorting the ions (a Thermo-Finnigan Element mass spectrometer at the University of Minnesota). Decay constants used to calculate ages from isotopic compositions are: for ^{230}Th : $9.1577 \times 10^{-6}/\text{y}$; for ^{234}U : $2.8263 \times 10^{-6}/\text{y}$; and for ^{238}U : $1.55125 \times 10^{-10}/\text{y}$. All errors are reported at the 2σ level of uncertainty

Sample number	$^{238}\text{U}^*$ (ppb)	$^{232}\text{Th}^*$ (ppt)	$^{230}\text{Th}/^{232}\text{Th}$ (atomic, $\times 10^{-6}$)	$\delta^{234}\text{U}^{**}$ (measured)	$^{230}\text{Th}/^{238}\text{U}$ (activity)	^{230}Th Age(y) (uncorrected)	^{230}Th Age(y)*** (corrected)
3	67.7 ± 0.2	$19,561 \pm 226$	12.5 ± 0.3	241.4 ± 3.1	0.2195 ± 0.0036	$21,111 \pm 390$	$14,190 \pm 4,200$
4	150.1 ± 0.7	$45,964 \pm 537$	56.3 ± 1.5	126.7 ± 3.9	1.044 ± 0.024	$249,350 \pm 21,500$	$242,000 \pm 21,000$
5a	37.6 ± 0.1	$99,040 \pm 1,340$	8.3 ± 0.1	281.6 ± 4.0	1.321 ± 0.012	$348,350 \pm 20,000$	$289,600 \pm 45,000$
5b	37.6 ± 0.1	$116,700 \pm 2,160$	7.2 ± 0.1	310 ± 11	1.363 ± 0.012	$356,390 \pm 29,000$	$287,170 \pm 60,000$

*ppb refers to parts per billion (10^9), ppt refers to parts per trillion (10^{12}); both by mass.

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

***Corrected ^{230}Th ages assume an initial $^{230}\text{Th}/^{232}\text{Th}$ atomic ratio of $(4.4 \pm 2.2) \times 10^{-6}$.

Table 2
List of vertebrate fauna from four caves in the Bubing Basin

Genus/species	Cunkong Cave	Lower Pubu Cave	Wuyun Cave (N = 5369)	Mohui Cave (N = 655)
	(N = 285) Holocene	(N = 665) Late Pleistocene	Middle to early Late Pleistocene	Late Pliocene to Early Pleistocene
<i>Alligator</i> cf. <i>A. sinensis</i>			1	
<i>Neotetracus</i> cf. <i>N. sinensis</i>			29	
<i>Soriculus</i> sp.			53	
<i>Crocidura</i> sp.			38	
<i>Anourosorex</i> sp.			13	
<i>Scotomanes</i> sp.			21	
<i>Hipposideros</i> sp.			65	
<i>Macaca</i> sp.	3	23	53	20
<i>Presbytis</i> sp.			39	
Hominoidea gen. et sp. indet.				17
<i>Pongo pygmaeus weidenreichi</i>			20	
<i>Gigantopithecus blacki</i>				16
<i>Homo sapiens</i>	4			
<i>Sciurotamias</i> sp.			59	
<i>Callosciurus</i> sp.			67	
<i>Belomys</i> sp.			56	
<i>Typhlomys cinereus</i>			102	25
<i>Hystrix subcristata</i>		122	251	
<i>Hystrix kiangsenensis</i>				77
<i>Hystrix magna</i>				10
<i>Hystrix</i> sp.	21			
<i>Rhizomys</i> sp.	4	5		
<i>Mus</i> cf. <i>M. pahari</i>			88	
<i>Hapalomys delacouri</i>			46	
<i>Hapalomys</i> sp.				30
<i>Chirodomys</i> cf. <i>C. gliroides</i>			102	
<i>Leopoldamys</i> sp.			65	19
<i>Niviventer</i> sp.			193	48
<i>Rattus</i> sp.			232	
<i>Cuon</i> cf. <i>C. javanicus antiquus</i>			26	
<i>Cuon dubius</i>				2
<i>Arctonyx collaris</i>		11	49	3
<i>Ursus thibetanus</i>	6	12	69	5
<i>Ailuropoda melanoleuca baconi</i>		3	17	
<i>Ailuropoda microta</i>				4
<i>Pachycrocuta licenti</i>				1
<i>Panthera</i> sp.				1
<i>Felis tigris</i>	2		3	
<i>Felis pardus</i>			19	
<i>Felis teilhardi</i>			23	2
<i>Paradoxurus</i> sp.			11	
<i>Stegodon orientalis</i>			59	
<i>Stegodon preorientalis</i>				15
<i>Elephas maximus</i>	3	2	3	
<i>Sinimastodon</i> sp.				1
<i>Tapirus sinensis</i>		1	22	
<i>Tapirus sanyuanensis</i>				4
<i>Hesperotherium</i> sp.				2
<i>Megatapirus augustus</i>			21	
<i>Rhinoceros sinensis</i>		2	69	18
<i>Equus hemionus</i>		2		
<i>Sus scrofa</i>	68	59	871	
<i>Sus xiaozhu</i>		7		31
<i>Sus peii</i>				53
<i>Dorcabune liuchengense</i>				3
<i>Muntiacus</i> sp.	28	123	995	72
<i>Cervus</i> cf. <i>fengqii</i>				62
<i>Cervus yunnanensis</i>				61
<i>Cervus</i> sp.	139	277	1296	49
<i>Capricornis sumatraensis</i>			125	
Bovinae gen. et sp. indet.	7	16	98	1
<i>Megalovis guangxiensis</i>				3

excavated in the Bubing Basin. Among these taxa are six rodents, including two species of *Hystrix*, which may implicate porcupine scavenging as the dominant taphonomic mode of bone accumulation and attrition of the assemblage.

The Mohui fauna is similar in its overall composition to the faunas from Longgupo (Chongqing, South China) and Liucheng (middle Guangxi, South China) (Han, 1987; Pei, 1987; Huang and Fang, 1991). Specifically, the presence of *Hesperotherium* and *Ailuropoda microta* are considered typical of the late Pliocene to earliest Pleistocene, which suggests that Mohui Cave also preserves fauna from this interval. The presence of these taxa supports the hypothesis that the highest cave preserves the oldest fauna among the four caves studied here.

Thirty-three isolated teeth of hominoid primates have also been identified in the Mohui sample (Table 2). Sixteen teeth from the middle stratigraphic unit are assigned to *Gigantopithecus blacki*. They include one RI₂, one LC₁, one LC¹ and one RC¹, three LP³, one LP₃, one RM_{1–2} and three LM_{1–2}, one RM^{1–2} and one LM^{1–2}, one LM₃, and one LM³ (Fig. 4). The size and morphological characters of these teeth are similar to those of *G. blacki* from Liucheng Cave (Woo, 1962) and Longgupo (Huang et al., 1995), and the sample exhibits substantial size variation.

A sample ($n = 17$) of smaller-sized hominoid molars, premolars, and an incisor were also found in the Mohui Cave excavation, and we provisionally assign this sample to Hominoida (gen. et sp. indet.). Our preliminary observations here are that this sample consists of two large molars with crown measurements outside the range of Chinese *H. erectus* at Zhoukoudian (Weidenreich, 1937), and a more abundant subsample of smaller teeth that includes molars similar to those from the Longgupo mandibular fragment (Huang et al., 1995). The latter specimen was originally claimed to represent *Homo*, but this interpretation has been questioned (e.g., Wu, 2000), and its classification as an ape is preferred by some specialists (Dennell and Roebroeks, 2005). This Mohui sample does not strongly resemble *Pongo* remains found in Wuyun Cave and other sites in China. One goal of our ongoing research in the Bubing Basin is to increase this sample and to refine the taxonomic assessment.

Isotopic results

$\delta^{13}\text{C}$ values range from -15.3 to -3.6‰ with a mean value of -12.5‰ relative to the PeeDee Belemnite international standard (PDB; Craig, 1957; Table 3). Two samples (LPC QL and LPC L7), both from Lower Pubu Cave, plot as significant outliers from the bulk of the data. $\delta^{18}\text{O}$ values range from 21.1 to 26.2‰ with a mean value of 23.8‰ relative to Standard Mean Ocean Water (SMOW; Craig, 1961). The two Lower Pubu Cave samples that are least depleted in $\delta^{13}\text{C}$ also show the least depleted $\delta^{18}\text{O}$ values. The first of these samples (LPC QL, *Elephas* sp.) is strongly discolored and shows dissolution texture on the surface of the enamel. This sample also shows the most extreme isotopic results reported in this study, plotting well away from the main data field. This is interpreted to result from diagenetic alteration and

post-depositional isotopic exchange. The second sample (LPC L7, *Ailuropoda melanoleuca baconi*) shows moderate discoloration but no obvious dissolution texture. The isotopic results from this sample plot closer to the main body of the data but still show some separation. No published data for the carbon stable isotopic composition of modern *Ailuropoda* could be found. However, the relatively simple morphology and low efficiency of the *Ailuropoda* gut (Dierenfeld et al., 1982) is not suggestive of significant isotopic modification by, for example, hind-gut fermentation. Thus, it seems most likely that the offset of the carbon isotopic data for this sample represents minor diagenetic alteration. The remaining data are consistent with the preservation of a primary environmental signal, with a mean $\delta^{13}\text{C}$ value of -13.6‰ and a range from -15.3 to -11.4‰ .

Discussion

The sequence of mammalian fossils

The mammalian remains from the four caves exhibit taxonomic variations that we attribute, at least in part, to a temporal sequence of faunal change. In this discussion, we focus on the presence/absence of taxa. Specimen counts given in Table 2 provide a general indication of how robust our interpretations are; estimates of the timing of first and last appearances, which are important to the interpretation of faunal change, will depend on detailed statistical treatment and the integration of the faunal data from elsewhere in China—both of which are a focus of our future work.

Cunkong Cave, which is the lowest elevation cave, provides the youngest faunal sample: *Stegodon* and *Ailuropoda* are absent, and the fauna consists entirely of extant species, which are similar to animals present in the area today. The Cunkong fauna is associated with pottery in the upper part of the stratigraphic profile. Therefore, we assign this fauna to the Holocene.

In Lower Pubu Cave, the fauna differs from the traditional *Stegodon*-*Ailuropoda* assemblages of South China. Although *Ailuropoda melanoleuca* is present, *Stegodon* is absent whereas *Elephas maximus* is present. The fauna also records the appearance of *Equus hemionus* in South China. This extant species is, at present, distributed broadly in northern China, Mongolia, and central and western Asia; fossils of this species have been recovered in late Pleistocene contexts of Gansu, Inner Mongolia, in northern China (Deng and Xue, 1999), and also at 20–40 ka in Nanshan Cave, Guangxi, southern China (Wang and Mo, 2004). It is possible that the presence of *E. hemionus* in South China reflects cooler environmental conditions associated with the last glacial epoch and the existence of at least a temporary corridor for migration between northern and southern China, which facilitated the range expansion of the rapidly dispersing *E. hemionus*. Further faunal evidence in precise chronological context is needed to test this idea. For now, we assign the Lower Pubu fauna to the late Pleistocene.

The Wuyun Cave assemblage differs from both the Lower Pubu (later) and Mohui (earlier) faunas. Remains of

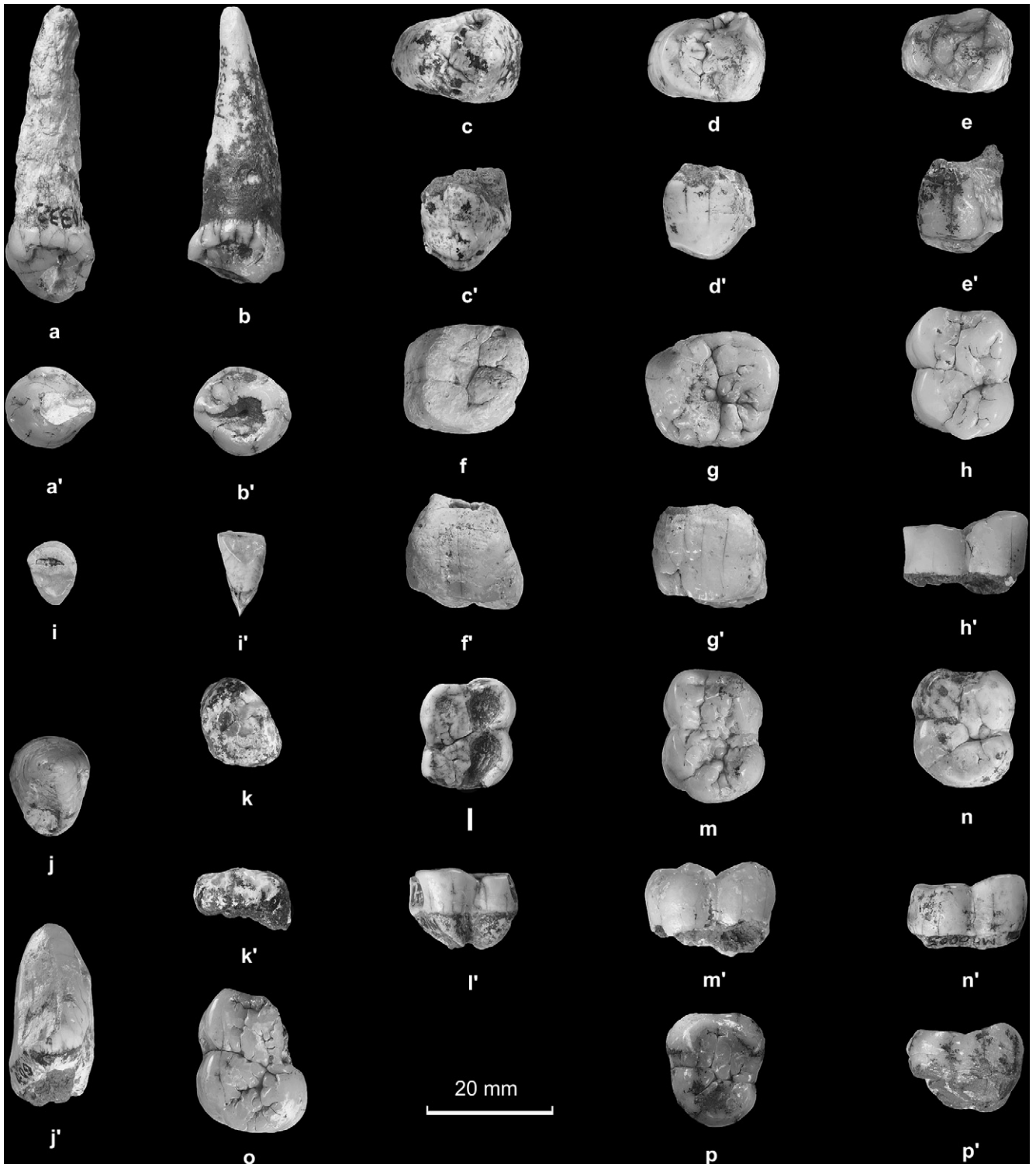


Fig. 4. *Gigantopithecus blacki* teeth from Mohui Cave. (a) MH0332, RC¹, lingual view and (a') occlusal view; (b) MH0548, LC¹, lingual view and (b') occlusal view; (c) MH0013, LP³, occlusal view and (c') lingual view; (d) MH0019, LP³, occlusal view and (d') lingual view; (e) MH0514, LP³, occlusal view and (e') lingual view; (f) MH0504, RM¹⁻², occlusal view and (f') lingual view; (g) MH0011, LM³, occlusal view and (g') lingual view; (h) MH0006, LM¹⁻², occlusal view and (h') lingual view; (i) MH0047, RI₂, occlusal view and (i') lingual view; (j) MH0409, LC₁, occlusal view and (j') lingual view; (k) MH0333, LP₃, occlusal view and (k') lingual view; (l) MH0513, RM₁₋₂, occlusal view and (l') lingual view; (m) MH0010, LM₁₋₂, occlusal view and (m') lingual view; (n) MH0005, LM₁₋₂, occlusal view and (n') lingual view; (o) MH0014, LM₁₋₂, occlusal view; (p) MH0623, LM₃, occlusal view and (p') lingual view. Scale bar = 20 mm.

Table 3

Isotopic data for eleven teeth representing a variety of mammalian taxa from the Bubing Basin caves, including samples LPC QL and LPC L7, which were excluded from the paleoenvironmental analysis due to probable diagenetic contamination. $\delta^{18}\text{O}$ SMOW values are calculated from the $\delta^{18}\text{O}$ PDB values by using the formula in [Coplen et al. \(1983\)](#)

Sample	Taxon	Comments	$\delta^{13}\text{C}$ PDB	$\delta^{18}\text{O}$ PDB	$\delta^{18}\text{O}$ SMOW
LPC QL	<i>Elephas</i> sp.	Discolored with dissolution texture	−3.62	−5.44	25.30
LPC L7	<i>Ailuropoda melanoleuca baconi</i>	Moderate discoloration	−10.97	−4.60	26.17
UPC A	<i>Elephas</i> sp.		−13.00	−6.15	24.57
UPC B	<i>Stegodon</i> sp.		−11.41	−6.56	24.14
UPC C	<i>Stegodon</i> sp.		−13.17	−7.89	22.78
MH 412	Cervidae indet.		−13.93	−8.71	21.93
MH 417	<i>Sus peii</i>		−14.79	−7.49	23.19
MH 478	<i>Sus xiaozhu</i>		−12.51	−7.80	22.87
MH 522	<i>Rhinoceros</i> sp.		−14.55	−6.34	24.38
MH 556	Bovidae indet.		−14.42	−6.48	24.23
MH 579	<i>Stegodon</i> sp.		−15.27	−8.21	22.45

Ailuropoda melanoleuca, *Stegodon orientalis*, and *Elephas maximus* occur together in Wuyun Cave. The latter species is unknown in early Pleistocene sites of China, which is consistent with U-series evidence presented here for the late middle Pleistocene age of the Wuyun fauna.

A different species of *Ailuropoda* (*A. microta*) is associated with *Stegodon* in Mohui Cave, and the *Stegodon* from Mohui (represented by a deciduous molar and dental fragments) differs from *S. orientalis* known from late Pliocene through middle Pleistocene sites in South China. Comparison among the Bubing Cave faunas also records the presence of the early Pleistocene suid *Sus peii* exclusively in Mohui, while *Sus scrofa* replaces *S. peii* in the later cave faunas.

The presence of both *Stegodon* and *Ailuropoda* in the recently dated Liujiang site (Guangxi, South China) at ~ 70 – 300 ka ([Shen et al., 2002b](#)) confirms the implications of this study that the simple presence of these two genera is not useful in distinguishing early from middle Pleistocene faunas. The comparison of faunas carefully excavated from caves of varying elevation in the Bubing Basin provides the first evidence of taxonomic variation and turnover within a relative temporal sequence of faunas from South China.

Isotopic results

There is an ~ 13 per mil enrichment in ^{13}C in tooth enamel over the dietary source of carbon ([Balasse, 2002](#)). On the basis of the mean $\delta^{13}\text{C}$ value of -13.6‰ obtained on this sample of mammalian herbivore teeth, the resulting estimate of about -26‰ is consistent with an entirely C_3 -plant-dominated assemblage. As some teeth show values significantly more depleted than -13‰ (as low as -15.3‰), it is possible that these specimens of *Stegodon* and *Sus* indicate a canopy effect (i.e., a recycling of already-depleted organic carbon within an enclosed heavily wooded environment; [Rodiere et al., 1996](#)). Our results are also consistent with $\delta^{13}\text{C}$ values reported for the Southeast Asian closed canopy fauna from Niah Cave, Sarawak ([Krigbaum, 2003](#)), and point toward a diet from a closed canopy habitat of dense woodland or forest.

Conclusion

Study of the karstic caves in the Bubing Basin has led to a geological hypothesis of cave formation and sedimentary infilling that helps in establishing a temporal sequence of fossils based on the excavation of caves of varying elevation. Our excavations of four such caves provide the first well-documented mammalian faunal sequence for South China. Faunal lists from the four caves indicate taxonomic variations in mammalian species over time that need to be assessed with further careful recovery of fauna from other caves in the region and statistical analysis. The taxonomic variations suggest that although the traditional *Stegodon-Ailuropoda* Fauna has served as a general description of the late Pliocene and Pleistocene fossil assemblages of South China, it is now a category with little value in the study of faunal dynamics, biochronology, and the biotic context of Pleistocene apes and hominins in this region.

The cave with the highest elevation, Mohui Cave, contains the oldest fauna of the four examined in this paper. This faunal assemblage is most similar taxonomically to others (e.g., Longgupo, Liucheng) thought to be of late Pliocene to early Pleistocene age. Eventually, the age of these faunas, including that of Mohui, will require independent verification by geochronological methods. For the time being, the Mohui tooth sample that is assigned here to an, as yet, unknown genus and species of hominoid, offers an opportunity to investigate dental morphology that superficially resembles Plio-Pleistocene hominins' but may instead represent a non-*Pongo* great ape lineage or clade that is not yet well-documented or understood.

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