Chinese Science Bulletin



# A newly discovered *Gigantopithecus* fauna from Sanhe Cave, Chongzuo, Guangxi, South China

JIN ChangZhu[1†], QIN DaGong[2], PAN WenShi[2], TANG ZhiLu[1], LIU JinYi[1], WANG Yuan[1], DENG ChengLong[3], ZHANG YingQi[1], DONG Wei[1] & TONG HaoWen[1]

[1] Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China;
[2] School of Life Sciences, Peking University, Beijing 100871, China;
[3] Paleomagnetism and Geochronology Laboratory, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing 100029, China

**Among the most important faunas in the Late Cenozoic, the *Gigantopithecus* faunas have received a good deal of attention. The *Gigantopithecus* fauna recently discovered in Sanhe Cave consists of more than 80 mammal species, including cf. Hominidae, *Pongo* sp., *Hylobates* sp., *Sinomastodon yangziensis*, *Stegodon preorientalis*, *Cervavitus fenqii*, *Dicoryphochoerus ultimus* and *Sus xiaozhu*. It is the southernmost *Gigantopithecus* fauna found so far in China. Its geological age is estimated to be Early Pleistocene based on the fauna and stratigraphic correlation. The significant increase in the estimated body sizes of *Ailuropoda*, *Gigantopithecus* and *Tapirus* shows that the Sanhe fauna is middle Early Pleistocene, later than those from Wushan and Liucheng (early Early Pleistocene). Paleomagnetic dating of the fossil-bearing strata in Sanhe Cave gives an age of approximately 1.2 Ma. The fauna is characterized by tropical-subtropical forest types, including *Pongo* sp., *Tupaia* sp., *Ia* sp., *Typhlomys intermedius*, etc., and it lacks Palaearctic types. It is a typical tropical forest fauna, suggesting an environment with a lush forest and a warm and humid climate. The discovery of the Sanhe *Gigantopithecus* fauna is significant for establishing the chronological stages of the *Gigantopithecus* faunas in China, and for discussing their origin, evolution and dynamics.**

Chongzuo, Guangxi, Sanhe Cave, early Pleistocene, *Gigantopithecus* fauna

As one of the most important Quaternary mammalian faunas, the *Gigantopithecus* fauna attracts much attention from Chinese scientists. In 1935, the Dutch paleontologist G.H.R. Von Koenigswald found a large cf. Hominidae lower molar in a Chinese traditional medicine store in Hongkong. The length of the molar is twice that of a human molar, and its occlusal surface area is 3 to 4 times larger. Von Koenigswald believed it to be a large relative of *Pithecanthropus* and therefore created a new genus *Gigantopithecus* and species *Gigantopithecus blacki*[1]. This discovery caused a sensation in paleontological circles. There was heated debate about whether this animal was an ape or a human, and about its height and size. The *Gigantopithecus* tooth was mixed with other "dragon bones", such as those of *Pongo, Ailuropoda,* and *Stegodon*, without any information on the stratum and locality of the specimen. Scholars referred to this assemblage as the "Drugstore fauna". Twenty years later (1956—1960), Pei Wenzhong, a famous Chinese Quaternary paleoanthropologist, carried out a large-scale investigation with his colleagues at cave sites in Guangxi. They discovered *Gigantopithecus* and associated mammalian fossils in Quaternary sedimentary sequences in caves in Tahsin, Liucheng, and a few other localities. Chow[2] thought that the mastodon and the

Received April 23, 2008; accepted October 14, 2008;
published online December 17, 2008
doi: 10.1007/s11434-008-0531-y
†Corresponding author (email: jinchangzhu@ivpp.ac.cn)
Supported by Key Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX2-YW-106) and National Basic Research Program of China (Grant No. 2006CB806400)

small sized tapirs from the Liucheng *Gigantopithecus* Cave were more primitive than the typical middle Pleistocene *Ailuropoda-Stegodon* fauna. He considered its age to be early Pleistocene (or the latest Pliocene) and named it the *Gigantopithecus* fauna. In the 1950s, there were only a few *Gigantopithecus* localities known with exact stratigraphic control. Today, the *Gigantopithecus* fauna is known from 12 localities distributed across 5 provinces in South China, in association with some important fossils and cultural relics of early humans. There has been considerable progress in the study of the geology, paleontology, paleoanthropology and chronology, and this provides a new perspective regarding the characteristics, age and environmental background of the *Gigantopithecus* fauna and its status in human evolutionary history. Due to the lack of systematic and comprehensive research on faunas in south China there have been controversies over the origin, evolutionary characteristics, age, and ecological environment of the *Gigantopithecus* fauna.

Recently, Pan Wenshi, a professor from Peking University (PKU), discovered *Gigantopithecus* fossils from Boyue Cave in Chongzuo Ecological Park, Guangxi. Since then the PKU Chongzuo Biodiversity Research Institute has cooperated with the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (CAS) to carry out further investigations, leading to the discovery of new strata with *Gigantopithecus* fossils in Sanhe Cave, Wuming Mountain. After trial excavation, a plethora of higher primate fossils, including *Gigantopithecus*, *Pongo* sp., *Hylobates* sp., *Macaca* sp., *Presbytis* sp., and cf. Hominidae have been collected, as well as other associated mammalian fossils. The newly discovered fossils provide important new evidence for the evolution and extinction of *Gigantopithecus* and the biochronological stages of the *Gigantopithecus* fauna.

## 1 Geographical background

Located 16 km to the northeast of Chongzuo urban district, Chongzuo Ecological Park (Chongzuo Biodiversity Research Institute, PKU) lies in Jiangzhou District between the Zuojiang River and the Sifang Mountain, and the junction between Banli and Luobai Country, covering an area of 24 km$^2$, with geographic coordinate: 22°16.493′N, 107°30.663′E (Figure 1). This park is also the main habitat for *Presbytis leucocephalus*, a rare and endangered primate. According to meteorological data, this area has a transitional climate between subtropical and tropical. However, the animal and plant species and other natural conditions indicate that this area belongs to



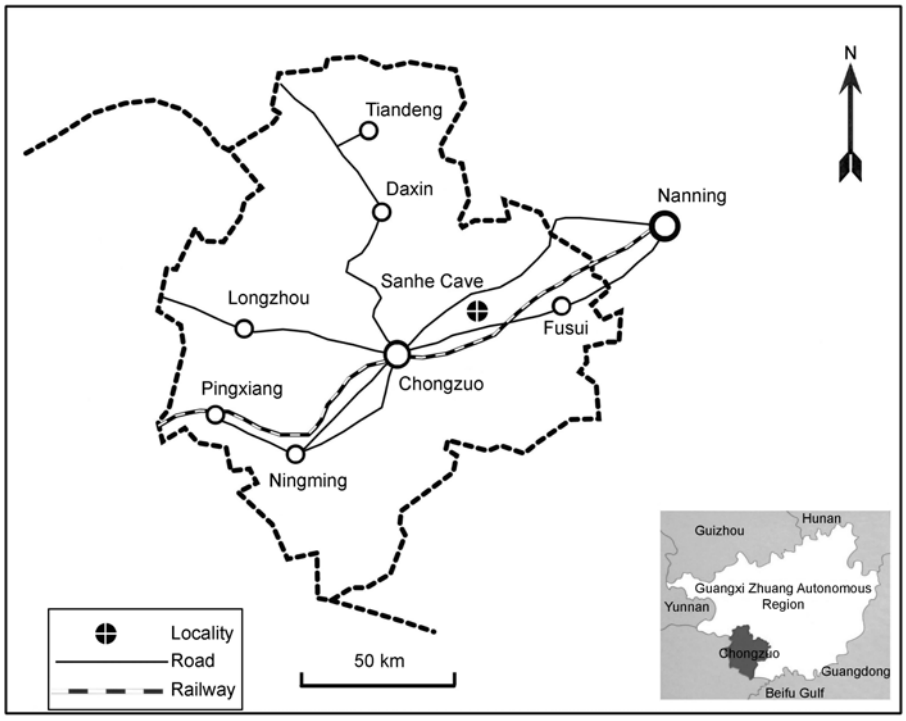


**Figure 1** Geographical location of the *Gigantopithecus* fauna in Sanhe Cave, Chongzuo, Guangxi.

the north tropical zone because it has more tropical than subtropical characters. Nevertheless, the tropical scenery is not as typical as that in Malaysia and Indonesia, and the temperature is relatively low with occasional frosts in winter. Due to the monsoon, rain and heat occur during the same period, so there is a marked climate change between cold-dry and hot-wet seasons. Therefore, the zoogeographical environment here has attracted much attention.

Chongzuo Ecological Park and its adjacent areas belong to the bare Karst area with a northern tropical climate. The Karst landscape includes two types: peak valleys and peak basins, but most of them are tropical peak basins with deep erosional cutting. The caves are well developed in the calcareous Karst rocks on both sides of the valley (or basin) (Figure 2). Six vertical level of caves are recognized in this area. The lowest layer (1st layer) of caves is about 130 m above sea level (ASL), while the highest layer (6th layer) of caves is 270 m ASL. *Gigantopithecus* fossils are mainly discovered from caves in the 5th layer, which is about 200 m ASL.

## 2 Geomorphology and stratigraphy of Sanhe Cave

Sanhe Cave is the largest tubular Karst cave in this area. The eastern cave entrance, 12.5 m wide and 15.6 m high, is 203 m ASL and located more than 70 m above the 1st terrace. The cave is 156 m long, with a maximum width of 100 m. The excavation area is a side branch of the cave, about 30 m to the southwest of the main cave opening. The direction of the chamber is oriented nearly south-north. The stratigraphic sequence can be divided into 7 layers from top to bottom (Figure 3):

1. Brown sandy clay with calcareous breccia, containing many spherical iron-manganese nodules, angled unconformably with the flowstone below. 160 cm
2. Gray-white flowstone. 15 cm
3. Yellow-brown sand with local nodules that are thinly zonal and relatively hard, containing many fossils. 125 cm
4. Brown-yellow sand, with thin calcareous stripe and tiny calcareous breccia whose diameters are 0.2－2 cm, yielding abundant fossils, such as cf. Hominidae, *Gigantopithecus* etc. 120 cm
5. Yellow sandy silt, relatively even and unconsolidated, with rare *Gigantopithecus* fossils. 420 cm
6. Yellow lutaceous silt, with a few tiny iron-manganese nodules, containing few fossils with thickness. 220 cm
7. Yellow sandy clay with few fossils and bottom not found. 230 cm

The sequence can be divided into upper and lower depositional units: layer 1 is the upper unit, also the secondary deposit; layers 2－7 form the lower unit (~11.3 m thick), from which *Gigantopithecus* and cf. Hominidae fossils have been found.

## 3 The characteristics and age of the Sanhe fauna

### 3.1 The characteristics of the Sanhe fauna

The vertebrate fossils excavated from Sanhe Cave include fish (4 species), amphibians (3 species), reptiles (6 species), birds (7 species) and mammals, with a total of about 100 species. The mammalian assemblage contains 10 orders, 24 families, 64 genera and more than 80 species (see Table 1 for the list of fauna), including 32 species of large mammals and 52 species of small mammals. The abundance of *Gigantopithecus* specimens suggests that *Gigantopithecus* was one of the most comon taxa at that time (Figure 4).


**Figure 2** Vertical distribution of Sanhe Cave and other caves showing multiple cave levels.

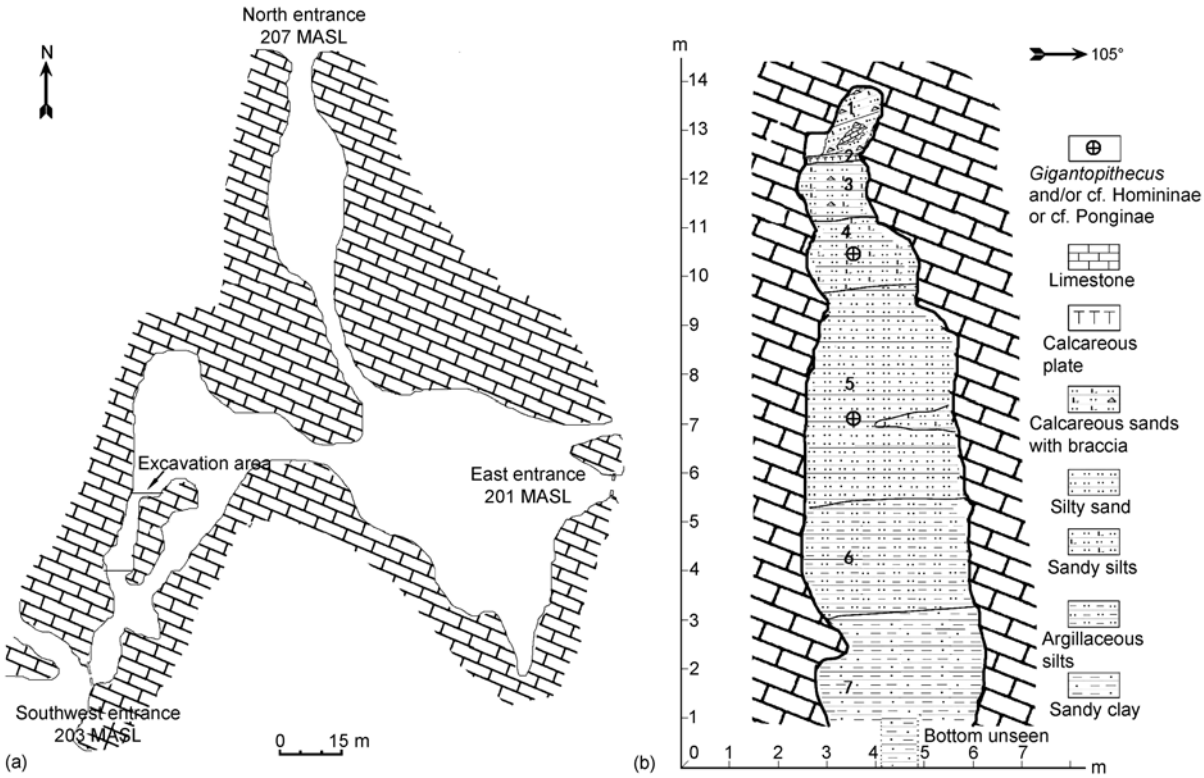


**Figure 3** Plan showing the position of the excavation area (a) and its geological section (b).



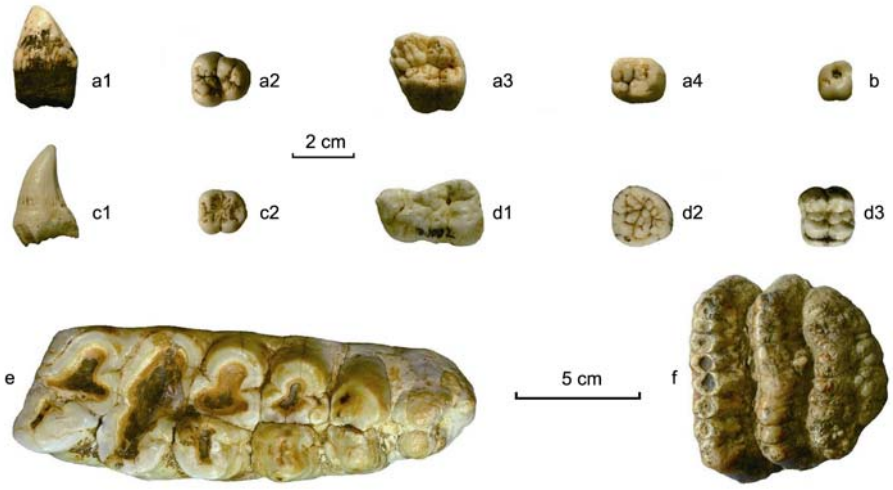


**Figure 4** *Gigantopithecus blacki*, cf. Hominidae or cf. Ponginae[1)] and other fossils from Sanhe Cave. a1—4, *Gigantopithecus blacki* (CSD0410-209, 230, 254, 257): a1, left canine; a2, right m3; a3—4, right M2—M3. b, cf. Homininae or cf. Ponginae (CSD0410-264): right M1. c1—2, *Pongo* sp. (CSD0410-179, 200): c1, left canine; c2, left m2. d1—3, *Ailuropoda wulingshanensis* (CSD0410-560, 568, 559): d1, left p4; d2, right m3; d3, left M1. e, *Sinomastodon yangziensis* (CSD0403): left 3. f, *Stegodon preorientalias* (CSD0401): left M3. (a1: labial view; the others: occlusal view).

1) Recently, the recovery of *Gigantopithecus* associated with important Hominidae fossils from early Pleistocene caves in south China (such as Longgupo in Chongqing, *Gigantopithecus* Cave in Liucheng, Mohui Cave in Guangxi, Longgudong Cave in Hubei and Sanhe Cave in Guangxi) has aroused much attention, providing important evidence for discussing hominid classification in EA and early hominid evolution. However, the limited material from the above sites results in intense debates about their taxonomy concerning whether they are Pongidae or Hominidae. We temporarily assign these teeth to cf. Hominidae or cf. Ponginae, awaiting systematic and detailed study.

The large mammals of the Sanhe fauna contain some Neogene remnant genera, such as *Sinomastodon*, *Dicoryphochoerus* and *Cervavitus*, and many Pleistocene extinct genera (for example, *Gigantopithecus*, *Procynocephalus*, *Erictis*, *Stegodon*, *Megalovis*, *Bibos*). The extinct genera account for 33% of the large mammals; while 26 extinct species represent 72% of all large mammal species. The small mammal fauna is characterized by common early Pleistocene Oriental species, including *Typhlomys intermedius*, *Hystrix magna*, *Belomys parapearsoni*, *Niviventer preconfucianus*, and *Leopoldamys edwardsioides*. Therefore, the fauna has a distinct early Pleistocene character.

To date, the earliest occurrence of *Gigantopithecus* is the late Miocene *Gigantopithecus giganteus* from India[3], while the latest record may be *Gigantopithecus blacki* in Vietnam dated to about 0.47 Ma[4]. The geographical distribution of *Gigantopithecus* ranges from China to Himachal Pradesh in north India, the Potwar Plateau in north Pakistan, and Tham Khuyen Cave in Vietnam, which borders Guangxi, China. The representative faunas are from Longgupo Cave in Wushan County, Chongqing, Liucheng *Gigantopithecus* Cave in Guangxi, Mohui Cave in Tiandong County, Guangxi, Longgudong Cave in Jianshi County, Hubei, Tahsin *Gigantopithecus* Cave in Guangxi, and Nongmo Hill in Bama, Guangxi These faunas represent different ages of the Pleistocene[5−13] and each of them has yielded *Gigantopithecus black*i. Research on the dental dimensions of *Gigantopithecus black* indicates that a certain consistency exists in terms of size variation and that there is a tendency for a gradual increase in the size of teeth from early to late Pleistocene[14−16]. Therefore, Zhang[17] divided *Gigantopithecus blacki* into two groups: a relatively small-sized group in the earlier period and a relatively large-sized group in the later period. The two groups seem to be different at the species level. The average size of the teeth of the *Gigantopithecus blacki* sample from Sanhe Cave generally falls between those of the two groups. The systematic classification, evolution and paleoecology will be discussed in a subsequent paper.

### 3.2 The age of the Sanhe fauna

The Sanhe fauna and its counterparts previously discovered in Guangxi, Hubei, Chongqing, and other localities mentioned above all belong to the Oriental realm. Therefore, their geological sequence has a relatively high degree of comparability (Table 1).

According to the biochronological characteristics of the fauna, the mammalian assemblages from Wushan, Liucheng, and Mohui are relatively primitive, with small-sized teeth in *Gigantopithecus blacki* and a higher proportion of Neogene relic species, such as *Hesperotherium*. Based on the results of paleomagnetic dating, the age of these sites is early Early Pleistocene[5−9]. The teeth of *Gigantopithecus blacki* in Sanhe Cave are significantly larger than their counterparts at the above sites. The *Gigantopithecus* faunas at the above sites have yielded primitive species, such as *Ailuropoda microta*[10], *Cuon dudius*, and *Tapirs sanyuanensis*; while the Sanhe fauna contains relatively advanced species, such as *Ailuropoda wulingshanensis*[10], *Cuon antiquus* and *Tapirus sinensis*. Moreover, the proportion of extant species in the Sanhe fauna is higher than those of the above early Early Pleistocene faunas. Therefore, the age of the Sanhe fauna is inferred to be younger than the early Early Pleistocene.

The age of the Longgudong fauna is middle Early Pleistocene[11,18,19]. Both the Longgudong fauna and the Sanhe fauna contain *Sinomastodon yangziensis*, *Stegodon prorientalias* and *Ailuropoda wulingshanensis*, implying contemporaneity. However, the average size of the teeth of *Gigantopithecus blacki* in the Longgudong fauna is slightly smaller than those in the Sanhe fauna. In addition, primitive *Tapirus sanyuanensis* is associated with *Tapirus sinensis*, and *Cuon dudius* also exists in the Longgudong fauna. The proportion of extant species of small mammals in the Longgudong fauna is also slightly lower than that in the Sanhe fauna. Accordingly, the age of the Longgudong fauna is inferred to be a little earlier than that of the Sanhe fauna.

Although controversy still exists about the age of the Tahsin fauna[11], the appearance of relatively primitive species, such as *Dicoryphochoerus ultimus*, *Sus bijiashanensis* and *Megalovis guangxiensis*, and the analysis of geomorphic characteristics of the cave (90 m higher than the valley floor, the same as the Liucheng *Gigantopithecus* Cave) show that the age of the Tahsin fauna may be late Early Pleistocene. There are more primitive species in the Sanhe Cave fauna than in that from Niushui Mountain Cave, Tahsin , so the age of the former is evidently earlier than the latter.

The *Gigantopithecus* in Sanhe Cave is different from

**Table 1** Comparison of *Gigantopithecus* faunas from Shanhe Cave and other Pleistocene localities in South China[a)]

| *Gigantopithecus* fauna from Shanhe Cave list of species | Longgupo in Chongqing[5] | Liucheng in Guangxi[6,7] | Mohui Cave in Guangxi[8] | Black Cave in Guangxi[12] | Longgudong in Hubei[11] | Bama in Guangxi[13] |
|---|---|---|---|---|---|---|
| **Mega-mammals** | | | | | | |
| *Gigantopithecus blacki* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ |
| *Pongo* sp. | | ◎ | ◎ | ◎ | | ◎ |
| *Procynocephalus* sp. | ◎ | | | | | |
| *Hylobates* sp. | | | ◎ | ◎ | | ◎ |
| *Rhinopithecus* sp. | | | ◎ | | ◎ | |
| *Macaca* sp. | ◎ | ◎ | ◎ | ◎ | ◎ | ◎ |
| *Presbytis* sp. | | | | | | |
| cf. Hominidae | □ | □ | □ | | □ | |
| *Ailuropoda wulingshanensis* | *A. microta* | *A. microta* | *A. microta* | *A. baconi* | ◎ ★ | *A. baconi* |
| *Ursus* cf. *thibetamus* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ | ◎ |
| *Arctonyx collaris* | | ◎ ★ | ◎ ★ | ◎ ★ | ◎ | |
| *Martes* sp. | | | ◎ | | ◎ | |
| *Viverra zibetha* | | ◎ | | | ◎ | |
| *Erictis* sp. | | | | | | |
| *Panthera pardus* | ◎ ★ | ◎ ★ | ◎ | | ◎ ★ | |
| *Felis teilhardi* | ◎ ★ | ◎ ★ | ◎ ★ | | | |
| *Felis* sp. | ◎ | ◎ | | | ◎ | ◎ |
| *Melogale* sp. | | | | | | |
| *Cuon antiquus* | *C. dubius* | *C. dubius* | *C. dubius* | ◎ ★ | *C. dubius* | ◎ |
| *Sinomastodon yangziensis* | ◎ ★ | ◎ ★ | ◎ ★ | | ◎ | |
| *Stegodon preorientalias* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | ◎ |
| *Tapirus sinensis* | *T. sanyuanensis* | ◎ | *T. sanyuanensis* | ◎ | *T. sanyuanensis* | ◎ |
| *Rhinoceros sinensis* | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | ◎ ★ | ◎ ★ |
| *Dicoryphochoerus ultimus* | ◎ ★ | ◎ ★ | | ◎ ★ | | |
| *Sus xiaozhu* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | ◎ ★ |
| *Sus peii* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | ◎ |
| *Muntiacus lacustris* | ◎ ★ | ◎ ★ | ◎ | ◎ | ◎ | |
| *Cervavitus fenqii* | ◎ | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | |
| *Cervus* (*Rusa*) *yunnanensis* | ◎ | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | |
| *Bibos* sp. | ◎ | ◎ | | ◎ | | |
| *Megalovis guangxiensis* | ◎ ★ | ◎ ★ | ◎ ★ | ◎ ★ | | |
| Caprinae | | ◎ | | | | |
| **Micro-mammals** | | | | | | |
| *Anourosorex quadratidens* | ◎ | | | | ◎ | |
| *Blarinella* sp. | ◎ | | | | ◎ | |
| *Soriculus* sp. | ◎ | | | | ◎ | |
| *Suncus* sp. | | | | | | |
| *Crocidura* cf. *C. hosfildi* | ◎ | | | | ◎ | |
| *Mogera* cf. *M. insularis* | | | | | | |
| *Parapanulus* sp. | | | | | | |
| *Uropsilus* sp. | ◎ | | | | ◎ | |
| *Tupaia belangeri* | | | | | | |
| *Rhinolophus pani* sp. nov. | | | | | | |
| *Rhinolophus* cf. *R. affinis* | | | | | ◎ | |
| *Rhinolophus* cf. *R. rouxi* | | | | | | |
| *Rhinolophus* cf. *R. pearsoni* | ◎ ★ | | | | ◎ ★ | |
| *Rhinolophus macrotis* | | | | | | |
| *Rhinolophus* sp. | ◎ | | | | ◎ | |
| *Hipposideros amiger* | ◎ | | | | | |
| *Hipposideros pratti* | ◎ | | | | ◎ | |
| *Hipposideros larvatus* | | | | | ◎ | |
| *Hipposideros bicolor* | | | | | | |

(*To be continued on the next page*)

(*Continued*)

| *Gigantopithecus* fauna from Shanhe Cave list of species | Longgupo in Chongqing[5] | Liucheng in Guangxi[6,7] | Mohui Cave in Guangxi[8] | Black Cave in Guangxi[12] | Longgudong in Hubei[11] | Bama in Guangxi[13] |
|---|---|---|---|---|---|---|
| *Aselliscus wheeleri* | | | | | | |
| *Myotis longipes* | | | | | ◎ | |
| *Ia* sp. | | | | | | |
| *Miniopterus schreibersi* | | | | | | |
| *Tylonycteris fulvidus* | | | | | | |
| *Kerivoula hardwickei* | | | | | | |
| *Nesolagus* sp. | | | | | | |
| *Sciurotamias davidianus* | ◎ | | | | ◎ | |
| *Dremomys* sp. | ◎ | | | | | |
| *Pteromys* sp. | ◎ | | | | | |
| *Belomys parapearsoni* | ◎ | | | | ◎ ★ | |
| *Petaurista brachyodus* | | | | | | |
| *Petaurista* sp. | | | | | | |
| *Typhlomys cinereus* | ◎ ★ | | ◎ | | ◎ ★ | |
| *Typhlomys intermedius* | ◎ ★ | | | | ◎ | |
| *Rhizomys brachyrhizomyoides* | ◎ | | | | ◎ | ◎ |
| *Atherurus* sp. | | ◎ | | ◎ | | ◎ |
| *Hystrix subcristata* | ◎ ★ | ◎ ★ | ◎ | ◎ ★ | ◎ | ◎ ★ |
| *Hystrix magna* | ◎ ★ | ◎ ★ | ◎ ★ | | ◎ ★ | |
| *Eothenomys* sp. | ◎ | | | | ◎ | |
| *Mus* cf. *M. pahari* | ◎ | | | | ◎ ★ | |
| *Apodemus draco* | | | | | | |
| *Apodemus* cf. *A. peninsulae* | ◎ | | | | ◎ | |
| *Hapalomys gracilis* | ◎ ★ | | ◎ | | ◎ | |
| *Hapalomys* cf. *H. delacouri* | ◎ ★ | | ◎ | | ◎ | |
| *Chiropodomys cf. C. gliorides* | ◎ | | | | ◎ | |
| *Niviventer preconfucianus* | ◎ | | ◎ | | ◎ ★ | |
| *Niviventer fulvescens* | ◎ ★ | | ◎ | | ◎ | |
| *Leopoldamys edwardsioides* | ◎ | | ◎ | ◎ | ◎ | |
| *Rattus norvegicus* | ◎ ★ | | | | ◎ | ◎ |
| *Rattus* sp. | ◎ | | | | ◎ | |

a) ◎ The same genera; ★ the same species; □ Hominidae.

its counterparts at the Middle Pleistocene sites, such as Nongmo Hill in Bama, Bulali Hill in Wuming, Guangxi[12,13] and Tham Khuyen Cave in Lang Son Province, Vietnam[4]. The teeth of *Gigantopithecus blacki* in Bama and Wumin are apparently larger than those in Sanhe Cave. In addition, the higher proportion of extant species (such as *Ailuropoda microta*) and the disappearance of Neogene relic genera (such as *Sinomastodon* and *Dicoryphochoerus*) in the Bama and Wumin fauna suggest that the age of the Bama and Wumin faunas are younger than that of the Sanhe fauna.

In sum, from the analysis of large mammal assemblage, the Sanhe fauna shares the most species with the Liucheng and Mohui faunas, secondly with the Wushan and Tahsin faunas (Table 2), which roughly reflects the differences in age and geographic distribution. By far, Longgudong is the northernmost *Gigantopithecus* fauna in China, which is characterized by a transitional zoogeography; while Sanhe is the southernmost *Gigantopithecus* fauna in China, with Oriental characteristics. The two faunas possess few overlapping species due to ecological and geographical factors.

The Wushan fauna has the lowest proportion of extant species or their affines among all faunas (Table 3), implying its earliest age. The proportion of extant species appears to increase in succession from the Liucheng fauna, the Mohui fauna, the Longgudong fauna to the Sanhe fauna, suggesting different ages. The highest proportion is found in the Tahsin fauna, suggesting a much later age.

The above comparison among different faunas reveals that the Tahsin fauna is a transitional fauna from the late Early Pleistocene to middle Pleistocene, and the Sanhe fauna is a transitional fauna from middle Early Pleistocene to late Early Pleistocene. The larger teeth of *Gigantopithecus blacki,* together with the faunal characteristics, suggest that the age of the Sanhe fauna is either middle or late Early Pleistocene. Paleomagnetic dating of the fossil-bearing strata in Sanhe Cave, conducted by Zhu Rixiang and Deng Chenglong from the Institute of

**Table 2** The common genera, species and proportions among faunas from Sanhe Cave and other early Pleistocene *Gigantopithecus* localities in South China[a)]

| *Gigantopithecus* Fauna | Common genera | Percentage occurring in Sanhe Cave | Common species | Percentage occurring in Sanhe Cave |
|---|---|---|---|---|
| Longgupo Cave in Wushan County, Chongqing | 21 | 67.74 | 12 | 60.15 |
| Liucheng Gigantopithecus Cave in Guangxi | 23 | 74.19 | 15 | 78.94 |
| Mohui Cave in Tiandong County, Guangxi | 23 | 74.19 | 12 | 63.16 |
| Longgudong Cave in Jianshi County, Hubei | 21 | 67.74 | 10 | 52.63 |
| Tahsin Gigantopithecus Cave in Guangxi | 17 | 54.83 | 7 | 36.84 |

a) There are 31 genera and 19 species in Sanhe Cave, Chongzuo, Guangxi.

**Table 3** The proportion of extant species in the Sanhe Cave fauna and other early Pleistocene *Gigantopithecus* localities in South China

| *Gigantopithecus* Fauna | Total number of genera and species | The number of extant species in the fauna | Percentage of extant species in the fauna |
|---|---|---|---|
| Longgupo Cave in Wushan County, Chongqing | 35 | 3 | 8.6 |
| Liucheng *Gigantopithecus* Cave in Guangxi | 28 | 3 | 10.7 |
| Mohui Cave in Tiandong County, Guangxi | 15 | 2 | 11.8 |
| Longgudong Cave in Jianshi County, Hubei | 16 | 2 | 12.5 |
| Sanhe Cave in Chongzuo, Guangxi | 18 | 3 | 16.7 |
| Tahsin *Gigantopithecus* Cave in Guangxi | 14 | 4 | 28.6 |

Geology and Geophysics, CAS (details will be published in another paper), shows that the geomagnetic polarity column from the third to fifth layer (Figure 3(b)) is covered mainly by Matuyama reverse polarity. The geomagnetic polarity column below the fifth layer has normal polarity, which roughly corresponds to Cobb Mtn and slightly earlier than Jaramillo normal event. Hence, the age of the strata yielding *Gigantopithecus* in Sanhe Cave is approximately 1.2 Ma[20].

In summary, the temporal sequence of *Gigantopithecus* faunas in East Asia from early to late Quaternary is Wushan-Liucheng-Mohui-Longgudong-Sanhe-Tahsin-Bama and Wuming-Tham Khuyen.

## 4 The characters and ecological environment of the Sanhe fauna

### 4.1 The characters of the Sanhe fauna

The composition of the Sanhe fauna is distinctive. Statistics on family-level taxa in the fauna show that 56% of the total classes occur in the Oriental realm (or old continent tropic to subtropics). These include Tupaiidae, Rhinolophidae, Hipposideridae, Platacanthomyidae, Rhizomyidae, Hystricidae, Ailuridae, Viverridae, Mastodontidae, Stegodontidae, Hominidae, Hylobatidae, Cercopithecidae, and Pongidae. Statistics at the genus-level show that 56 genera, more than 87% of the total genera, belong to the Oriental realm. These include *Suncus*, *Parapanulus*, *Tupaia*, *Hipposideros*, *Ia*, *Kerivoula*, *Belomy*, *Rhizomys*, *Atheruru*, *Typhlomys*, *Eothenomys*, *Leopoldamys*, *Viverra*, *Ailuropoda*, *Arctonyx*, *Sinomastodon*, *Tapirus*, *Rhinoceros*, *Muntiacus*, *Gigantopithecus*, *Pongo*, *Hylobates*, *Rhinopithecus*, *Macaca*, and *Presbytis*. Comparisons at the species-level shows that the typical Palaearctic species are absent, except for widespread taxa. Apparently, this fauna is a typical Oriental tropical fauna (Figure 5).

The Sanhe fauna is quite different from other *Gigantopithecus* faunas in South China. As one of the northernmost sites yielding *Gigantopithecus blacki*, the Wushan fauna contains both Palaearctic (such as Cricetidae, *Mimomys* and Hyaenidae) and Oriental elements, highlighting its transitional characteristics. The Longgudong fauna also has transitional features due to its relatively northern location the and appearance of many Palaearctic taxa (such as Cricetidae, *Mimomys*, Hyaenidae and Leptobox). The close geographical proximity of the Liucheng fauna and the Sanhe fauna leads to the occurrence of similar general features in the two faunas. However, the former includes some Palaearctic taxa (such as Hyaenidae, *Felis teilhardi* and Equidae), suggesting that zoogeographic connections between south and north China still existed during the early Early Pleistocene.

Given the combination of mammals in the assemblage, the Sanhe fauna can be characterized as an Oriental tropical fauna. To date, it is the most typical tropical Quaternary mammalian fauna in South China.

### 4.2 The Paleoecology of the Sanhe fauna

Among the Sanhe fauna, tropical mammals (including Tupaia belangeri, Tylonycteris fulvidus, Ia sp., Kerivoula hardwickei, Nesolagus sp, Belomys parapearsoni, Typhlomys, Arctonyx collaris, Viverra zibetha, Muntiacus

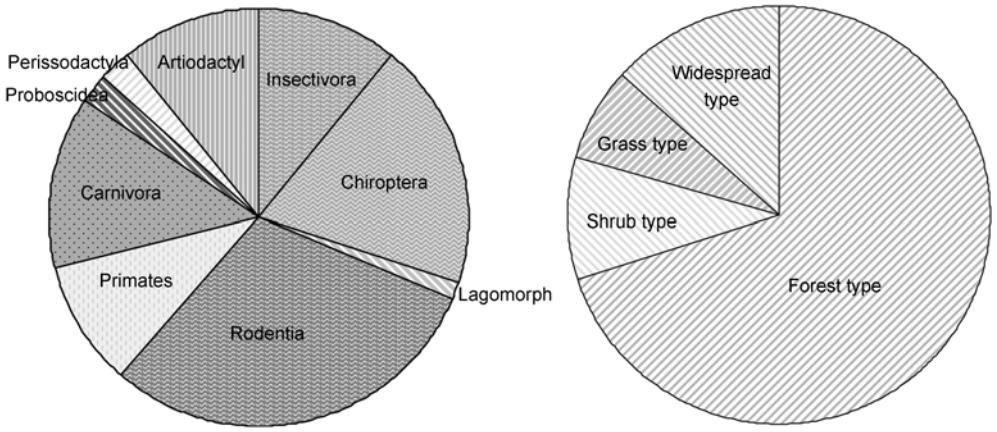


**Figure 5** Composition of the Faunal Elements and Ecological Types of the Sanhe fauna.

lacustris, Pongo sp., Hylobates sp., and Presbytis sp.) are dominant. There are no typical Palaearctic taxa in the fauna apart from a few widespread murids and carnivores. Therefore, it can be inferred to have been a hot tropical climate.

There are some Oriental forest mammals of the Hengduanshan Mountains in this fauna, such as *Anourosorex quadratidens*, *Blarinella* sp. and *Soriculus* sp. Today, they mainly live in montane seasonal rainforest around 1000 m above sea level. However, Sanhe Cave is only 203 m above sea level and the highest peak in the Chongzuo area is just about 600 m, indicating that topographic relief was more pronounced in the past. Besides hills and valleys, high mountains and gorges also existed, with greater elevational variation.

The arboreal Chiropteran fossils, such as *Tylonycteris fulvidus*, *Kerivoula hardwickei* are common in the fauna. There is also a high diversity of arboreal rodent species, including *Pteromys* sp., *Chiropodomys* cf. *C. gliorides*, and semi-arboreal rodents, *Niviventer preconfucianus* and *Leopoldamys edwardsioides*. In addition, there are also many mammals preferring forests, such as *Tupaia belangeri*, *Nesolagus* sp., *Viverra zibetha*, *Muntiacus lacustris* and various suids. The primate taxa, *Pongo* sp., *Hylobates* sp., *Rhinopithecus* sp., *Macaca* sp. and *Presbytis* sp., are typically arboreal. Consequently, the paleoecological setting at Sanhe can be reconstructed as tropical forest and shrub.

## 5 Conclusions

There has been considerable progress in research on the *Gigantopithecus* fauna, owing to recent discoveries of some important *Gigantopithecus* sites from different periods in South China. It has been demonstrated that differences exist between *Gigantopithecus* faunas in China and neighboring countries that relate to faunal characteristics, ecology and age. Based on the fauna and chronology obtained using various methods, such as paleomagnetism, ESR and Amino Acid dating, the *Gigantopithecus blacki* fauna in southeast Asia can be divided into three temporal stages.

The early stage (between the Gauss-Matuyama boundary and the Olduvai normal subchron, 2.58－1.8 Ma[20]) is represented by the Wushan, Liucheng and Mohui faunas. This stage is characterized by *G. blacki* of relatively small body size, and an associated fauna with Neogene relic species, such as *Sinomastodon*, *Hesperotherium*, and *Dicoryphochoerus*, and primitive species that first appeared in the Pleistocene, such as *Ailuropoda microta*, *Cuon dubius*, *Stegodon preorientalis,* and *Tapirus sanyuanensis*.

The middle stage (between Olduvai and Jaramillo subchrons, 1.77－1.07 Ma[20]) is represented by the Longgudong and Sanhe faunas. This stage is characterized by the increased body size of *G. blacki, Ailuropoda and Tapirus* (compared to the previous stage), the disappearance of primitive species, such as *Ailuropoda microta*, *Cuon dubius*, and *Tapirus sanyuanensis,* and the first appearance of *Ailuropoda wulingshanensis*, *Cuon antiquus*, and *Tapirus sinensis*. The faunas of this stage possess transitional feature.

The late stage (between the start of the Jaramillo and the middle of the Brunhes normal chron, 1.07－0.42 Ma) is represented by the Tahsin, Bama, Wuming and Tham Khuyen faunas. The latest *G. blacki* had a smaller body size compared to those in the preceding stages[4]. In

these faunas, more advanced species, such as *A. baconi*, and *Megatapirus augustus,* replace the Neogene relic species, and there is a higher proportion of extant species (30% for large mammals and more than 45% for small mammals).

Based on the *Gigantopithecus* fossils discovered in Indo-Pakistan and in the various sites in China and Vietnam, the *Gigantopithecus* teeth show an evolutionary tendency to first increase in size then decrease in size through the Miocene to early and middle Pleistocene. It is worth considering whether the observed changes in tooth size reflect changes in the paleoenvironment and food resources during the Pleistocene.

*We would like to thank PKU Chongzuo Biodiversity Research Institute for the valuable support in field excavations. We are grateful to Prof. Qiu Zhanxiang and Zheng Jiajian for revising a draft version of this manuscript and for providing valuable suggestions. We also thank Prof. Terry Harrison from New York University for revising the English version.*

1 Koenigswald G H R von. *Gigantopithecus blacki* von Koenigaswald, a giant fossil hominoid from the Pleistocene of southern China. Anthropological Paper, Amer Mus Nat Hist, 1952, 43(4): 295－325
2 Chow M C. Characteristic and correlation of the Tertiary and early Quaternary mammalian faunas from southern China (in Chinese). Chin Sci Bull, 1957, 13: 394－399
3 Hartwig W C. The Primate Fossil Record. Cambridge: Cambridge University Press, 2002. 1－530
4 Ciochon R, Long V T, Larick R, et al. Dated co-occurrence of *Homo erectus* and *Gigantopithecus* from Tham Khuyen cave, Vietnam. Proc Natl Acad Sci USA, 1996, 93: 3016－3120
5 Huang W P, Fang Q R, et al. Wushan Hominid Site (in Chinese). Beijing: Science Press, 1991. 1－205
6 Pei W Z. Carnivora, Proboscidea and Rodentia from Liucheng *Gigantopithecus* cave and other caves in Guangxi (in Chinese). Memoirs of Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, No.18. Beijing: Science Press, 1987. 1－134
7 Han D F. Artiodactyla fossils from Liucheng *Gigantopithecus* cave in Guangxi (in Chinese). Memoirs of Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, No.18. Beijing: Science Press, 1987. 135－208
8 Wang W, Potts R, Hou Y M, et al. Early Pleisotcene hominid teeth recovered in Mohui cave in Bubing Basin, Guangxi, South China. Chin Sci Bull, 2005, 50(17): 2777－2782
9 Wang W, Potts R, Yuan B Y, et al. Sequence of mammalian fossils, including hominoid teeth, from the Bubing Basin caves, South China. J Hum Evol, 2007, 52: 370－379
10 Jin C Z, Ciochon R L, Dong W, et al. The first skull of the earliest giant panda. Proc Natl Acad Sci USA, 2007, 104: 10932－10937
11 Zheng S H. Jianshi Hominid Site (in Chinese). Beijing: Science Press, 2004. 1－412
12 Han D F. Mammalian fossils from Tahsin County, Guangxi (in Chinese). Vertebrata PalAsiatica, 1982, 20(1): 58－63
13 Zhang Y Y, Wang L H, Dong X R, et al. Discovery of a *Gigantopithecus* tooth from Bama District in Guangxi (in Chinese). Vertebrata PalAsiatica, 1975, 13(3): 148－153
14 Zhang Y Y, Wu M L, Liu J R, et al. Newly recovered *Gigantopithecus* fossils from Wuming, Guangxi (in Chinese). Chin Sci Bull, 1973, 18(3): 130－133
15 Zhao L X, Tong H W, Xu C H, et al. New Discovery of *Gigantopithecus blacki* tooth fossil from Bijie, Guizhou and its Significance. Quat Sci, 2006, 26(4): 548－554
16 Wang W, Tian F, Mo J Y. Recovery of *Gigantopithecus blacki* fossils from the Mohui cave in the Bubing Basin, Guangxi, South China (in Chinese). Acta Anthropol Sin, 2007, 26(4): 330－343
17 Zhang Y Y. Variability in tooth size of *Gigantopithecus blacki* and the dietary hypothesis for Australopithecines. Acta Anthropol Sin, 1983, 2(3): 205－217
18 Ji H X. The subdivision of the *Gigantopithecus* faunas from south China (in Chinese). J Stratigr, 1990, 14(1): 57－62
19 Shi L F. Comments on "the Gaoping Formation——a new Stratigraphic unit with the *Gigantopithecus* fossils from West Hubei" (in Chinese). J Stratigr, 2006, 30(2): 183—186
20 Cande S C, Kent D V. Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. J Geophys Res, 1995, 100(B4): 6093－6096