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Paleoenvironmental and chronological analysis of the mammalian fauna from Migong Cave in the Three Gorges Area, China

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A B S T R A C T

Migong Cave is an important Late Pleistocene fossil locality in the Three Gorges Area, and many mammalian fossils were excavated from this cave. The faunal characteristics of the small mammals from the Migong Cave are closest to the Oriental and the South China Region faunas, but also with some elements of the Himalaya-Hengduan Mountains Region and the Monsoon Region faunas. Most of the large mammals are typical members of the "*Ailuropoda-Stegodon*" fauna, but lack some common Late Pleistocene taxa of South China, such as *Elaphas maximus*, *Rhinoceros sinensis*, *Cervus unicolor* and *Muntiacus*. On the other hand, there are several large mammals of the Palaearctic Realm Pattern and the Monsoon Region Pattern in this locality. Through analyzing the features of the mammalian fauna and regional geomorphology, it is concluded that during the period of the Migong Cave fauna, seasonal temperature difference was obvious; the valleys were wider than the present; forests were relatively sparse, and the impact of the East Asian monsson was relatively strong. Combined with the isotope dating result, it is presumed that the age of Migong Cave is correlated to MIS 2. The unusual composition of the Migong Cave fauna challenges the past principle that the alternations of glacial period and interglacial period have no or very little influence on the mammalian fauna of Southwest China.

1. Background

The Three Gorges Area of Yangtze River is a hub located at the middle part of the second landform of China, which is an important channel for north-south migration of mammals in the Quaternary. A great many Quaternary fossil localities have been found in this area, including several important paleoanthropological sites, such as the Longgupo Site (Huang and Fang, 1991), the Jianshi Man Site (Zheng, 2004), the Yunxian Man Site (Echassoux et al., 2008) and the Fengjie Man Site (Huang et al., 2002). These fossil localities provide a large number of powerful evidences for researches on mammalian evolution and paleoenvironment. In this article, a Late Pleistocene fossil locality in the Three Gorges Area, Migong Cave, is studied. From Migong Cave, a fossil mammalian fauna with numerous specimens and unique composition has been unearthed (Hang et al., 2000). This article attempts to analyze the paleoenvironment and the age for this fossil mammalian fauna.

Migong Cave, located at Maping Village, Baolong Town, Wushan County, Chongqing Municipality (Fig. 1), is to the east of the Qinghai-Tibetan Plateau, north of the Wushan Mountains and northeast of the Sichuan Basin, belonging to the middle subtropical warm moist monsoon climate zone. Biogeographically, this locality is situated in the eastern Sichuan Basin Province, Western Mountain Subregion, Central China Region, Sino-Indian Subrealm, Oriental Realm, next to the Qinba-Wudang Province. Geomorphically, the area around this locality is complex and diverse, with altitudes generally under 1000 m, rarely more than 2000 m. Migong Cave has developed in the Triassic Jialingjiang Limestone of the Wushan Mountain, formed by a pocketed karst cave and four layers of irregular tubular tunnels (Fig. 2). The altitude of the tunnel entrance of the first layer is 165 m, and the fourth layer is 258 m. After being discovered, this locality received a systematic excavation in 1999. At that time, five locations within the cave were chosen to be excavated, among which the fifth location produced no fossils, but the first to the fourth locations produced a large number of fossils. The layers of the four fossil locations were

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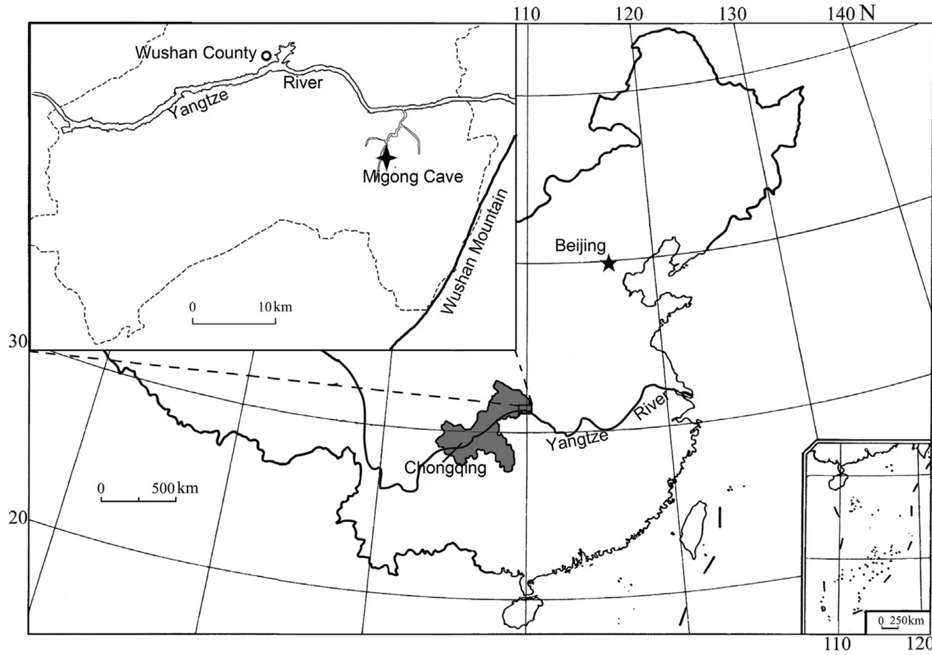

Fig. 1. Location map of Migong Cave.

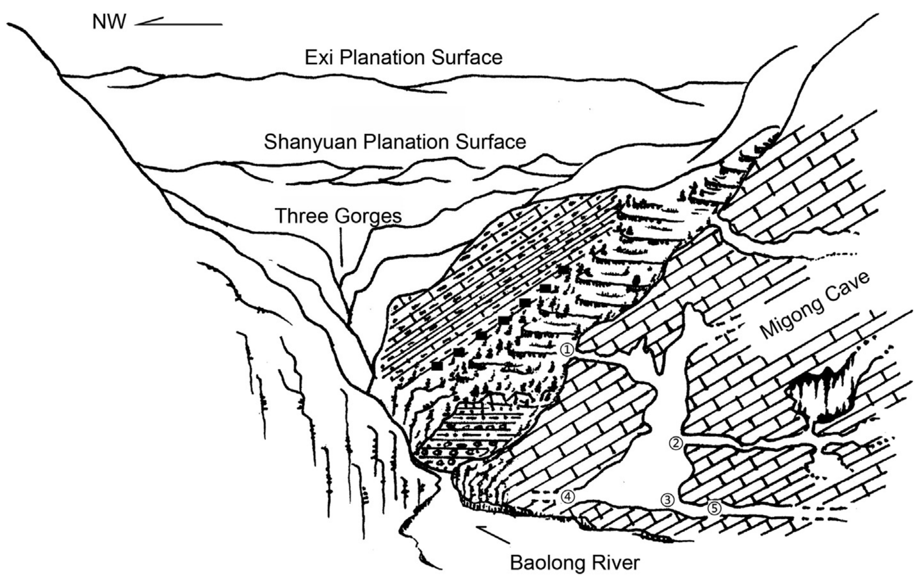

Fig. 2. Regional geomorphologic landscape and the shape of Migong Cave. 1–5, the five excavated locations in Migong Cave.

similar: the upper layer was calcareous plate or disturbed layer; the middle layer was brown or light brown sandy clay, rich in fossils; the lower layer was gravel or directly exposed bedrock (Hang et al., 2000). Therefore, the fossil layers of the four locations could be of the same or similar age. Hang et al. (2000) have made a preliminary report on the fauna of this locality. The fossils excavated include fish, reptiles, insectivores, chiropterans, rodents, lagomorphs, primates, carnivores, proboscideans, perissodactyls, and artiodactyls.

2. Materials and methods

The distribution of mammals is closely linked with the natural environment (Zhang, 2002). Previous research has shown that mammalian distribution and evolution of the Late Pleistocene experienced strong environmental stresses (Graham et al., 1996). Most species of the Late Pleistocene faunas have survived to the present and the ecological studies of these extant animals can provide good references for paleoenvironmental analyses of Late Pleistocene communities. Therefore, mammalian fauna is an important basis for speculating the paleoenvironment of the Late Pleistocene. In addition, Liu et al. (2000) created a stratigraphical table of Quaternary deposits in China based mainly on the correlation with the marine isotope stages (MIS). Therefore, the age of the Late Pleistocene mammalian fauna can be further determined through the paleoenvironment reflected by the fauna itself.

The materials studied in this article all belong to the mammal fossils collected and washed from the middle layer of the second to the fifth locations in excavation. The lithology of the middle layer is sandy clay, with thickness from 0.5 to 1.8 m. There is no significant lithological change from bottom to top, which indicates that the sediment was formed by steady continuous accumulation in a relatively short time and the climate should have no steep fluctuation during this period. These mammalian fossils include: *Erinaceus* sp., *Scaptonyx fusicaudatus*, *Crocidura suaveolens*, *Crocidura attenuata*, *Soriculus parva*, *Soriculus hypsibius*, *Blarinella quadraticauda*, *Sorex* sp. and *Anourosorex squamipes* of Insectivora; *Rhinolophus rouxi*, *Rhinolophus pearsoni*, *Hipposideros armiger*, *Myotis* sp. and *Murina leucogaster* of Chiroptera; *Pipistrellus* sp., *Callosciurus erythraeus*, *Eothenomys* sp., *Atherurus macrourus*, *Mus* cf. *musculus*, *Mus* sp., *Micromys* sp., *Apodemus* sp.1, *Apodemus* sp.2, *Apodemus* sp.3, *Vernaya foramena*, *Leopoldamys edwardsi*, *Niviventer fulvescens*, *Niviventer confucianus* and *Niviventer andersoni* of Rodenta; *Ochotona thibetana* of Lagomorpha; *Macaca* sp. of Primates; *Nyctereutes* sp., *Ailuropoda melanoleuca baconi*, *Ursus* sp., *Meles* sp., *Mustela putorius*, *Viverra* cf. *zibetha* and *Crocuta crocuta ultima* of Canivora; *Stegodon orientalis* of Proboscidea; *Megatapirus augustus* and *Stephanorhinus kirchbergensis* of Perissodactyla; *Sus scrofa*, *Elaphurus davidianus*, *Cervus elaphus xanthopygus*, *Capricornis sumatraensis*, *Spirocerus* sp. and *Bubalus* sp. of Artiodactyla.

Small mammals are sensitive to the environmental change, having rapid evolutionary rates and spreading relatively slowly. On the other hand, different species of the same genus may have different ecological habits. Therefore, when studying the small mammal fossils, this article selects taxa that could be identified to the species level for statistical analysis. The selected small mammal fossils are all extant species, respectively belonging to Insectivora, Chiroptera, Rodenta and Logomorpha. Their distribution patterns, regional distributions, and correlated abbreviations follow Zhang et al. (1997) and Zhang (2011). The large mammal fossils belong to Primates, Carnivora, Proboscidea, Perissodactyla and Artiodactyla, respectively. As the real geographic ranges of the large mammals are much larger than the ranges of their distribution patterns and the record of the large mammals is more easily confined by the sedimentary environment of the cave, only qualitative analyses are made.

The lowest taxonomic unit that could be identified is used when determining whether the taxon is extinct. For example, *Ailuropoda melanoleuca* is an extant species, but the specimens of this species from Migong Cave could be identified to subspecies level, *A. m. baconi*, an extinct subspecies, so it is considered as an extinct taxon.

In addition, there is the concept of regionally extinct taxon, which means a taxon is not extinct but disappears in a certain area. In this article, we presume that the living area of the Migong Cave fauna is south of the Yangtze River and north of the Wushan-Qiyueshan Mountains, involving Wushan County, Fengjie County, Yunyang County, and Wanzhou District. If a taxon is not recorded in this area but still survives in other areas, it is a regionally extinct taxon in this research.

3. Paleoenvironmental analysis

3.1. Small mammal fauna

Among the small mammal fossils from the Migong Cave, there are 240 pieces which could be identified to species. They respectively belong to 19 species, including 7 species of insectivores, 4 species of chiropterans, 7 species of rodents, and 1 species of lagomorph, which are all extant (Supplement Table 1). There are 5 distribution patterns of these species: 1) the Himalaya-Hengduan Mountains Region Pattern (H), here only containing the subpattern of Hengduan Mountains in Chief (Hc); 2) the South China Region Pattern (S), here only containing the subpattern of Tropics to Northern Subtropics (Sd); 3) the Monsoon Region Pattern (mainly of the eastern humid regions) (E), here only containing the subpattern of Amur or Extending to Russian Far East (Eb); 4) the Oriental Pattern (W), here containing the subpatterns of Tropics to Northern Subtropics (Wb), Tropics to Middle Subtropics (Wc), Tropics to Southern Subtropics (Wd) and Tropics to Temperate Zone (We); 5) other distribution patterns difficult to categorize (O). Fig. 3 shows all these species except the O Pattern *Crocidura suaveolens*.

Among all the specimens of small mammals, fossils of *N. fulvescens* are the most numerous, representing 15.83% of all specimens, and are *C. attenuata* (14.17%), *R. rouxi* (12.92%), *N. confucianus* (12.50%) and *R. pearsoni* (8.75%). These five species account for 64.17% of the total specimens that could be identified. They all belong to the S and W distribution patterns, widespread in South China. If counted by distribution pattern, it is also the specimens of these two patterns that dominate, and other patterns have very small proportions (Fig. 4A). The large proportions of the S and W patterns among fossil specimens reflects a typical character of the Oriental Realm fauna.

There are 6 species of the Hc Subpattern and 1 species of the Eb Subpattern in the small mammal fossils of the Migong Cave. They are *S. fusicaudatus*, *Soriculus parva*, *S. hypsibius*, *B. quadraticauda*, *V. foramena* and *O. thibetana* of the Hc Subpattern and *M. leucogaster* of the Eb Subpattern. Alhough their number is not dominant, with only 11.67% of the total specimens that could be identified (Fig. 4A), if counted by species richness, the Hc Subpattern is second only to the W Pattern and exceeds all the subpatterns of the W Pattern (Fig. 4B). It can be concluded that the species of the Hc Subpattern is the richest among the small mammal species from the Migong Cave. Therefore, it can be presumed that the small mammal fauna of the Migong Cave is closely connected with the modern fauna of the Hengduan Mountains.

The 7 species of the Hc Subpattern and Eb Subpattern are all the regionally extinct species in the small mammal fauna of Migong Cave, and thus they are most significant for indicating the paleoenvironment. *S. fusicaudatus* is an ancient species and lives in brush habitats with an altitude of 1200–1300 m, now mainly distributed in the area of the Hengduan Mountains and the Qinling Mountains, and having a small distribution in Nanchuan District and Chengkou County of Chongqing (Wang and Zhang, 1997; Zheng and Song, 2010). *Soriculus parva* is distributed mainly at an altitude of 2000–3500 m in the Hengduan Mountains now and also has a small distribution in shrub-grass area of forest margins at an altitude of 900–1500 m in the Qinling Mountains (Zhang et al., 1997; Zheng and Song, 2010; Sun et al., 2013). *S. hypsibius* is distributed mainly in northwestern Sichuan to the Qinling Mountain at an altitude of 1200–2100 m, as well as in a very small range with an altitude of about 300 m in Beijing. Recently, a few specimens of this species have also been found in Ningwu County, Shanxi Province, at an altitude of about 2000 m (Liu et al., 2011). *B. quadraticauda* now lives mainly in the Hengduan Mountains and the Qinling Mountains, slightly in Nanchuan District of Chongqing and in the north of Guizhou Province, at an altitude of about 1200–3000 m (Zhang et al., 1997; Zhang, 2011; Sun et al., 2013). *V. foramena* is a very rare rodent, firstly discovered in Pingwu, Sichuan Province by Wang et al. (1980), and later also found in the Wanglang National Nature Reserve of Sichuan Province (Zhang et al., 1991) and in the Qinling Mountains of Gansu Province and Shaanxi Province (Li and Wang, 1995). It lives at an altitude of about 2000–2500 m. *O. thibetana* now lives on the Qinghai-Tibetan Plateau, the Qinling Moutains and the Shennongjia area, at an altitude of 1800–4200 m (Feng and Zheng, 1985; Li, 2007). *M. leucogaster* is a widespread species, living in caves of cool temperature. All of these species nowadays live at higher altitude or in further north latitude, representing lower temperatures than the modern Migong Cave area.

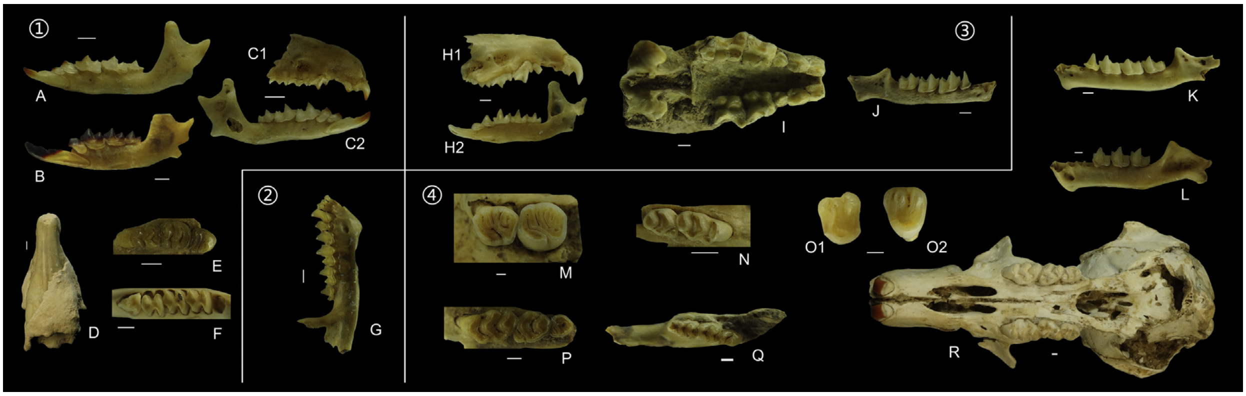

Fig. 3. Partial small mammalian fossils from Migong Cave. 1, Hc Subpattern, A, *Soriculus parva*; B, *Blarinella quadraticauda*; C, *Soriculus hypsibia*; D, *Scaptonyx fusicaudatus*; E, *Vernaya foramena*; F, *Ochotona thibetana*. 2, Eb Subpattern, G, *Murina leucogaster*. 3, Sd Subpattern, H, *Crocidura attenuata*; I, *Anourosorex squamipes*; J, *Rhinolophus rouxi*. 4, W Pattern, K, *Rhinolophus pearsoni*; L, *Hipposideros armiger*; M, *Atherurus macrourus*; N, *Niviventer fulvescens*; O, *Callosiurus erythraeus*; P, *Niviventer andersoni*; Q, *Niviventer confucianus*; R, *Leopoldamys edwardsi*. Scale bar: 2 mm.

The fossil small mammal fauna in Migong Cave has more insectivores than other Late Pleistocene faunas in the Three Gorges Area, but the rodents are relatively fewer in number of taxa, and lack representatives of the arboreal Petaurisidae and the bamboo feeding Rhizomyidae, which are common in other modern and Late Pleistocene mammalian faunas. This observation suggests that forests were relatively sparse and brushwoods were relatively prosperous in this area at the time when the Migong Cave fauna lived.

3.2. Large mammal fauna

There are 17 species of large fossil mammals in Migong Cave, and most of them are the typical members of the "*Ailuropoda-Stegodon*" fauna, such as *Ailuropoda melanoleuca baconi*, *Viverra* cf. *zibetha*, *Crocuta crocuta ultima*, *Stegodon orientalis*, *M. augustus* and *Capricornis* cf. *sumatraensis*, reflecting a relatively strong feature of South China Pleistocene faunas. However, there are some special species in this fauna, which reflect a different climatic environment from other periods of the Mid-Late Pleistocene in South China. Several aspects of environmental characteristics reflected by this large mammal fauna are discussed below.

(1) Giant panda lives only in the area of middle to high altitude in the Hengduan Mountains and the Qinling Mountains today. It is found in colder climates. However, in Pleistocene, this species, especially *Ailuropoda melanoleuca baconi*, was found throughout South China,and the northernmost distribution may have reached Zhoukoudian of Beijing (Pei, 1934). *S. orientalis* and *M. augustus* in the Migong Cave fauna are extinct species, and they are usually found with *A. m. baconi*, indicating that their ecological requirements were similar. The combination of these three species not only occurred widely in South China, but also has been found in the Gongwangling Hominoid Site of Lantian, north of the Qinling Mountains (Hu and Qi, 1978). This combination in the Migong Cave fauna indicates that the climate was not extremely dry or cold at that time.

(2) The Migong Cave fauna includes several Palaearctic species (Fig. 5A–E), which are *S. kirchbergensis*, *Spirocerus* sp., *Cervus* (*Elaphus*) *xanthopygus* and *M. putorius*.

S. kirchbergensis is an extinct species, and its fossil records are found in temperate regions of Eurasia. In recent years, it has been also found in Hulu Cave of Nanjing, Jiangsu Province (Huang, 1996; Tong, 2002) and Xiniu Cave of Shennongjia, Hubei Province (Tong and Wu, 2010). Migong Cave is the southernmost fossil record of this species (Chen et al., 2012). The nasal bones of *S. kirchbergensis* have a partially ossified nasal septum, indicating that its cold tolerance is inferior to *Coelodonta* (Deng et al., 2011), but much superior to other rhinos, such as *Rhinoceros* and *Dicerorhinus*. Therefore, *S. kirchbergensis* is usually considered as a typical representative of temperate environments. The limbs of *S. kirchbergensis* are slender, and the articular surfaces are broad, indicating its agility and adaptation to forest margins.

Spirocerus is an extinct genus. Except for the Longgupo Site (Huang and Fang, 1991) and the Migong Cave Locality, its fossils have been only discovered in the area from North China to the Baikal Area in Russia (Sokolov, 1959). Sokolov (1959) has described the limbs of *Spirocerus kiaktensis*: humerus short, metacarpus short and wide, and phalanx long and slim. It has characters of antelope, buffalo, and musk ox, indicating that it inhabited semi-open mountain or open forest-meadow habitats, with relatively poor mobility, and fed on grass.

Cervus (Elaphus) xanthopygus now only lives in Hebei Province, Northeast China and in areas further north. Other species of the same subgenus now mainly live in Northwest China and the Hengduan Mountains (Zhang et al., 1997). *C.* (*E.*) *xanthopygus* inhabits mountain forest and forest-meadow environments, and feeds on leaves and grasses.

Except for Migong Cave, the fossil record of *M. putorius* has only been found in Zhoukoudian of Beijing (Pei, 1934) and some fossil localities in Northeast China (Heritage Management Committee of Heilongjiang Province (1987); Museum of Liaoning Province and Museum of Benxi Museum of Liaoning ProvinceMuseum of Benxi City (1986)). It lives in North China, Northeast China, the Hengduan Mountains and the Qinghai-Tibetan Plateau. It is a typical small carnivore adapted to cool climate, and is found in open mountain, grassland, and shrubs (Zhang et al., 1997).

These palearctic species from the Migong Cave indicate that certain North China species migrated to the central part of the Three Gorges Area, reflecting a dry and cold climate in the Three Gorges Area when the accumulation in the Migong Cave was formed.

(3) *E. davidianus*, a Monsoon Region Pattern species, is found in the Migong Cave fauna (Fig. 5F–G). The wild population of *E. davidianus* is extinct. Its original range included the lower reaches of the Yellow River and the Yangtze River, and it was once widespread in East Asia as a typical monsoon region

species. Ji (1985) has analyzed its geographical distribution and thought that its distribution was closely related to climate. This species lived in warm humid swamps and fed on tender grasses or leaves. Its appearance in Migong Cave indicates that the East Asian monsoon had a great influence on the Three Gorges Area at that time.

(4) Some common species of the Late Pleistocene in South China are absent in Migong Cave, such as *Elaphas maximus*, *Rhinoceros sinensis*, *Cervus unicolor*, and *Muntiacus*. They live in warm humid environments, especially *C. unicolor* and *Muntiacus* which mainly feed on fresh leaves and branches and are relatively abundant and likely hunted by ancient humans. Their absence in Migong Cave indicates that forests were relatively sparse and climate was relatively dry at that time.

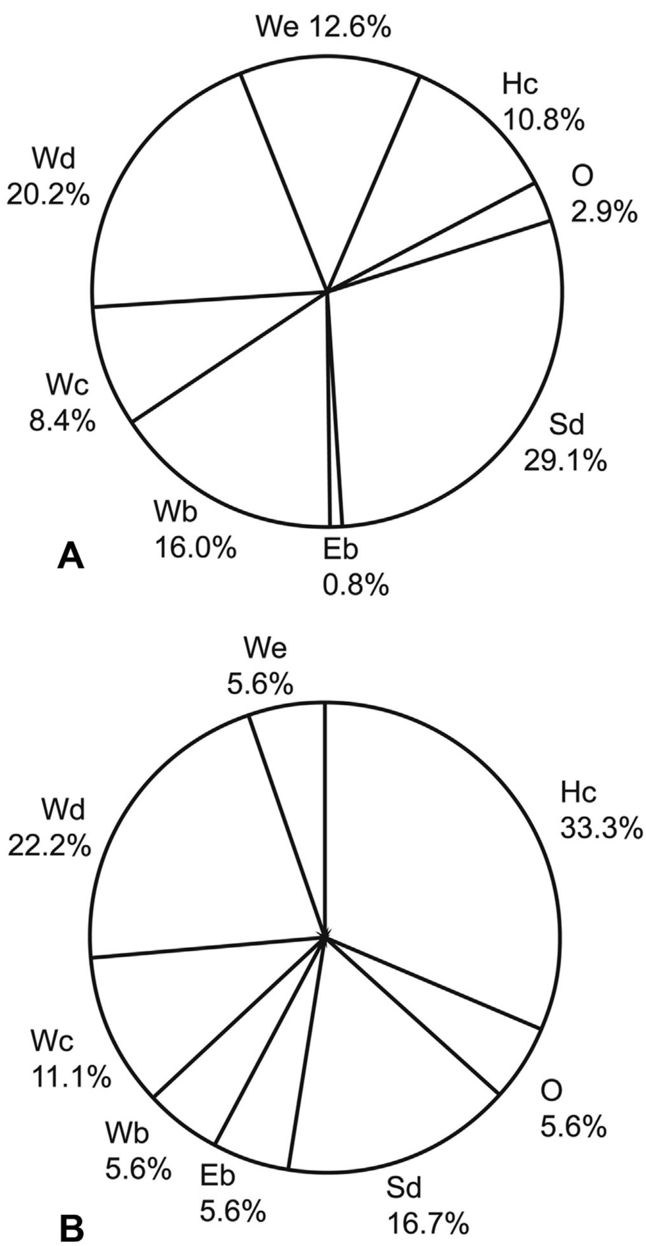

Fig. 4. Distribution patterns of the small mammals from the Migong cave. A, proportions counted by number of specimens; B, proportions counted by species richness.

3.3. Paleoenvironment

The unusual composition of the Migong Cave fauna is not a result of migration of the regionally extinct species or other occasional incidents. Most of these regionally extinct species have very similar geographical distributions now, but their abilities to disperse are not similar. It is the environmental change that produces similar stress on these species and causes the change of their distribution. The remarkable environmental change since the Late Pleistocene is the most important factor leading to this geographical distribution.

Among the Migong Cave fauna, the species of the W Pattern and the S Pattern occupy a large proportion. Combined with multiple small mammals of the Hc Subpattern in this fauna, it is indicated that at that time, there was a variety of ecological space in this area that could meet the survival needs of animals living in different temperatures. However, vertical change of temperature in this area is not significant, so it is more likely due to seasonal temperature changes. Based on the species of the W Pattern and the S Pattern, it is speculated that temperature in summer at that time was similar to or slightly lower than in other periods of the Late Pleistocene. Temperature in winter should be lower than now, because the small mammals of the Hc Subpattern at the similar latitude with the Migong Cave Locality live usually at an altitude above 2000 m, but the elevation around Migong Cave is mainly lower than 1000 m. According to calculations of temperature decrease of 6 °C with each 1000 m increase in altitude, it is calculated that temperature in winter might be at least 6 °C lower than nowadays in the Migong Cave area. The palearctic species among the large mammals, such as *S. kirchbergensis* and *Cervus* (*Elaphus*) *xanthopygus*, also support the existence of a cool environment. Meanwhile, two species of the Monsoon Region Pattern in the fauna, especially *E. davidianus*, a typical representative of the East Asian monsoon region species, indicate that at that time the impact of the East Asian monsoon in the Migong Cave area was stronger than in any other period of the Late Pleistocene. In addition, *Spirocerus* sp. reflects a more open mountain forest environment than nowadays.

The environment in which the Migong Cave fauna lived could be generally described as follows: seasonal change of temperature was obvious and temperature in winter was lower than nowadays, which was probably similar with modern southern North China; humidity was lower than now, but higher than modern North China; mountain valleys were wider than now, and forests were relatively sparse, with developed scrubs and grasslands; the East Asian monsoon was relatively strong, which could bring much summer precipitation.

4. Chronological analysis

Ailuropoda melanoleuca baconi, *Crocuta crocuta ultima*, *S. orientalis* and *M. augustus* from Migong Cave indicate that the age of this fauna should be correlated to the Late Pleistocene, possibly the earliest Holocene. The ^{14}C dating result of the specimen unearthed from the top of the middle layer gives an age of latest Pleistocene (13150 ± 190 BP), but only based on one sample (Hang et al., 2000). Another U-series date shows that the age of the calcareous plate under the fossil layer is about 30 ka (unpublished data). Although this result remains to be improved, there should be no problem in considering the age of this fauna as late Late Pleistocene. In this fauna, *S. kirchbergensis*, *Spirocerus* sp., *Cervus* (*Elaphus*) *xanthopygus* and *M. putorius* are very typical palearctic species. Their migration south in this period reflects a cooling climate. The paleoenvironment of Migong Cave was obviously cooler than most periods of the Late Pleistocene and today. In MIS 2, the global climate was unprecedentedly dry and cold in general. Xu (1986, 1992) determined

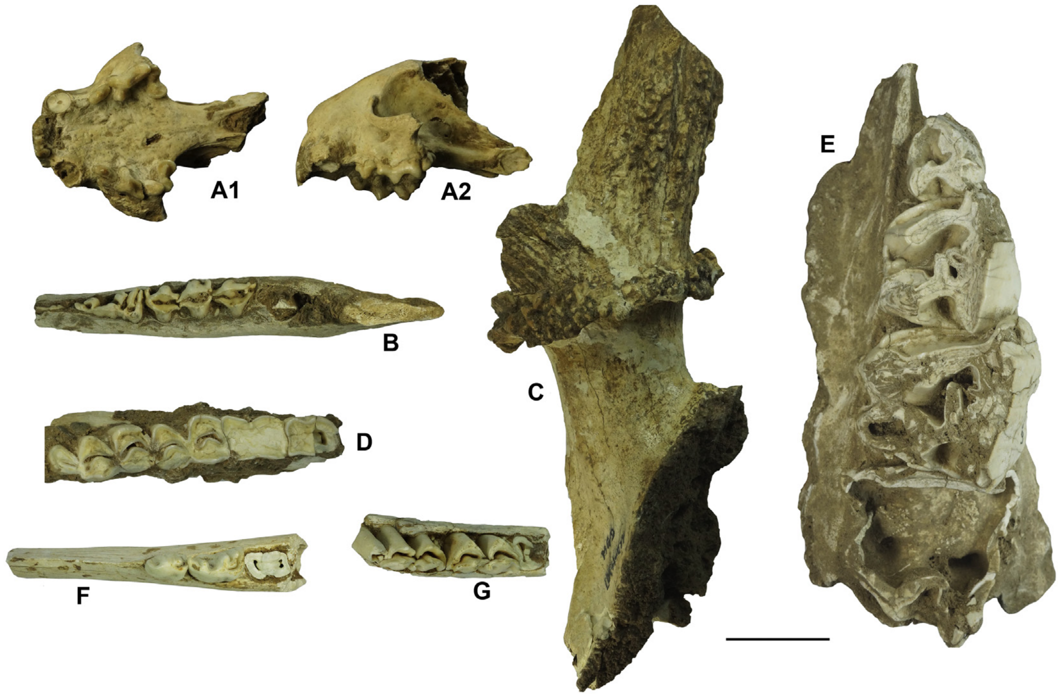

Fig. 5. Palaearctic and Monsoon Region Pattern large mammalian fossils from the Migong Cave. A, *Mustela putorius*; B and C, *Cervus* (*Elaphus*) *xanthopygus*; D, *Spirocerus* sp.; E, *Stephanorhinus kirchbergensis*; F and G, *Elaphurus davidianus*. Scale bar: for A 2 cm, others 4 cm.

that during this period, there was southward migration of animals in East China. Combined with the isotope dating result, it is reasonable to correlate the age of the Migong Cave fauna to MIS 2.

5. Conclusion

In the Quaternary, the alternation of glacial and interglacial periods greatly influenced the climate of China and the rest of the world, but most paleontologists believed that the alternation had no or very little influence on the mammalian fauna of South China. However, with so many species adapted to dry and cool climate found in Migong Cave of this period in the Three Gorges Area, there is evidence that the Quaternary global climate change did influence the mammalian distribution in South China. In the Three Gorges Area, there is another contemporaneous fossil locality, Zhangnao Cave of Fang County, Hubei Province (Huang et al., 1987). Fossil species excavated from this locality are relatively few, but the presence of *S. kirchbergensis* could also reflect a cool environment. In addition, during the Last Glacial Maximum, the “Wushan Loess”, over 10 m thick, developed on the terrace in the middle reach of the Yangtze River, which was an aeolian deposit as indicated by multiple indices (Li et al., 2010; Zhang et al., 2010, 2013). This also illustrates the dry and cool climate of the Three Gorges Area during MIS 2.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.11.039.

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