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Occurrences of warm-adapted mammals in north China over the Quaternary Period and their paleo-environmental significance

TONG HaoWen

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
(email: tonghaowen@ivpp.ac.cn)

The north and south China faunas are subdivided along the line of Huaihe River-Qinling Mountains-Hengduan Mountains-Himalayas, to the north is the Palearctic Region, and to the south is the Oriental Region, which is the result of long-time evolution. Hundreds of Quaternary fossil localities have been known up to now, more than 60 of which contain warm-adapted elements which can be referred to 20 species. Among the warm-adapted elements appearing in north China, *Hystrix*, *Macaca*, *Palaeoloxodon*, *Dicerorhinus* and *Bubalus* are the most frequently recorded genera. There are three kinds of causal explanation about the frequent appearance of warm-adapted elements in north China: The first hypothesis attributed them to the dispersal events of warm-adapted mammals from the south during warm stages or warm seasons; the second scenario thinks that these warm-adapted mammals in north China were once derived there *in situ* and subsequently emigrated to the south with the cooling down of the global climate; the last hypothesis believes that these warm-adapted elements were not real warm-climate animals at that time. This study shows that almost none of the warm-adapted mammals in north China was recovered in the loess, and also almost all of the fossil localities which bear warm-adapted mammals fall within the warm temperate zone of nowadays. In fossil assemblage, those warm-adapted elements rarely co-exist with the cold-adapted mammals. All these evidences mentioned above indicate that the warm-adapted mammals in north China represent warm climate, but not hot one. Because all these warm-adapted mammals are widely distributed oriental elements, some of them even still exist north of the Huaihe River today. Up to now, no typical oriental elements have ever been recovered in north China, such as pangolin, primitive primates (e.g. loris and tarsier), big apes (e.g. *Gigantopithecus*, *Pongo* and *Hylobates*), etc. The Late Pleistocene lasted a relatively shorter time, but the appearance of warm-adapted mammals during that span were the most frequent and most widespread. It means that the climate of the Late Pleistocene experienced the most frequent fluctuation over the whole period of Quaternary.

mammals, oriental elements, north China, Quaternary, paleoenvironment

1 Introduction

The boundary between the Palearctic Region and the Oriental Region of zoogeography passes across east China. In the modern zoogeography patterns, north China belongs to the Paleartic Region, South China falls within the Oriental Region. Although the communications between north and south China are inevitable, both of them are distinct enough in fauna compositions. But in the Pleistocene, the situation was a little different from that of today. In the Pleistocene epoch, quite a

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number of warm-adapted mammals once inhabited north China, which is well known in the paleontological world. But no body knows exactly how many species of warm-adapted mammals and how many records in north China have been recognized. The spatiotemporal distributions of these mammals in north China are not clear yet. The paleoenvironmental implications of the occurrences of warm-adapted mammals in north China remain unsolved. To answer these aforementioned questions will be the main goal of the present paper.

Concerning the exact boundary between the north China and south China faunas, there exist different opinions. Some authors regarded the line of Yangtze River-Qinling Mountains as the fauna divide[1]. Another hypothesis thinks that the north and south China faunas can be distinguished along the line of Huaihe River-Qinling Mountains-Himalayas, which coincides with the north boundary of north subtropical zone[2]. The third hypothesis regards the line along the Huaihe River-Qinling Mountains-Hengduan Mountains as the fauna divide between north and south China, but to some extent, the Yangtze River prevents the communications of some taxa between the north and south faunas[3].

For the sake of the correspondence of the second hypothesis with the current geographical pattern, which coincides with the climate zones and humidity distribution, this paper adopted the second hypothesis. In this paper, the north China and south China faunas are going to be distinguished according to the line along the Huaihe River-Qinling Mountains. In consideration of the frequent communications between the north and south faunas in the east part of China during the whole period of Quaternary, the present author agrees with the previous authors[4] in regarding the Qinling-Dabashan Mountains and the areas between the Huaihe River and Yangtze River as the transitional zone.

Abbreviations: C.K.T. Choukoutien (Zhoukoudian).

2 The taxa of warm-adapted mammals once inhabited north China

In Europe, *Macaca*, *Palaeoloxodon*, *Dicerorhinus*, *Hippopotamus* and *Bubalus* are treated as warm-adapted animals during the Middle Pleistocene[5].

Quite a lot of warm-adapted mammals once left their records in north China, such as *Ia io*, *Hipposideros*, *Macaca*, *Rhinopithecus*, *Sciurotamias*, *Aeretes*, *Rhizomys*, *Hystrix*, *Ailuropoda*, *Arctonyx collaris*, *Paguma larvata*, *Acinonyx*, *Stegodon*, *Palaeoloxodon*, *Elephas maximus*, *Hesperotherium*, *Megatapirus*, *Tapirus*, *Dicerorhinus*, *Muntiacus muntjak*, *Hydropotes*, *Cervus unicolor*, *Bubalus* and *Capricornis* (see Table 1). The defining of the warm-adapted elements is according to the criteria given by Zhang[2]. Among all these taxa mentioned above, *Hystrix*, *Macaca*, *Palaeoloxodon*, *Dicerorhinus* and *Bubalus* are the most frequently appearing genera (see Table 1). Most of the taxa are not very difficult to be identified. Some comments will be given for the taxonomic determination of some important genera and species.

Hipposideros is a kind of big bat which has a relatively easy distinguishing lower dental formula (2.1.2.3), but sometimes it is not easy to tell it from *Megaderma lyra* if only based on the mandible. It is a typical oriental element today, but there are some reports of Pleistocene records of this genus at C.K.T. Loc. 3[6] and C.K.T. Donglingzi Cave[7].

Ia io is a south China type of mammal[2] whose fossil in north China is very rare, the only known locality is C.K.T. Loc.1[8]. Actually, the record of this species is also very limited in south China.

Bats usually inhabit cave, forest and bamboo environments, most of which occur in south China today; very few species can survive to the north of Yellow River. In the loess deposits and the arid area, the records of bat are very rare. It seems that *Rhinolophus ferrumequinum* can be treated as a warm-adapted species.

The fossil records of *Macaca* in north China concentrated in the Zhoukoudian area and Liaodong Peninsula[9,10], which is also within the range of the warm temperate zone. All those records of *Macaca* were recovered in cave deposits. It is worth mentioning that there is only one occurrence of *Macaca* in loess deposit of Early Pleistocene at Longdan locality in Gansu Province in northwest China[11]. Several decades ago, the wild population of *Macaca* still could be observed around Beijing, but today's northern most occurrence of the natural groups of *Macaca* only can be found in the Jiyuan, Henan, in the Taihang Mountains.

Rhinopithecus is not a typical oriental element, because its ranges are situated within the transitional zone. It is true that this kind of mammal left very few records in north China, up to now, only the Gongwangling Locality in Lantian[12], Baoji[13] and Xin'an in Henan[14] bear *Rhinopithecus* fossils. The skull of *Rhinopithecus* is

Table 1 Fossil and subfossil records of oriental elements in north China

Taxa	Number of records				
	Early Pleistocene	Middle Pleistocene	Late Pleistocene	Neolithic-Historic Period	Recent
Ia io	—	2	—	—	—
Hipposideros	—	—	2	—	—
Rhinolophus	—	2	5	—	*
Macaca	3	11	4	5	*
Rhinopithecus	1	?1	—	1	—
Aeretes	—	—	2	—	*
Rhizomys	—	2	—	4	—
Hystrix	7	10	6	1	*
Ailuropoda	1	?2	—	1	—
Arctonyx collaris	—	2	1	1	*
Paguma larvata	—	—	2	—	*
Acinonyx & Sivapanthera	2	4	3	—	—
Stegodon	4	10	—	—	—
Palaeoloxodon	19	12	28	—	—
Elephas maximus	?1	?2	?3	3	—
Hesperotherium	5	—	—	—	—
Megatapirus	1	2	—	—	—
Tapirus	1	—	—	1	—
Dicerorhinus	5	14	5	1	—
Muntiacus muntjak	3	2	1	2	—
Hydropotes	—	6	4	5	—
Cervus unicolor	—	2	1	1	—
Bubalus	1	13	14	3	—
Capricornis	1	—	2	1	—
Total	55	99	83	30	6

—Without record; * with record.

characterized by very small nasal bone and shortened muzzle. But concerning the isolated teeth, they are not easy to be distinguished from that of *Macaca*. There is no evidence of *Rhinopithecus* found to the north of Yellow River, this kind of mammal should be regarded as warm-adapted.

Xiaonanhai (=Hsiaonanhai) was once thought to be the only occurrence of *Pongo* locality north of the Yangtze River[15], but it was denied by Zhou subsequently, who thought both the morphological characters and odontometric data of the materials show that they belong to human, but not to *Pongo*. That is to say, up to now, there is no definite record of *Pongo* north of the Yangtze River[16].

Aeretes is an endemic mammal of China, it is also a monospecific genus, the only species is *Aeretes melanopterus*. This genus is characterized by its grooved broad upper incisors. The type locality is Xinglong in Hebei Province. In the modern zoogeographical classification, *Aeretes melanopterus* was grouped with oriental elements. The oldest occurrence of this genus is from Longgupo, an Early Pleistocene locality just on the southern bank of the Yangtze River. There were no records of this genus around Beijing until the Late Pleistocene[17,18]. The Late Pleistocene and recent occurrences of this genus around Beijing are still within the range of warm temperate zone.

Bamboo rat (*Rhizomys*) is mainly feeding on bamboo roots. Its range is related to the range of bamboo to some extent. The range of the recent bamboo rat stops at the north boundary of the north subtropical zone. There are only two fossil records in north China, one is Gongxian in Henan[19], the other is Lantian in Shaanxi[20]. Additionally, there are three Neolithic localities[21] and one

historical site at Anyang[22] with bamboo rat records in north China. Concerning the occurrence of *Rhizomys* at the Peking Man site at Zhoukoudian, it is still open to question. In several bibliographies, it was cited that *Rhizomys* existed in the Peking Man fauna, but the present author did not find the original description of the materials. The only original description is in the monograph on microfauna of Peking Man Site by Young[22], but the *Rhizomys* materials described in it were from the upper travertine of Pliocene age, but not from the Peking Man site. In some important bibliographies on the Peking Man fauna[23,24], *Rhizomys* was not mentioned. So it seems that the existence of *Rhizomys* at the Peking Man site should be denied.

During the Quaternary Period, *Hystrix* once appeared in north China quite often. There are more than 20 records of fossil *Hystrix*[25], most of which are of Middle Pleistocene age. *Hystrix* fossils are mainly recovered in cave deposits. Only one record is from lacustrine deposit in Nihewan, two records are from the loess in Gongwangling and Mianchi. Most of the *Hystrix* materials are isolated teeth, they are very easy to be recognized. So the determinations of the *Hystrix* fossils are usually reliable at the generic level. Concerning the record from Chenjiawo, it is still open to question, because no actual fossil was found, the existence of *Hystrix* was inferred from the gnawing marks left on the bone, the width of the tooth mark is 3.5 mm[26]; based on the study on the *Hystrix* materials from Tianyuan Cave, the width of the lower incisor ranges between 4.5 and 6.5[25], so the record of *Hystrix* at Chenjiawo is still not sure. Up to now, there is no sound evidence of the existence of *Hystrix* in typical loess deposits.

Ursus thibetanus used to be one of the most important members of the *Ailuropoda-Stegodon* fauna in south China. The recent forms are also mainly distributed in south China, so this species used to be used as an indicator of warm climate[23]. But the subsequent discovery of the living *Ursus thibetanus* in Northeast China made us have to doubt its significance in the paleoenvironmental reconstruction.

In summer, the recent range of giant panda (*Ailuropoda*) can reach the north slope of the Qinling Mountains in Zhouzhi, Shaanxi. But in winter, it will move to the south slope. So it is reasonable to regard *Ailuropoda* as oriental element whose fossil records were really widespread in south China even with an outreach to Southeast Asia. There is only one confirmed record of *Ailuropoda* in north China, that is Gongwangling. The report on the *Ailuropoda* from Peking Man site at Zhoukoudian is still open to question, because only few postcranials have been attributed to *Ailuropoda* with uncertainty, and the materials are not available today. Someone proposed that it may be possible to have *Ailuropoda* at Peking Man Site with the coexistence of *Bubalus* and *Hystrix*[23]. The records of *Ailuropoda* from the Middle Pleistocene deposits in Pinglu, Shanxi, are still uncertain, because only two teeth (V5779) have been measured, but without description and illustration[27], and the present author failed in finding the fossil materials. The occurrence of *Ailuropoda* to the north of Yellow River is not definite yet.

Arctonyx collaris can survive in north China, but it is more widespread in south China both in fossil records and living forms. *Arctonyx collaris* appeared in north China at the Tianyuan Cave at the late Late Pleistocene[18, 28]. The upper M1 of *Arctonyx collaris* is quite different from that of *Meles meles*, the former is much narrower; additionally, its hard palatine extends more backward than in *Meles meles*. In the lower m1, these two species are also very different[29]. Because *Arctonyx collaris* moved to north China very late, its fossil records there are very limited.

The records of *Paguma larvata* are very similar with that of *Arctonyx collaris*, and its first appearance was in the Zhoukoudian area during the last interstadial[17,18,28]. The fossil record of this species is very rare in north China, but the living form still exists near Beijing.

The Cheetah (*Acinonyx)* is not one of the Great Cats, because it does not have a floating hyoid bone in its neck, so it cannot roar. Additionally, *Acinonyx* also owns some of its special characters, e.g. skull relatively small and compact (greatest length: 162—203 mm), rostrum (snout) very shortened, domed skull, nasal profile straight to concave (dipped), small short canines, canine grooves absent or faint, broad frontal[30,31]. The upper p4 of *Acinonyx* is also very characterized by the greatly reduced and more posteriorly positioned protocone; the lower premolars have developed parastylid and metastylid. This kind of mammal surely represents warm climate. The recent cheetahs only exist in Africa, southwest Asia and Middle East. But the occurrences of this kind of mammal in north China are quite often. One quite complete mandible was recovered in the Early

Pleistocene lacustrine deposits in Nihewan[32]. The materials from the Upper Cave in Zhoukoudian were very well preserved as described in the preliminary excavation report by Pei, but it is a pity that the materials now are not available, and only one upper p4 was studied by Pei[17]. All these evidences indicate that the existence of *Acinonyx* in China is definite. But the fossil records from Northeast China (Miaohoushan, Jinniushan[33], Gulongshan, Xiaogushan, etc.) are still open to question, because of the poor materials. Concerning the systematical paleontology work on the early cheetah fossils in China, the current proposal is to put the Early Pleistocene materials into the genus *Sivapanthera*, such as *Sivapanthera linxiaensis* from Longdan, Gansu[11] and *Sivapanthera pleistocaenica* from Gongwangling. Although someone proposed that the cheetah material from Nihewan is very similar with the living form, but definite records of *Acinonyx jubatus* only appeared in the Late Pleistocene in north China[34], and most of them concentrated in the Zhoukoudian area and Liaodong Peninsula[35]. In consideration of the poor knowledge about the paleoecological feature of the early cheetah-like mammals, in this paper only the materials referred to the living species are regarded as warm-adapted elements.

Most of the *Stegodon* fossils recovered in north China concentrate in the upper and middle reaches of the Yellow River[36]. Additionally, some *Stegodon* localities were also recovered in the west Qinling Mountains which falls into the transitional zone. *Stegodon* can be employed as a reliable indicator of warm climate, because of its brachyodont cheek teeth and the dependence on the branches and foliage in its diet. Besides, the fossil records of *Stegodon* mainly occur in the *Ailuropoda-Stegodon* Fauna in south China and Southeast Asia region, in north China its occurrences are much less than that of *Palaeoloxodon*. From all these evidences mentioned above, it seems that *Stegodon* prefers much more warmer climate than *Palaeoloxodon*. It is worth mentioning that there are many species under the genus *Stegodon*, the species appearing in north China are primitive and large-bodied ones, such as *Stegodon zdanskyi*, (*Stegodon chiai*) and *Stegodon huanghoensis*[37], and their occurrences did not extend into Late Pleistocene. On the other hand, the evidences of derived and small ones were also detected in north China, such as the *Stegodon orientalis* from Gongwangling.

Dicerorhinus-Palaeoloxodon fauna was the typical interglacial assemblage[23]. They adapted to live in the temperate forest and grassland biomes, and made their first appearance during Günz-Mindel interglacial (or Cromer interglacial)[5] in Europe. In the central and northern parts of Europe, *Palaeoloxodon* fossils are always associated with interglacial deposits, but disappear in the *Mammuthus* fauna preserved in the glacial deposits (Lister, personal communication). Up to now, almost no record of *Palaeoloxodon* was reported from the loess deposits. All these evidences indicate that *Palaeoloxodon* appeared to prefer warm and moist climate. *Palaeoloxodon* used to be a fairly widespread animal over the time span of the whole period of Quaternary in China, its fossil records occurred almost all over the country except very few regions, e.g. Tibet and the northern part of Northeast China[38]. In north China, *Palaeoloxodon* sometimes coexisted with *Coelodonta*[39]. From this point of view, *Palaeoloxodon* was not a typical warm-adapted mammal. More than 60 *Palaeoloxodon* localities have been reported in north China, except the three exceptions, almost all of them exclusively fall within the warm temperate zone. During the Late Pleistocene, *Palaeoloxodon* used to be quite common in the fauna in the Beijing area.

The history of *Elephas* in north China is not quite clear yet. Some proboscidean materials from Dingcun once were put into the genus *Elephas*[40], but they were moved to *Palaeoloxodon* for the sake of narrowness and loosely arranged lamellar of the cheek tooth (lower lamellar frequency)[41]. The subfossil materials from the Dingjiabu reservior in Hebei Province was definitely referred to *Elephas maximus*[42], up to now, there is no challenge to this determination. The age of the materials was dated at 3 ka, which is the most recent record of *Elephas maximus* in the far north of China. Additionally, the remains of *Elephas maximus* at the historical site of Anyang are also very interesting. Because the materials were preserved together with cultural relics, it is very possible that they were human introduced, but not natural group[43].

Chalicotheres is a group of extinct mammal which dwelt in dense forests. The teeth of chalicothere are characterized by buno-lopho-selenodont cheek teeth, the buccal wall is sharp and can be used to cut, and the lingual cusps are bunodont and can be used to crush foods. Their relatively low-crowned teeth are not suited for a

fibrous, gritty diet, but specialized for dealing with leaves and other browse[11,44]. So it is reasonable to suppose that chalicotheres are adapted to warm climate. In China the only known Quaternary species of chalicothere is *Hesperotherium sinense*, which represents the last occurrence of this kind of animal on the earth. *Hesperotherium sinense* also occurred in north China in several localities, such as Nihewan, Tianzhen, Gongwangling and Linyi, etc.

Traditionally the diceratherine rhinocerotid fossils found in north China were put into *Dicerorhinus mercki* (*Dicerorhinus kirchbergensis*) and *Dicerorhinus yunchuchunensis*, the former was supposed to be the largest species under the genus *Diceorhinus*[45]. The only recent species under *Dicerorhinus* is *Dicerorhinus sumatrensis* which dwells in the dense forests[46]. The cheek teeth of this kind of animal is characterized by the lowest hypsodonty index and the relatively least length of premolar series[47]. It should be warm-adapted and a browser. The present author does not agree with the hypothesis which proposed that the grazing rhinos usually enlarge the premolar tooth row for greater grinding area and the browser usually has less lengthy premolar series[47], because *Coelodonta* and *Elasmotherium* are two very well-known steppe grazers, but both of them with very short premolar tooth row, the latter even only has two premolars on each side, which is less than usual.

Extant tapirs are found primarily in tropical forests, and appear to be water-dependent. Tapirs not only can inhabit the lowland forests, but also can survive in the mountains at an altitude of 2000 to 4000 m. The distinctive bilophodont molars of tapirs, with wear on the cross lophs only, appear to be specialized for dealing with relatively low cellulose content foliage, such as leaves, fresh sprouts, and small branches as well as fruit, sometimes also including some aquatic plants[48]. Simpson once indicated that all the records of tapirs in America are limited to the mesothermal area[49]. Janis proposed that the endemic genus *Megatapirus* in Asia presumably occupied a hippopotamus type of niche[48], this inference coincides with the fact that in China there are no reliable records of *Hippopotamus*. The Asian tapir, *Tapirus indicus*, prefers closed forest to forest edge[50]. On the other hand, some disagreements on the paleoenvironmental implications of tapirs have been proposed by Graham who proposed that about 168 localities of Quaternary tapir fossil have been known in North America, most of which are far from the ranges of the living forms, so he proposed that tapirs can tolerate relatively lower temperature[51]. According to the ranges of fossil *Tapirus* and *Megatapirus* in China, the present author thinks that they represent warm climate, because almost all of the tapir records exclusively occur in south China[52], and only one fossil and one subfossil locality were found in the southern part of north China.

The Chinese water deer (*Hydropotes inermis*) is a kind of small cervid which is very similar with *Moschus moschiferus* in small body size, lacking of antlers and with sabre-like upper canine in male individuals, but *Hydropotes inermis* is a little different in the following aspects: slightly larger size, with developed mesostyle in the upper molars, sabre-like canine is relatively robuster and shorter, with fossa in front of the mental foramen. The most important difference between the two species lies in the absence of lacrimal sac in *Moschus* and the occurrence of very developed lacrimal sac in *Hydropotes inermis*. The living *Hydropotes inermis* today is only restricted to the areas to the south of Huaihe River, the records of this group in north China should be reconfirmed.

The sambar (*Cervus unicolor*) is characterized by its rough antler and the brow-tine is borne on the beam at a higher position above the burr, the angle between the brow-tine and the beam is acute. The extant *Cervus unicolor* in China only exists in south and southwest China. But its northern most record of fossil is in Miaohoushan, Liaoning, which was questioned subsequently. Concerning the related species *Cervus elegans* of Early and Middle Pleistocene, its paleoenvironmental implication is not so clear.

Water buffalo is a kind of large bovid, the only wild species is *Bubalus arnee* which is restricted to a very small area in the southeast part of Tibet today[53]. But the range of the domestic species *Bubalus bubalis* covers a huge area to the south of the Huaihe River. During the Pleistocene epoch, the occurrences of *Bubalus* used to be quite common in north China, at least 27 records are known[54,55]. Up to now, no *Bubalus* fossil was found in the loess deposits[56], which is in the same situation as *Palaeoloxodon*. This should be sound evidence for its preference of warm climate for *Bubalus*. There are three possibilities to explain the frequent appearances of *Bubalus* in north China during the Pleistocene epoch[57]. The fossil species of *Bubalus* found in north China are

exclusively extinct species, which makes it more difficult to reconstruct their paleoenvironmental features. But more evidences and more authors support the proposal that occurrences of *Bubalus* usually indicate warm climate[55].

Among all the fossil *Bubalus* localities in north China, Salawus (Sjara-osso-gol) is the most northwest one[58]. Some reports mentioned the discovery of fossil *Bubalus* in Qingyang, Gansu, which should be reconfirmed owing to the poor materials. The most unbelievable thing is the occurrence of *Bubalus* extending to the high latitude in Northeast China. The fossils of *Bubalus wansjocki* found in Zhaoyuan, Heilongjiang, were very complete with both skull and postcranials. Its geologic age is around 25 ka B.P.[57], which falls within the interstadial. In north China, there are two Holocene occurrences of *Bubalus*, one is Sanhe, Hebei[59]; the other is at the historical site of the Shang dynasty at Anyang[43]. But Jia proposed that the *Bubalus* at the Sanhe site probably came from much lower horizon in the profile than originally inferred by Andersson, it should be between 5000—2000 a B.P.[60].

In regard to *Bos primigenius*, some authors once proposed that it should be interglacial animal[23]. But in China, quite a lot of *Bos primigenius* were preserved in loess, so the present author does not think it is warm-adapted.

The paleoenvironmental features of *Crocuta crocuta ultima* and *Crocuta crocuta spelaea* are still controversial, though Kahlke[61] once proposed that both subspecies were inhabitants of temperate to boreal, but by no means arctic, zones.

3 Distributional patterns of the occurrences of warm-adapted mammals in north China

3.1 Amounts of locality of warm-adapted mammals in north China

Based on the incomplete statistic, there are hundreds of Quaternary fossil localities in north China, more than 60 of which contain warm-adapted elements (Figures 1 and 2), and more than 60 of which bear *Palaeoloxodon* fossils (some of them coexisted with other warm-adapted animals) (Figure 3). Most of the warm-adapted mammals in north China were once distributed in the Zhoukoudian area, Liaodong Peninsula and the Lantian area. In consideration of the uncertainty of the exact location and horizon, the following occurrences of warm-adapted mammals at Mianchi (with *Macaca* and *Hystrix*), Xin'an (with *Rhinopithecus*) and Gongxian (with *Rhizomys*) are not taken into consideration in Figures 1 and 2. Besides, the faunas composed of materials from different locations, such as Linyi[62] and Tunliu[63] in Shanxi and Laochihe[64] in Shaanxi, are not going to be discussed in this paper too.

Zhoukoudian is the evolutionary center for warm-adapted mammals in north China, more than 10 different groups once inhabited there for quite a long time. The most important elements are *Macaca*, *Hystrix*, *Dicerorhinus*, *Bubalus*, etc. The present author once proposed that in east China there is no natural barrier which can prevent the free communication of faunas, and the boundary between north and south China has been continuing to shift with the fluctuations of climates[54].

Because the localities are numerous and the bibliographies are huge, it is very possible that some of the occurrences of warm-adapted mammals found in north China were not included in this paper.

3.2 The occurrences of warm-adapted mammals and their geological background in north China

In the tectonic framework of China, the occurrences of warm-adapted mammals in north China fall into the region of North China Platform, except few exceptions, such as the presence of *Dicerorhinus mercki* and *Bubalus* in Heilongjiang, *Palaeoloxodon* in Xinjiang, etc. (Figures 2 and 3).

Most of the warm-adapted mammalian fossils were found in cave deposits which were distributed mainly in the Zhoukoudian area, Liaodong Peninsula and the Taihang Mountains. But proboscidean and *Bubalus* fossils are mainly from lacustrine and fluvial deposits which mainly appeared in the Nihewan basin and Dingcun area. Nihewan is a very productive Quaternary fossil locality which bears a large quantity of freshwater mollusks but contains relatively less warm-adapted mammals compared with the Zhoukoudian area.

In China, loess is a very important type of deposit which is of distinct paleoenvironmental implications. Concerning the origins of loess, Liu once proposed in the 1960s that loess in China represents arid and semi-arid grassland environment, and the loess fauna is mainly composed of steppe types[56], such as *Marmota*,

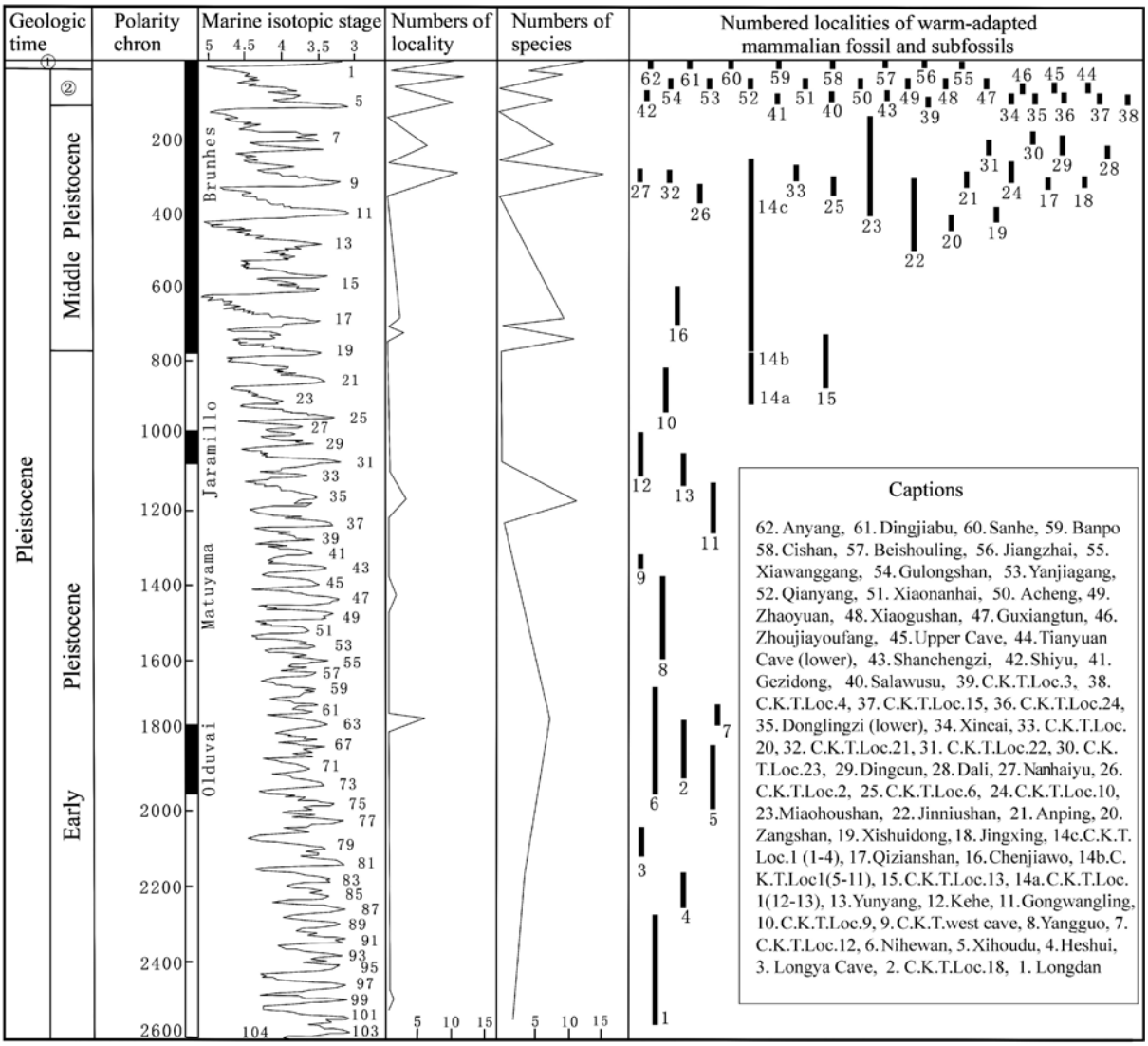

Figure 1 The occurrences of warm-adapted mammals in north China and their temporal distributions over the Quaternary Period. ① Holocene; ② Late Pleistocene; deep-sea oxygen isotope stages and paleomagnetic chronology are according to Lisiecki & Raymo[65]; The geological time table is after Zhang et al.[66].

Allactaga, *Cricetinus*, *Meriones*, *Myospalax*, *Ursus*, *Meles*, *Vulpes*, *Panthera pardus*, *Hipparion*, *Equus sanmeniensis*, *Equus hemionus*, *Equus przewalskii*, *Coelodonta*, *Sinomegaceros*, *Cervus grayi*, *Capreolus*, *Camelus*, *Spirocerus*, *Gazella przewalskii*, *Gazella subgutturosa*, *Bos primigenius*, *Bison exiguus* and *Struthio anderssoni*, among which *Myospalax* is the most frequently appearing element, and large mammals are relatively sparse. In the loess fauna the warm- adapted elements are absent. But in the lacustrine and fluvial deposits which are located in the loess region, it is possible to find some warm-adapted mammals, such as *Stegodon*, *Palaeoloxodon*, *Dicerorhinus* and *Bubalus,* etc.[56,67]. In regard to the *Bubalus* fossils found in the loess region, it is still open to question, but it is definite till now that there is no record of *Bubalus* found directly in loess. The *Bubalus* fossils found near Mianchi was from the bottom of the reddish bed, maybe it belongs to the Wucheng Loess[55], but not the typical one.

The loess in the Lantian area, Shaanxi, is an exception, because the fauna there contains quite a number of warm-adapted elements, such as *Rhinopithecus*, *Hystrix*, *Ailuropoda*, *Sivapanthera*, *Stegodon*, *Palaeoloxodon*, *Hesperotherium*, *Tapirus*, *Dicerorhinus*, *Elaphodus*, *Capricornis*, etc. Additionally, the loess fauna from Longdan, Gansu, also contains some warm-adapted

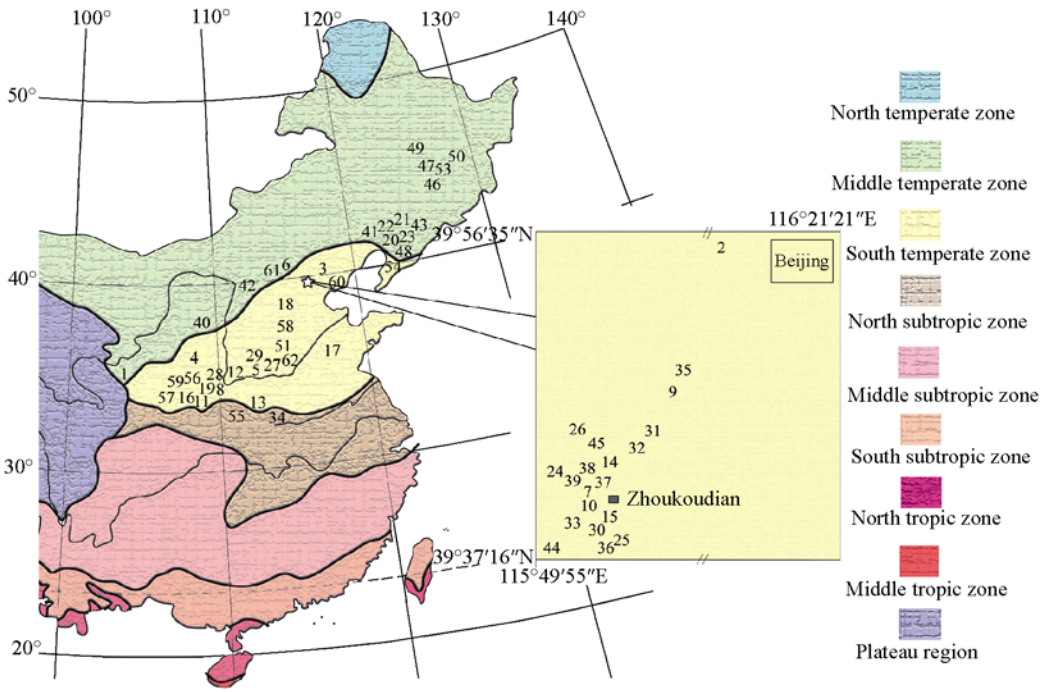

Figure 2 Map showing the distribution of the occurrences of warm-adapted mammals other than *Palaeoloxodon* in north China, compared with the subdivisions of modern climate zones. The numbers of the localities are the same as in figure 1. The subdivisions of climate zones is after the National Meteorological Bureau (1966)[78].

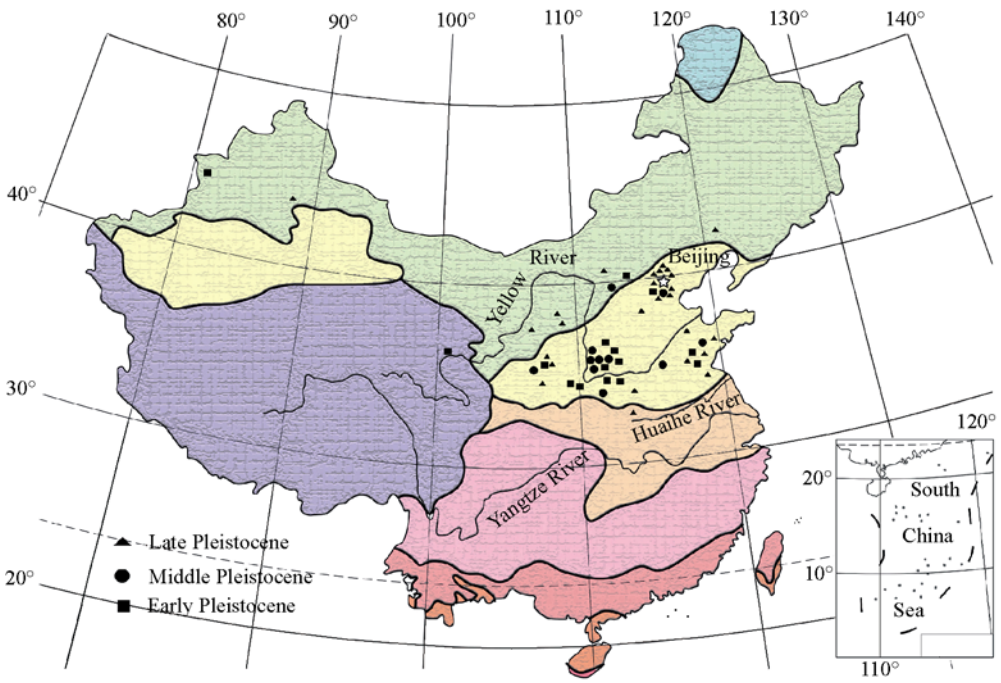

Figure 3 The occurrences of *Palaeoloxodon* in north China (The physical geographical subdivision is the same as in Figure 2).

elements, such as *Macaca* and *Sivapanthera*[11]. The warm-adapted mammals dominated assemblage of the Gongwangling Fauna conflicted with the result from the study on the non-biological indices which indicated that the L15 should be deposited under dry and cold conditions[68]. It is worth mentioning that all the examples of the warm-adapted mammals preserved in loess are located on the edge of the Loess Plateau, especially the Gongwangling Fauna is near the transitional zone. The loess which contains warm-adapted mammals is pre-

sumably not typical one.

3.3 Warm-adapted mammals and their fossil assemblages

In north China the warm-adapted mammals seldom coexisted with cold-tolerant mammals. During the last ice age, the cold-tolerant mammalian assemblages appeared in the northern part of Palearctic Region, which dealt with the following taxa: *Lepus arcticus*, *Alopex lagopus*, *Gulo gulo*, *Lynx lynx*, *Panthera leo spelaea*, *Ursus spelaeus*, *Ursus maritimus*, *Ursus arctos*, *Mammuthus primigenius*, *Alces alces*, *Rangifer tarandus*, *Bison priscus*, *Saiga tatarica*, *Ovibos moschatus*, etc., some of which once appeared in Northeast China, such as *Ursus arctos*, *Ursus spelaeus*, *Lynx lynx*, *Mammuthus primigenius*, *Rangifer tarandus*, *Alces alces* and *Bison priscus*[39]. The only example of coexistence of warm-adapted elements with *Mammuthus* is the *Bubalus*[57]. But among the seven *Bubalus* localities, four of which, such as Yushu, Gulongshan, Xiaogushan and Yanjiagang, have the *Bubalus*-*Mammuthus* assemblage, but they did not need to appear in the same horizon.

In the past, the following taxa once appeared in Zhoukoudian area used to be supposed to represent cold climate, such as *Marmota complicidens, Marmota robustus, Gulo gulo*, *Ursus spelaeus*, *Lynx lynx*, *Coelodonta*, *Boopsis*, etc.[23]. But today most of the taxa had their taxonomic identifications changed, and others' preference for warm climate has been questioned. That is to say, in the Zhoukoudian area, there existed no typical cold-tolerant elements.

3.4 Correspondence between the occurrences of warm-adapted mammals and the geologic ages as well as with the paleoclimatic stages

Most of the warm-adapted mammals appearing in north China corresponded with the warm stages (interglacial and/or interstadial). Although some localities' time span once were correlated with glacial stages, such as the Gongwangling with the Günz Glacial and C.K.T.Loc.1 with Riss Glacial, some of the *Bubalus* fossil records also corresponded with glacial, but the most recent study shows that some layer (layers 10—12) at C.K.T.Loc.1 can be correlated with S5 (0.62—0.48 Ma), which represents warm climate, in the loess sequences; and the Gongwangling Fauna is a little earlier than L15[34] which indicates that even during the glacial, there existed some warm substages. It worth mentioning that in Early and Middle Pleistocene faunas there are very few cold-tolerant taxa. It is supposed that the climate during that time span was quite warm, another possibility is that the taxa dominated that time span is mainly extinct one, the knowledge about their paleoecological features is very poor. Most of the modern mammal species appeared since the middle Middle Pleistocene[5].

There are only 11 Early Pleistocene localities which bear warm-adapted mammals, but the diversity of the taxa which amounts to 16 species is very high. Though the time span of Middle and Late Pleistocene is shorter than that of Early Pleistocene, the latter two have more occurrences of warm-adapted mammals, 22 localities fall into Middle Pleistocene, 21 localities fall within Late Pleistocene. It indicates that during the Middle and Late Pleistocene, the climate was more fluctuated. The result from the mammalian fossil records corresponds with that of other studies such as the evidence from loess. The sequences of the loess-paleosoil show that the fluctuations of the climate became more sharp since 0.8 Ma[69]. In the Late Pleistocene the fluctuations became more frequent, which made the frequent turnover of faunas possible, and the range of warm-adapted mammals expanded into the largest ever since in north China. The records of warm-adapted mammals to the far Northeast China occurred during this time span, which is not compatible with the range of loess and the cold-tolerant assemblage of mammals, it is well known that the Late Pleistocene loess is the most widespread one[56] and the cold-tolerant assemblage of mammals of the Late Pleistocene is the dominant fauna in the Palearctic Region[39]. All these different phenomena mixed together. The only reasonable explanation is the frequent change of climate during Late Pleistocene, which coincided with the frequent sea level changes during Late Pleistocene[70]. Recently more evidences show that some interstadial was as warm as the interglacial. Before the last glacial maximum, there existed a dispersal event of mammals from south to north in China, in which such mammals as *Aeretes*, *Arctonyx*, *Paguma* and *Capricornis* extended their occurrences to the far north near Beijing[18,28]. During the post-glacial time, there occurred also some migrations of warm-adapted mammals to the north, such as in the period of Yangshao, around 6000 a B.P., whose age falls within the Neolithic age[71].

3.5 Records of warm-adapted mammals and the current climate zones

The overwhelming majority of the records of the warm-adapted mammals occurred in north China fall within

the range of south temperate zone in the modern subdivisions of physical geography and concentrated in the moist subzone (Figure 2). The south temperate is characterized by deciduous forest and its south boundary neighbors with the north boundary of the north subtropical zone[72]. There existed some exceptions, such as the few occurrences of warm-adapted mammals in the far northeast and far northwest of China, which only deals with the megafauna, such as *Palaeoloxodon*, *Dicerorhinus* and *Bubalus*. The medium-sized and microfauna of warm-adapted mammals never reach too far to the north, such as *Macaca*, *Hystrix*, *Rhizomys*, *Arctonyx*, *Acinonyx*, etc. Additionally, the farthest oc- currence of *Stegodon* in Heshui is located at the northern edge of the south temperate zone.

3.6 Records of warm-adapted mammals in north China and the current zoogeography

The overwhelming majority of the records of the warm-adapted mammals occurred in north China fall within the range of North China Region which includes the Huanghuai Plain subregion and the Loess Plateau subregion whose fauna is not only a mixture of the Palearctic and the Oriental elements, but also a mixture of the fauna from the monsoon area and the Mongolia-Xinjiang faunas[73]. So this region almost has no endemic mammal of its own. It appears that the feature of the north China fauna during the Pleistocene epoch was similar with the situation of today.

4 Discussions on the paleoenvironmental implications

The frequent appearances of warm-adapted mammals in north China can be attributed to the following causations: The first possibility is that in the past, there existed some warm stages in north China, which resulted in the invasions of the fauna from the south. Some non-biological indices indicate that the global climate was continuing cooling down since the end of Neogene. The second possibility is the seasonal dispersal, such as the seasonal migrations of *Ailuropoda* between the two slopes of Qinling Mountains, and the great migrations of wildebeest and zebra in Africa. The latter migration can travel as long as 1600 km which is equal to the distance between the north and south boundaries of the south temperate zone in China. The third possibility is that the warm-adapted mammals dispersed to north China are not typical warm-like elements, they can tolerate relatively wide variations of climate, for example, *Macaca* and *Hystrix*, both of them can survive cool conditions. Their disappearance in north China was caused by human activities. The fourth possibility is that some of the groups made their first and early appearances in North China, such as *Acinonyx*, Chalicothere, *Dicerorhinus*, *Palaeoloxodon* and *Stegodon* as well as *Bubalus*[74−76], some of which got extinct with the cooling down of the global climate, others moved from north to south. The previous studies show that the changing of the zoogeography to the modern patterns took place around the transition between Neogene and Pleistocene[2,3].

The four possibilities mentioned above have enough reasons to have occurred, which makes it more difficult to interpret the paleoenvironmental implications of these warm-adapted mammals in north China. But the present author inclines to suppose that the seasonal and climate-driven dispersals were the root causations, because there exists no natural barrier between the Palearctic and the Oriental Regions in east China, which made it possible for the faunas between the north and the south to exchange freely[54,77].

Although some debates still exist in the interpretation of the significance of the occurrences of the warm-adapted mammals in north China, it is true that almost none of those mammals were preserved in the typical loess deposits, which is a sound evidence to support the assumptions that those warm-adapted mammals should represent warm climates in the past. But it should be pointed out that those warm-adapted elements are not typical warm-like mammals, they can tolerate relatively wide variations. Up to now, no records of the truly warm-like mammals, such as *Gigantopithecus*, *Pongo*, *Hylobates*, *Presbytis*, *Nycticebus* and *Manis*, were detected north of the Yangtze River. The existence of the dominant taxa of *Ailuropoda-Stegodon* fauna in north China is still uncertain. Besides, most of the warm-adapted mammals that once occurred in north China are extinct species, such as the fossil species under the following genera *Macaca*, *Palaeoloxodon*, *Dicerorhinus* and *Bubalus*, their paleoenvironmental implications are not quite sure yet. The appearance of the living species from the Oriental Region is not so often. All these evidences show that the warm stages that once occurred in north China were never as warm as in the subtropic even tropic zones. Some one once proposed that during Early Pleistocene the northern boundary of the tropic zone

extended northward across the Yangtze River, and the northern boundary of the subtropic zone reached the middle temperate zone of today[2]. But it seems that the present study does not support this hypothesis.

It is true that the interpretations on the paleoenvironmental implications of the warm-adapted mammals that once occurred in north China are far from definite. Some of the taxonomic work should be reconfirmed, and lots of dating work should be added. The correct conclusions only can be reached based on the correct dating data and the correct taxonomic determination of the fossils.

5 Conclusions

The warm-adapted mammals dispersed to north China are not typical warm-like elements, such as *Macaca*, *Hystrix*, *Palaeoloxodon*, *Dicerorhinus*, *Bubalus*, etc., they can tolerate relatively wide variations of climate. Most of the warm-adapted mammalian fossils were found in the cave deposits, and almost none of those mammals were preserved in the typical loess deposits. In north China the warm-adapted mammals seldom coexisted with cold-tolerant mammals. Most of the warmadapted mammals appearing in north China corresponded with the warm stages (interglacial and/or interstadial). The overwhelming majority of the records of the warm-adapted mammals occurring in north China fall within the range of south temperate zone of the current climate subdivisions and the range of North China Region of zoogeography. The warm stages that once occurred in north China during Pleistocene were never as warm as in the subtropic, let alone tropic zones of today.

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