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中国与欧洲晚中新世猪类比较研究：生物地层学及古生态学

刘建辉[1]　Martin PICKFORD[2]
（1 云南省文物考古研究所　昆明　650118）
（2 法国国家自然历史博物馆　巴黎　75005）

摘要：猪类对比研究表明，从晚中新世初期到晚中新世末（或上新世初期），中国与欧洲的古气候、古环境和猪类演化都受到了全球性自然变化的影响，有着相同或相似的发展经历。晚中新世早期（early Vallesian（MN9））中国与欧洲的猪类显示它们均受到先前来自南亚猪类的影响，南亚猪类可能通过东南亚扩散到中国南方，通过西亚扩散到欧洲。晚中新世中期（late Vallesian（MN10）and early Turolian（MN11）），中国和欧洲的猪类与南亚已基本没有交流，在各自地区相对独立地演化发展。晚中新世晚期（late Turolian（MN12、MN13））中国北方除了保留有从南方迁移来的种类外，欧洲的猪类也已出现，此时中国（北方）动物群与欧洲动物群关系较为密切。南亚动物群在晚中新世早期（或者更早些）似乎已经和中国及欧洲的动物群分离。受青藏高原隆升等自然因素的影响，晚中新世中后期中国南方的古环境有一个从较为封闭、湿热的森林类型向相对开阔、干冷稀树草原类型的演变过程，而在此期间北方的自然环境则可能是从早期的半干旱疏林草原逐步发展到晚中新世末期的湿润林地。晚中新世欧洲自然环境有一个与中国南方相似的变化过程，比较而言，晚中新世中后期欧洲的环境可能比中国北方更为开阔和干冷。古气候和古环境变化是影响晚中新世猪类分布演化的决定性因素。

关键词：中国，欧洲，晚中新世，猪类，生物地层学，古生态学
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COMPARISON OF EUROPEAN AND CHINESE LATE MIOCENE SUOIDEA：IMPLICATIONS FOR BIOSTRATIGRAPHY AND PALAEOECOLOGY

LIU Jian-Hui[1]　Martin PICKFORD[2]
(1 *Yunnan Institute of Culture Relics and Archaeology* Kunming 650118)
(2 *Collége de France*, *and Département Histoire de le Terre*, *Muséum national d' Histoire naturelle*, *UMR* 5143 *du CNRS* Case Postale 38,8, rue Buffon, F－75005, Paris)

Abstract Global physical events during the Late Miocene affected not only the European and Chinese Suoidea but also the environment. In the early Vallesian (MN9) the suoid assemblages indicate that both areas were influenced by previous immigration from the Indian Subcontinent, whereas in the late Vallesian (MN10) and early Turolian (MN11) they evolved independently in each area. In the late Turolian (MN12, MN13) European and southern Chinese suid lineages appeared for the first time in northern China. It seems that the Indian Subcontinent biome was isolated from that of Europe

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and China during the early Late Miocene or even earlier. The Late Miocene environment in southern China ranged from humid, warm and closed to relatively arid, cold and open. A comparable pattern is seen in Europe during this period. In contrast, the environment changed from open, cold and arid to close, warm and humid in northern China. During the same time suids spread gradually from southern China northwards and Europe eastwards to northern China. The European environment was slightly colder and more open than the Chinese one.

Key words China, Europe, Late Miocene, Suoidea, Biostratigraphy, Palaeoecology

1 Introduction

There is a long history of European palaeontological studies, and recently there have been major advances in Neogene mammal research. European suoids research has made remarkable progress in taxonomy, chronology, palaeogeography, biostratigraphy and palaeoecology. In contrast, in the Chinese literature there are many parochial descriptions of specimens, but a general lack of synoptic systematic research. In the past decade many new suoid fossils have been found, especially from Yuanmou and Hezheng (Liu and Pan, 2003; Liu et al., 2004; Pan et al., 2006) and a comprehensive review of Chinese suoids has been undertaken (Liu, 2003), which offer a good chance to extend the systematic work on Chinese suoids. This paper attempts to make a preliminary comparison between Chinese and European Late Miocene suoids focusing on biostratigraphy and palaeoecology. The stratigraphic distribution of European suoids is reasonably well established. The European data utilized in this paper is based on Pickford (1993), Made (1989 ~ 1990), Made and Moyá-Solá (1989) and Fortelius et al. (1996). For the sake of comparisons the biozonation of Mein (1990) is used. A synopsis of the Chinese Late Miocene Suoidea is provided in Table 1.

2 Biostratigraphy

Suoids are typically omnivorous, especially the bunodont forms, and they are adapted to a broad range of environments. Because they have such characteristic they were well adapted to exploit new environments, and once they arrived in new territories, they tended to radiate, often quite rapidly as the environment changed. In contrast, other mammals which were more restricted in diet migrated to other places or became extinct. As a result suoids survived for long time periods as shown by their extensive fossil record. They can thus be used for "fine focus" biostratigraphy in some areas and for some time periods (Pickford, 1993).

Biostratigraphy requires detailed provenience records, precise identification of specimens and accurate dating of the strata (Pickford, 1988). Most suoid fossils from China and Europe have clear provenience, especially the material obtained in recent years. Some taxa are based on a few or even isolated specimens and some are the subject of debate and in these cases we make a decision according to presently available knowledge and use the taxa that most people have accepted. Some deposits lack age determinations based on palaeomagnetic and isotopic methods, as a result some of the proposed time ranges of suoids are not well constrained. The temporal distribution of the Late Miocene Suoidea in China and Europe is provided in Table 2.

Palaeochoeridae (Old World peccaries) are rare in China, *Pecarichoerus* sp. was recorded from the Early Miocene Sihong fauna and it also occurs at Zhongxiang (Hubei) (Qiu and Qiu, 1995; Gu, 1980; Pickford, 1993), *Yunnanochoerus lufengensis* was reported from the Late Miocene Lufeng and Yuanmou faunas of southern China. In Europe Palaeochoeridae was abundant in the Middle Miocene deposits, but most of them going extinct after MN9, with only *Schizochoerus vallesiensis* persisting into MN10.

Yunnanochoerus was erected by Made and Han (1994) for the palaeochoerid from Lufeng. Similar fossils occur in another Late Miocene site, Yuanmou, about two hundred kilometres from

Table 1 Late Miocene Suoidea of China

	Locality	Description	Referable fauna	Age	Age reference	Lithology
Chleuastochoerus	Shihuiba, Lufeng, Yunnan	Made & Han, 1994	Lufeng①	Upper Nagri or Lower Dhok Pathan	Made & Han, 1994	lignite
				8 Ma (MN12)	Flynn & Qi, 1982	
				MN11	Qiu & Storch, 1990	
				9 Ma	Pickfor & Liu, 2001	
				MN11~12	Qiu et al., 1999	
	Qingyang, Gansu and western area of Gansu, Shanxi and east of Shanxi	Pearson, 1928	Qingyang; Mahui, Yushe ②	Pontian	Pearson, 1928	"*Hipparion* red clays"
				Late Miocene (Turolian)	Li et al., 1984; Qiu & Qiu, 1995	
				MN11~12 (Baode local faunas)	Qiu et al., 1999	
	Xiaohe and Leilao, Yuanmou, Yunnan	Pan, 1997 (*Sus* sp. (sp. nov. 1)); Pan et al., 2006	Yuanmou③	3~4 Ma	Zhang et al., 1987	gray-yellow sandy bed
				3.4~6 Ma	Qian, 1997	
				8~7 Ma	Liu & Pan, 2003; Yue et al., 2003	
				9 Ma	Ni & Qiu, 2002	
	Laogaochuan, Fugu, Shaanxi	Xue et al., 1995	Miaoliang	5.3 Ma	Xue et al., 1995	"*Hipparion* red clays"
	Potouchun, Binxian, Shaanxi	Tang et al., 1985	Binxian	Late Miocene	Tang et al., 1985	red and brown sandy mudstone
Hippopotamodon hyotherioides	Shihuiba, Lufeng, Yunnan	Made & Han, 1994 (*Propotamochoerus hyotherioides*); Pickford & Liu, 2001	Lufeng	Same as ①	Same as ①	lignite
	Xiaohe and Leilao, Yuanmou, Yunnan	Pan, 1997 (*Propotamochoerus* sp.); Pan et al., 2006	Yuanmou	Same as ③	Same as ③	gray-yellow sandy bed
	Xiaolongtan, Kaiyuan, Yunnan	Chang, 1974 (*Listriodon* sp.); Dong, 1987 (*Dicoryphochoerus* sp.);	Kaiyuan④	Late Miocene (Chinji)	Chang, 1974	lignite
				MN9 (Vallesian)	Dong, 1987	

Continued

	Locality	Description	Referable fauna	Age	Age reference	Lithology
Hippopotamodon hyotherioides		Pickford & Liu, 2001		10 Ma (MN9/10)	Pickford & Liu, 2001	
				12~11 Ma	Pickford et al., 2004b	
				MN7~8	Qiu et al., 1999	
	Qingyang, Gansu and western area of Gansu, Shanxi and east of Shaanxi	Pearson, 1928 (*Propotamochoerus hyotherioides*)	Qingyang Mahui, Yushe	Same as ②	Same as ②	"*Hipparion* red clays"
	Dalai-nor, Ximeng, Nei Mongol	Fahlbusch et al., 1983 (*Propotamochoerus hyotherioides*)	Ertemte	Latest Miocene MN13, Early Pliocene (Ruscinian MN14)	Fahlbusch et al., 1983; Li et al.,1984	Gray and yellow sandy clay
				MN13	Qiu et al., 1999	
	Potouchun, Binxian, Shaanxi	Tang et al., 1985 (*Dicoryphochoerus binxianensis* sp. nov.)	Qingyang	Late Miocene	Tang et al., 1985	red and brown sandy mudstone
Microstonyx major	Lantian, Shaanxi	Liu et al., 1978 (*Dicoryphochoerus medius*); Zhang Z Q et al., 2002; Liu et al., 2004	Mahui, Yushe	Pontian	Liu et al., 1978	"*Hipparion* red clays"
				Late Miocene	Zhang Z Q et al., 2002; Liu et al., 2004	
	Locality 114, 44, Shanxi	Pearson, 1928 (*Microstonyx erymanthius*)	Mahui, Yushe	Pontian	Pearson, 1928	
	Hezheng area, Gansu	Liu et al., 2004	Hezheng	MN13	Liu et al., 2004	
Propotamochoerus parvulus	Xiaolongtan, Kaiyuan, Yunnan	Chang, 1974 (*Potamochoerus parvulus*); Dong, 1987; Pickford & Liu, 2001	Xiaolongtan	Same as ④	Same as ④	lignite
Propotamochoerus wui	Shihuiba, Lufeng, Yunnan	Made & Han, 1994; Pickford & Liu, 2001 (*Propotamochoerus parvulus*)	Lufeng	Same as ①	Same as ①	lignite
Molarochoerus yuanmouensis	Xiaohe and Leilao, Yuanmou, Yunnan	Pan, 1997 (Suinae gen. et sp. indet.); Liu & Pan, 2003; Pickford et al., 2004a	Yuanmou	Same as ③	Same as ③	gray-yellow sandy bed
Parachleuastochoerus sinensis	Xiaolongtan, Kaiyuan, Yunnan	Chang, 1974 (*Potamochoerus parvulus*); Dong, 1987 (*Propotamochoerus parvulus*); Pickford & Liu, 2001	Xiaolongtan	Same as ④	Same as ④	lignite
Yunnanochoerus lufengensis	Shihuiba, Lufeng, Yunnan	Han, 1983 (*Lophochoerus lufengensis* sp. nov.); Made & Han, 1994	Lufeng	Same as ①	Same as ①	lignite
	Xiaohe and Leilao, Yuanmou, Yunnan	Pan, 1997 (*Lophochoerus* sp.); Pan et al., 2006	Yuanmou	Same as ③	Same as ③	gray-yellow sandy bed

Lufeng. The Yuanmou specimens are larger than *Y. lufengensis* but smaller than *Schizochoerus gandakasensis*(= *Yunnanochoerus gandakasensis* Made and Han, 1994) from Pakistan and *S. vallesiensis* from Europe. The Yuanmou specimens are more derived than those from Lufeng, the cheek teeth being more bunoselenodont (Pan et al., 2006). *Y. lufengensis* shows affinities with *Schizochoerus*(Made, 1997a) and *Schizochoerus* is closely related to *Taucanamo*(Pickford and Ertürk,1979; Made, 1989 ~ 1990), and both of these Late Miocene genera are likely to have evolved from *Taucanamo* or a similar form (Made, 1997a). *Schizochoerus vallesiensis* occurs in MN9 and MN10, *Yunnanochoerus lufengensis* ranges from MN11 to MN12 and there is no overlap between their ranges. *Yunnanochoerus gandakasensis* ranges through the upper half of the Nagri unit (MN10) and into the base of the type succession of the Dhok Pathan unit (MN11) (Pickford, 1988). *Yunnanochoerus* probably immigrated to China from the Indian Subcontinent. It is unknown in the younger northern Chinese faunas and is rare in the faunas of southern China.

In Europe the latest record of *Listriodon splendens* is in MN9, but it is unknown from the Late Miocene of China.

Chleuastochoerus is a diminutive endemic Chinese suine, widely distributed in the Late Miocene sediments of China. It is found in the Baode mammalian faunas of northern China (including the Qingyang, Mahui, Binxian and Miaoliang faunas) (Pearson, 1928; Liu et al.,1978; Tang et al.,1985;Xue et al.,1995) and Lufeng and Yuanmou faunas of southern China (Made and Han, 1994; Pan et al., 2006).

Chleuastochoerus specimens from northern China show a range of body sizes but are morphologically similar (Pearson, 1928; Tang et al., 1985; Pan et al., 2006). The specimens from Lufeng, Yuanmou and Binxian belong to the small type. The genus is common in northern Chinese faunas and Yuanmou, whereas it is rare at Lufeng and has not been found at Kaiyuan. Its earliest record is in the Lufeng local fauna (MN11, 9 Ma) and the latest record is in the Miaoliang fauna(5.3 Ma, Xue et al., 1995). They gradually spread from southern to northern China and disappeared during the early Pliocene.

The dental characters indicate the derivation of *Chleuastochoerus* from a primitive, probably Asiatic *Palaeochoerus*-like form (Pearson, 1928). *Chleuastochoerus* is quite similar to *Hyotherium* in its diminutive body size, similar tooth morphology, and in details of skull configuration such as expanded zygomatic arches, short snout and distally positioned orbit. It possibly diverged from *Hyotherium* during the late Middle Miocene.

Much of the material attributed to *Propotamochoerus parvulus* (Dong, 1987) was reassigned to *Parachleuastochoerus sinensis* (Pickford and Liu, 2001). The latter species has a small and low p2 in contrast to the longer and taller p3 ~ 4, both of which are longer than the m1. It represents a large species of the genus, being slightly larger than *P. huenermanni* from Europe and much larger than the type species *P. crusafonti* from Spain (Pickford and Liu, 2001). The European taxa range from MN7 ~ 10 and the genus appeared in China in MN9. The same species occurs at Chiang Muan, Thailand, where it ranges from 12 ~ 11 Ma (Pickford et al., 2004b). *P. sinensis* was probably derived from a European species and dispersed through Thailand to southern China.

"*Sus*" *hyotherioides* was erected by Schlosser (1903) based on specimens from China. Pearson (1928) attributed the original fossils to *Propotamochoerus hyotherioides*. Pickford and Liu(2001) referred it to *Hippopotamodon hyotherioides*.

Microstonyx is distinguished from *Hippopotamodon* by its small canine(even in males), its long snout and absent p1 (Pilgrim, 1926; Pickford, 1988, 1993). The female of *Hippopotamodon* has small lower canines (Pilgrim, 1926, Pl. XIII,fig. 2), so to identify specimens that only have the lower tooth row, it is important to observe whether it possesses p1. However, in

Table 2 Temporal distribution of the Late Miocene Suoidea in China and Europe

AREA	SUOIDEA	Middle Miocene	Late Moiocne					Pliocene	Gedogic Age
		Astaracian	Vallesian		Turolian			Ruscinian	Mammal Age
		>11.2	11.2~9.5	9.5 ~ 9.0	9.0~8.2	8.2~7.1	7.1~5.3	>5.3	Absolute Age (Ma)
			MN9	MN 10	MN11	MN12	MN13		Mammal Zone
CHINA	*Yunnanochoerus lufengensis*			---	---	---			
	Parachleuastochoerus sinensis		---						
	Chleuastochoerus stehlini			---	---	---	---		
	Hippopotamodon hyotherioides		---	---	---	---	---		
	Microstonyx major					---	---		
	Propotamochoerus parvulus		---						
	Propotamochoerus wui			---	---				
	Molarochoerus yuanmouensis				---	---			
EUROPE	*Albanohyus pygmaeus*	MN4---							
	Taucanamo grandaevum	MN5---							
	Conohyus ebroensis	MN8---							
	Schizochoerus vallesiensis	MN6---	---	---					
	Listriodon splendens	MN6---	---						
	Parachleuastochoerus steinheimensis	MN7---	---						
	Parachleuastochoerus huenermanni		---						
	Propotamochoerus palaeochoerus	MN8---	---	---	---	---	---		
	Propotamochoerus provincialis						---	MN15	
	Hippopotamodon antiquus		---						
	Microstonyx major		---	---	---	---	---		
	Microstonyx erymanthius			---	---	---			
	Eumaiochoerus etruscus				---	---	---		

some modern pig p1 is a variable tooth, some individuals having it, while in some it is absent, and even in the same individual the right tooth row may have one and in the left it is absent. However, detailed observations indicate that in *Sus* these teeth are degenerate, whereas in *Hippopotamodon* from Turkey (Yassioren) and India, the p1 is well formed and is constantly present, so its use as character for classification is credible. "*Dicoryphochoerus binxianensis*" has a small lower canine (it represents a female individual), a short symphysis and p1 is present (Tang et al., 1985). It is unlikely to belong to *Microstonyx*, and we here attribute it to *Hippopotamodon hyotherioides*.

In China the earliest record of *Hippopotamodon hyotherioides* is MN9 (Kaiyuan, Pickford and Liu, 2001) and the latest report is from MN13 (Ertemte, Fahlbusch et al., 1983), and it frequently occurs alongside *Chleuastochoerus*. In Europe the equivalent suid is *Hippopotamodon antiquus*, which is found in MN9, and is bigger than the Chinese species. Both of these lineages probably originated from the Indian Subcontinent, but evolved in different trajectories, the European species retaining a large body size and going extinct after MN9, the Chinese species reducing its body size somewhat and surviving to the latest Miocene. *Hippopotamodon* is also found in Chiang Muan, Thailand (Pickford et al., 2004b).

There are two species of *Propotamochoerus* in Europe. *P. palaeochoerus* has a long range from MN8 to MN13, and *P. provincialis* (= *Postpotamochoerus*) appears in the latest Late Miocene MN13 and is still found in MN15. There is a similar taxon (*Potamochoerus chinhsienensis*) in the Pliocene deposits at Qinxian, northern China (Lee, 1963). The lineage probably spread into China from Europe during the latest Late Miocene, but further study is required. China has two species of *Propotamochoerus*, *P. parvulus* at Kaiyuan (MN9), and *P. wui* at Lufeng (MN10). *P. wui* measures 104% of *P. palaeochoerus*, 110% of *P. provincialis*, 78% of *P. hysudricus*, and there are minor but constant dental morphological differences between them (Made and Han, 1994). *P. wui* is the dominant species of suid in the Lufeng fauna. Pickford and Liu(2001) considered *P. wui* to be a junior synonym of *P. parvulus*. After revision *P. parvulus* from the type locality, Kaiyuan, was left with only three isolated teeth (Pickfordand Liu, 2001). Based on such few specimens, it is difficult to make a detailed comparison, but the holotype from Kaiyuan falls within the range of variation of *P. wui*. *Propotamochoerus* has a long chronological range both in Europe and the Indian Subcontinent, but in China it only extends from MN9 to MN10. The basis for this difference is not clear, but it may be related to erroneous identifications. *Propotamochoerus* seems to have been derived from *Hyotherium* which occurs at Chinji in Pakistan (Pickford,1988).

Molarochoerus is an endemic suid from Yuanmou (MN12). It shows affinities with *Propotamochoerus*, but it is distinguished from this genus by the presence of a unique configuration of the zygomatic arches and the presence of completely molarized p 4/4. It is possible that it was derived from *Propotamochoerus* or a *Propotamochoerus*-like form. It has some progressive characters compared to *Propotamochoerus*(Liu and Pan, 2003; Pickford et al., 2004a). *Molarochoerus* and *Chleuastochoerus* are the dominant suids in the Yuanmou local fauna, the former being a bit more abundant than the latter(Pan et al., 2006).

Microstonyx is a common faunal element in the Late Miocene faunas of Europe, known from many fossiliferous sites. It ranges from MN10 to MN13, and is the preponderant suid in late Late Miocene deposits of Europe where two species are known (*M. major*, *M. erymanthius*). Some authors have subdivided the species into several subspecies (Made, 1997b; Kostopoulos et al., 2001). The systematics of this genus is still subject to debate, the small differences in morphology and dimensions that occur among the *M. e. brevidens* – *M. e. erymanthius* lineages show increase in I 2 ~ 3 length, a moderate increase in M3 length, and a reduction in relative premolar size (Made, 1997b, 2003), the complexity and size increase of M3/3 from late Vallesian to late Turolian (Made et al., 1992; Bonis and Bouvrain, 1996; Kostopoulos et al.,2001), but whether these changes can be attributed to chronology or geography is uncertain. *Microstonyx* from the *Hipparion* fauna of northern China was described by Pearson (1928). *Dicoryphochoerus medius*(Liu et al., 1978) is attributed to *Microstonyx*(Zhang Z Q et al., 2002; Liu et al., 2004). Recently, *Microstonyx major* was unearthed from the Hezheng area, Gansu Province, and confirms the presence of the genus in the Late Miocene of China (Liu et al., 2004). It is clear that *Microstonyx* is a common suid in the Baode mammalian faunas, ranging in age from MN12 to MN13. The Chinese specimens of *Microstonyx* are smaller than their European counterparts, and they have reduced and relatively narrow premolars. Nevertheless, the skull and mandible from Hezheng are very similar to those of *Microstonyx* from Pikermi (Greece) and Kalimance (Bulgaria), except for their smaller size. They approach even more closely the material from Maragheh in Iran (Liu et al., 2004). The genus is unknown from southern China and has not been recorded in northern China in deposits older than MN12. It is likely that the genus spread to China via western Asia early during MN12.

Eumaiochoerus etruscus is an endemic island suid from Tuscany (Italy). It ranges in age from MN12 to MN13. It may have been derived from *M. m. major* and for that reason the species would have split off in the early part of MN12, which has been corroborated by radiometric dating of the V2 level at 8 Ma (Made and Moyá-Solá, 1989).

During the Late Miocene suoids were successful both in Europe and in China. During the Vallesian (MN9 and MN10) the diversity of suoids is higher in Europe than in China, owing to the survival of Palaeochoeridae from the Middle Miocene and previous immigration of suoids from the Indian Subcontinent. During the same period Chinese suoid diversity was low, the only fossils known being from Kaiyuan. During the Turolian, Chinese suoid diversity was higher than in Europe, with the appearance of some endemic genera such as *Chleuastochoerus* and *Molarochoerus*. This higher diversity is related to immigration of suoids from Europe and the Indian Subcontinent followed by autochthonous evolution. *Hippopotamodon* disappeared from Europe after MN9, but continued to survive in China until MN13. During the Late Miocene the suoid fauna of Europe was dominated by two taxa and can be called the *Propotamochoerus-Microstonyx* fauna (Pickford, 1988). In China the situation is more complex, and we tentatively refer to the southern Chinese fauna as the *Propotamochoerus-Chleuastochoerus* fauna and the northern Chinese one as the *Microstonyx-Chleuastochoerus* fauna.

The red clay deposit of northern China began to accumulate about 8 Ma (Lü et al., 2001) or slightly earlier than 7 Ma (Sun et al., 1997), so the fossils from this deposit must be younger than 8 Ma (upper MN12 ~ 13), and belong, in the narrow sense, to the Baode epoch (Li et al., 1984; Zhang Z Q et al.,2002), no fossil suids have been recovered from Bahean Land Mammal Age of northern China (Liu, 2003). In Contrast, southern China suoids are found at Kaiyuan (11 Ma), Lufeng (9 ~ 8 Ma) and Yuanmou (8 ~ 7 Ma), but in MN13 (7.1 ~ 5.3 Ma) no suoids have been found yet. The striking difference between northern and southern Chinese suoid faunas is their stratigraphic distribution. If this difference is not an artefact, the fossil record suggests a gradual spread of suids (*Chleuastochoerus*, *Hippopotamodon*) from south to north during the Late Mioceneof China.

3 Analysis of palaeoecology based on suoid body mass, species diversity and morphology

On the basis of the study of modern suids, most authors accept that they are adapted to a broad variety of environments, which is why they are not often regarded as important for analysis of palaeoecology. However, comparisons of the different configuration and body size etc. indicate that suoids show a diversity of adaptations to the environment, especially the early forms (Legendre, 1986; Pickford, 1993, 1988; Fortelius et al., 1996; Made and Han, 1994). They diverged to produce many offshoots with different characters, most of which developed as adaptations to different environments. We find that these different characters provide useful information about past environments. For example, from the peculiar dental and skull structure of the extant wart hog, *Phacochoerus* we can be sure that it was agrazer (Ewer, 1958).

European suoid body mass calculations are cited from Fortelius et al. (1996, table 28.2) in Table 3. Although their data do not include all European suoids, it represents the group well. For the sake of comparisons, we use the same body mass equation (Body mass $= 10^{1.08} \times (\mathrm{LM2})^{2.99}$) and class divisional criteria defined by Fortelius et al. (1996) for the Chinese Suoidea, the data is provided in Table 3.

Class 1 taxa were probably forest forms. Class 2 did not inhabit open environments. In class 3 the majority of taxa exhibit open habitat associations. Class 4 contains forms from woodland-grassland mosaic habitats and (later on) forms more definitely associated with open woodlands (Fortelius et al., 1996).

In China there are five suoids in class 2. Both *Schizochoerus* from Europe and *Yunnanochoerus* from China have lophodont teeth, *Schizochoerus vallesiensis* is dentally similar to *Listriodon splendens*, and it probably evolved to occupy the niche that the extinction of *L. splendens* left vacant (Pickford, 1978). *Yunnanochoerus* is smaller with lophodont teeth suggesting that it was probably a folivore, and thus a forest type. *Chleuastochoerus* was adapted to life in open steppes. It was omnivorous, but it apparently did not have the rooting behaviour of modern pigs (Pearson, 1928), the thin enamel and the wear facets on the cusps of the cheek teeth suggest

Table 3　Body mass of Chinese and European Suoidea estimates based on second upper molar length

Europe

Taxon/Locality	Reference	Number	Length of M2 (mm)	Body mass (kg)
Class 1 (1 ~ 20 kg)				
Taucanamo grandaevum (Steinheim)		4	9.9	11
Albanohyus pygmaeus (LaGrive)		4	9.2	9
Class 2 (21 ~ 80 kg)				
Conohyus simorrensis (various localities)		3	18.1	69
Parachleuastochoerus huenermanni (various localities)		4	14.9	39
Parachleuastochoerus steinheimensis (Steinheim)		2	18.4	73
Class 3 (81 ~ 200 kg)				
Listriodon cf. *L. splendens* (Pasalar)		21	19.8	91
Schizochoerus vallesiensis (Middle sinap)		1	21.7	120
Propotamochoerus palaeochoerus (various localities)	Hünermann, 1968	21	22	120
Propotamochoerus provincialis (various localities)			23.9	160
Class 4 (201 ~ 1000 kg)				
Microstonyx erymanthius (Pikermi)	Pearson, 1928	13	28.6	270
Microstonyx major (various localities)	Van der Made et al., 1992	12	30.5	330
Hippopotamodon sivalensis (for *H. antiquus*)	Pickford, 1988	6	35.3	510

China

Taxon/Locality	Reference	Number	Length of M2 (mm)	Body mass (kg)
Class2 (21 ~ 80 kg)				
Yunnanochoerus lufengensis (Lufeng)	Made & Han, 1994			45 1)
Parachleuastochoerus sinensis (Kaiyuan)	Pickford & Liu, 2001	3	18.8 2)	78
Chleuastochoerus stehlini (various localities)	Pearson, 1928; Tang et al., 1985; Made & Han, 1994; Pan et al., 2006	40	15.3	42
Propotamochoerus wui (Lufeng)	Made & Han, 1994	31	17.2	60
Propotamochoerus parvulus (Kaiyuan)	Pickford & Liu, 2001	1	17.8 3)	66
Class 3 (81 ~ 200 kg)				
Hippopotamodon hyotherioides (various localities)	Pearson, 1928; Tang et al., 1985; Made & Han, 1994; Pan et al., 2006	12	24.5	171
Molarochoerus yuanmouensis (Yuanmou)	Liu & Pan, 2003	10	21.8	121
Microstonyx major (Hezheng)	Liu et al., 2004	7	25.2	186

Note: 1) The M2 of *Y. lufengensis* is not preserved, the body mass was estimated from the size of m1 (Made & Han, 1994);

2) The M2 of *P. sinensis* is not preserved, but *P. crusafonti* has similar proportion with length of m2 approximately 106% of M2 (Pickford, 1981), the estimated M2 of *P. sinensis* is 18.8 mm;

3) The M2 of *P. parvulus* is not preserved, but *P. wui* has similar proportion with length of M3 approximately 141% of M2 (Made & Han, 1994), the estimated M2 of *P. parvulus* is 17.8 mm.

that it lived on soft food such as tender leaves and soft grass.

Parachleuastochoerus sinensis is similar to *Conohyus*. It is unlikely that *Parachleuastochoerus steinheimensis* in Europe was adapted to dry conditions (Fortelius et al., 1996). In Thailand and China it probably lived in marshy forest.

Propotamochoerus is adapted to forest habitats and *P. provincialis* was adapted to savanna (Thenius, 1950). *Propotamochoerus* survived a long time during which the environment may have changed many times. The molar cusps are not high, the enamel is medium thick, the groove pattern complicated and the furchen are shallow, all of which are features showing that it was probably a typical omnivore and adapted to a wide variety of habitats.

In China there are three suid species belonging to class 3. *Hippopotamodon* and *Microstonyx* lived in open habitats, a suggestion that is accepted by many people (Thenius, 1972; Bernor, 1984; Solounias, 1981; Kostopoulos et al., 2001; Made, 2003). The dental morphology of *Microstonyx* and *Hippopotamodon* is similar to that of *Propotamochoerus* and modern pigs, and they are likely to have been omnivorous suids. *Molarochoerus* has unique features of the dentition and skull showing that it had very strong rostral and masseteric musculature, was well adapted for the 'rooting' behaviour and was eating hard food (Pickford et al., 2004a). It was comparable in some ways to the bush pig (*Potamochoerus*).

In mammals increase in mean body size and a concomitant loss of environmental diversity, usually occurs with the reduction of forest habitats. Fortelius et al. (1996) contrasted modern mammals living in hot and humid, forest environments with those that live in cold, dry, open environments. They showed that between the same or similar species body size is generally smaller in the forested, hot and humid environment.

Suoids of class 1 and class 4 are absent from the Late Miocene faunas of China. In Europe, class 1 is the surviving palaeochoerid from the Middle Miocene. The only Chinese palaeochoerid of Late Miocene age, *Yunnanochoerus lufengensis* is a small and progressive one, but it belongs to class 2, the comparable taxon in Europe is *Schizochoerus vallesiensis* which belongs to class 3. Because of their small body sizes, Chinese *Hippopotamodon* and *Microstonyx* belong to class 3, *Propotamochoerus* species from China are attributed to class 2, unlike their counterparts in Europe which belong to class 4 and 3. The difference of souid Body mass between China and Europe are most likely being due to different palaeoecology, the suoids inhabiting slightly different ecotypes. In late Late Miocene the environment was more closed, more humid and warmer in China than in Europe.

Five taxa from southern China belong to class 2 and two taxa to class 3, in northern China a single species belongs to class 2 and two species to class 3. In southern China the taxonomic diversity of suoids is higher than in northern China and it possesses more species with small body size, suggesting that the environment of southern China was relatively warmer, more humid and more closed than that of northern China. Lufeng and Kaiyuan faunas indicate a warm, humid, subtropical to tropical forest (Qiu, 2002; Made and Han, 1994; Badgley et al., 1988; Dong, 2001). The Yuanmou fauna indicates awarm, humid, subtropical forest to grassland (Qian, 1997; Dong et al., 2003; Zhang et al., 2001a). The northern Chinese faunas suggest the presence of semi-arid steppe with scattered trees (Zhang et al., 2001b; Zhang Z Q et al., 2002). *Chleuastochoerus* is abundant in the Baode mammalian faunas and the Yuanmou local fauna, whereas in the Lufeng local fauna it is rare, and in the Kaiyuan local fauna it is not present. A similar pattern is found in hipparionine horses (Zong, 1997, 1998) which also implies environmental differences.

In Vallesian and early Turolian (MN9 ~ 11), suoids of class 3 in China (south) with only *Hippopotamodon hyotherioides*, in late Turolian (MN12 ~ 13) with appearance of *Molarochoerus* in southern China and *Microstonyx* in northern China, suoid diversity went up to 3 species. In Vallesian (MN9 ~ 10) *Propotamochoerus parvulus* and *Parachleuastochoerus sinensis*

(Kaiyuan) went extinct, suoid diversity of class 2 dropped to zero, but it came back to 3 in early Turolian (MN11 ~ 12) with *Propotamochoerus wui* (Lufeng), *Chleuastochoerus* and *Yunnanochoerus* (Lufeng and Yuanmou) appearance, in late Turolian (MN13) only *Chleuastochoerus* survived in northern China (Fig. 2). Body mass analysis of Chinese suoids of late Miocene indicates there was a relatively stable humid forest environment in southern China during the Vallesian and early Turolian, moreover the environment of northern China was semi-arid steppe with scattered trees.

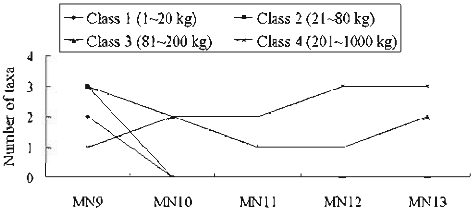

Fig. 1 European suoids distribution of size class 1 ~ 4

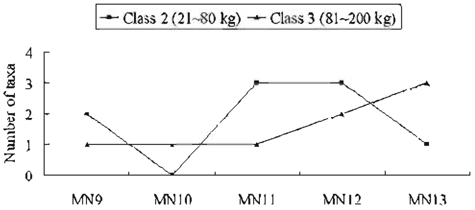

Fig. 2 Chinese suoids distribution of size class 2 ~ 3

In the early Vallesian (MN9), suoid diversity in Europe was high; the four size classes were all present suggesting high ecological diversity, meaning that the environment was likely warm and included humid dense forest. In the late Vallesian (MN10) all palaeochoerids (except *Schizochoerus*) and *Parachleuastochoerus* went extinct, suoid diversity dropped from 9 to 3 species (MN11), the strong decrease reflecting major changes in the palaeoenvironment. The loss of class 1 and class 2 taxa and the appearance of *Microstonyx major* reflect a decrease in dense forest and a change from a humid, warm climate, to a colder, more open steppe-like environment by the late Turolian (Fig. 1).

4 Discussion and conclusion

There were three faunal turnover (extinction) events in the middle and Late Miocene (MN6, MN9, MN12/13), it is likely that these events were synchronous with physical changes (Fortelius et al., 1996). The physical changes noted in China are mostly attributed to uplift of the Tibetan Plateau, which occurred in two main phases at the beginning of the Middle Miocene (Coleman, 1995; Wang et al., 2003) and the beginning of late Late Miocene (about 8 Ma, Lü et al., 2001; Sun and An, 2001; Sun et al., 1997). These two phases of uplift were part of more widespread geotectonic events or phases known as the Styrian and Rhodanian tectonic phases (Scherba, 1987) which caused uplift in many sectors of the Alpine-Himalayan orogenic belt (Pickford, 1996).

In China, Europe and Africa, there was a major faunal change at the end of the Middle Miocene (12 ~ 11 Ma), a well known result of which was the spread of the equid *Hipparion* from the New World to the Old. There appears to have been no major tectonic activity in the Tibetan sector of the Himalayan belt at this time (Song et al., 2001), but elsewhere in the Alpine orogeny there was major activity known as the Attic tectonic phase (12.5 ~ 10 Ma) (Scherba, 1987). The main areas affected by this terminal Middle Miocene phase of tectogenesis were the Carpathians, the Appennines and the Atlas. The effect on the faunas of Africa and Eurasia was marked, with lineages such as *Listriodon*, *Kubanochoerus* and some Palaeochoerids going extinct, and others such as propotamochoerines and equids spreading throughout the regions (Table 2).

The Late Miocene uplift of the Tibetan Plateau (part of the Rhodanian phase, 8 ~ 7 Ma), coincided in time with the onset of the monsoon weather system in the Indian Ocean, particularly affecting the climates of the Indian Subcontinent and eastern Africa (Quade et al., 1989).

With the growth of the Arctic Ice cap to continental proportions, and there could well be a link between the geotectonic event and the growth of the ice cap, in north central Africa, the onset of widespread aridification occurred at this time leading to the formation of the Sahara Desert (Pickford and Senut, 2003). While in China uplift of the Tibetan Plateau caused the onset of the Asian winter monsoon, which transported immense quantities of loess into northern China and caused the climate in northern Asia to become drier (Lü et al., 2001; Sun and An 2001; Sun et al., 1997), a sharp faunal change is seen (Liu, 2003; Zhang Z Q et al., 2002). In southern China the environment turn into an unrest, transitional one from the forest to bushveld (Zhang Y X et al., 2001a, 2002; Dong, 2001, 2003). At the end of the Late Miocene climates became more seasonal and became warmer and more humid (Zhang Z Q et al., 2002; Liu, 2003; Liu et al., 2004; Zhang et al., 2001b). Concomitant these change, the Chinese and European suoids expand to open country woodlands and some spread gradually to northern China, most of them going extinct after MN13 (Table 2).

In the Late Miocene the palaeoenvironments of both China and Europe were affected by global physical events, and the faunal turnover events are almost synchronous in the two areas. The palaeoenvironment ranged from warm, humid, subtropical and tropical forest to semi-arid steppe with scattered trees in southern China and Europe, there is a contrary process in northern China. In the early Vallesian (MN9) both China and Europe were affected by immigrants from the Indian Subcontinent (the immigration seems to have happened just before MN9), the route to southern China was through south-east Asia while to Europe it was through south-western Asia. In the late Vallesian (MN10) and early Turolian (MN11) the suoids evolved independently in southern China and Europe, as there is no connection between their faunas. However, in the late Turolian (MN12, MN13) European and southern Chinese suids migrated to northern China. In the late Turolian (about 7 Ma ago) a great discrepancy in suid faunas occurs between Eurasia and the Indian Subcontinent with the appearance of *Sivachoerus*, *Hippohyus* and *Sivahyus* in the latter area (Pickford, 1988). This suggests that the Indian Subcontinental biome was isolated from Eurasia in the early Vallesian or earlier. In the late Late Miocene northern China mammal was in communication with Europe, but in southern China the situationis not clear, perhaps being isolated from northern China.

This study examines in detail the Chinese and European Late Miocene suoids, as both areas are in the northern hemisphere and there were no major physical barriers between their populations. We observe several differences between the histories of the suoids in each area, which we consider to reflect latitudinal and environmental signals (ultimately controlled by palaeoclimate) rather than the presence of physical barriers to the spread of genes.

There are many gaps in the fossil suoid record, and new evidence is needed to refine our understanding of this group of mammals.

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