

Major events of Paleogene mammal radiation in China

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On the basis of mammalian biostratigraphical study, the Paleogene was subdivided into 11 land mammal ages in China: the Paleocene Shanghuan, Nongshanian and Gashatan; the Eocene Lingchan, Arshantan, Irдинmanhan, Sharamuruniаn, Naduan and Ulangochuan; and the Oligocene Ulantatalian and Tabenbulukian. Biostratigraphical correlation with North American Land Mammal Ages, plus some palaeomagnetic, isotopic and radiometric results, established the indirect connection with the international time scale. Under this biochronological framework, the compositional change of mammalian faunas and the evolution of major groups are discussed. Three stages are recognized in the Paleogene mammalian radiation: (1) the Paleocene flourishing of archaic groups, (2) the Eocene rising and development of modern major groups and (3) the Oligocene faunal reorganization. During the Paleocene, the mammalian radiation was dominated by the archaic groups and the faunas showed apparent endemism. The radiation was characterized by faunal turnovers due to the flourishing of different families in archaic groups. During this period, ancestral forms of modern glires emerged and the first Rodentiaformes appeared in the late Late Paleocene. Such faunal changes corresponded to the successive rise of temperature after the transition from the Mesozoic to the Cenozoic. The Initial Eocene Thermal Maximum resulted in a significant decrease of the archaic groups and the faunal composition became more similar to that of modern ones. At the beginning of the Eocene, Artiodactyla and Euprimates appeared and Rodentia and Perissodactyla began to differentiate. During the Eocene, Mixodontia, Arctostyloidae, Dinocerata, Pantodonta, Tillodontia and Creodontia disappeared in succession. Perissodactyla became the dominant group in the faunas. The faunal turnovers were characterized by the alteration of dominant families due to the appearance, differentiation and flourishing of families in modern orders. The severe cooling events at the Eocene–Oligocene transition resulted in the development of open grassland, that further contributed to the great mammalian faunal turnover. The perissodactyl-dominant Eocene faunas were replaced by the rodent/lagomorph-dominant Oligocene faunas. The appearance and radiation of hypsodont mammal groups characterized the mammalian evolution in the Oligocene. Copyright © 2007 John Wiley & Sons, Ltd.

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1. FRAMEWORK OF CHINESE MAMMALIAN BIOCHRONOLOGY

Paleogene terrestrial stratigraphy and palaeontology in western North America has been the most thoroughly studied of anywhere in the world. The land mammal ages proposed on the basis of mammalian biostratigraphy formed the foundation for the discussion of related issues (Archibald *et al.* 1987; Emry *et al.* 1987; Krishtalka *et al.* 1987; Tedford *et al.* 1987, 2004; Lofgren *et al.* 2004; Prothero and Emry 2004; Robison *et al.* 2004). Palaeomagnetic studies, isotopic work and radiometric dating have established the correlation of North American Land Mammal Ages with the international time scale (Woodburne 2004). Thus, the North American Land Mammal Ages were used as references in the intercontinental biochronological correlation of the continental Paleogene.

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TIME (Ma)	CHRONS	POLARITY	EPOCH	AGE	NORTH AMERICAN LAND MAMMAL AGES	CHINESE LAND MAMMAL AGES	ASIAN LAND MAMMAL AGES
			MIOCENE				
24	C6C		OLIGOCENE	LATE CHATTIAN	Arikareean	Tabenbulukian	Tabenbulukian
	C7						
	C7A						
26	C8						
28	C9						
	C10		EARLY RUPELIAN	Whitneyan	Ulantatalian	Hсандgolian	
30	C11						
32	C12						
34	C13		LATE PRIABONIAN	Chadronian	Ulangochuan	Ergilian	
	C15						
36	C16						
38	C17		MIDDLE BARTONIAN	Duchesnean	Naduan	Sharamurunian	
40	C18						
42	C19						
44	C20		LUTETIAN	Uintan	Irdinmanhan	Irdinmanhan	
46	C21						
48	C22						
50	C23		EARLY YPRESIAN	Bridgerian	Arshantan	Arshantan	
52	C24						
54	C25						
56	C26		LATE SELANDIAN	Clarkforkian	Gashatan	Gashatan	
58	C27						
60	C28						
62	C29		EARLY DANIAN	Torrejonian	Shanghuan	Shanghuan	
64	C29						
			CRETACEOUS		Lancian		

The age determination of Chinese Paleogene continental deposits has relied on biostratigraphical studies for a long time. The mammalian biostratigraphical work established the base of the framework for Chinese Paleogene biochronology. Ever since Romer (1966) proposed some Asian land mammal ages, the framework of Chinese Paleogene Land Mammal Ages has been recognized and improved (Li and Ting 1983; Tong 1989; Wang 1992, Tong *et al.* 1995; 1997a,b,c; Ting 1998). Many of these studies have been used in discussions on the intercontinental biostratigraphic correlation and mammalian dispersal (e.g. Archibald *et al.* 1987; Berggren and Prothero 1992; Lucas and Williamson 1995; Beard 1998; Beard and Dawson 1999; Lofgren *et al.* 2004). Some were adopted as representatives of Asian land mammal ages (Luterbacher *et al.* 2004).

In this paper, 11 land mammal ages are adopted in the subdivision of Chinese Paleogene biostratigraphy. They are: the Paleocene Shanghuan, Nongshanian and Gashatan; the Eocene Lingchan, Arshantan, Irdinmanhan, Sharamuronian, Naduan and Ulangochuan; and the Oligocene Ulantatalian and Tabenbulukian. The definition and correlation of these land mammal ages follow Tong *et al.* (1995), Wang (1997c) and Ting (1998), except for those discussed below. The lack of age constraints of Chinese Paleogene mammal-bearing strata has hampered the direct correlation with the international standard. Attempts have been made to correlate Chinese Paleogene Land Mammal Ages with North American Land Mammal Ages on the basis of faunal comparison (Tong *et al.* 1995; Ting 1998; Wang *et al.* 1998). Such correlations provide an indirect connection between Chinese Paleogene Land Mammal Ages with the international standard (Figure 1).

1.1. Paleocene

1.1.1. Subdivision

Tong *et al.* (1995) incorporated the Gashatan into the Nongshanian and subdivided the Paleocene into two land mammal ages: the Shanghuan and the Nongshanian. However, the Nongshanian mammalian fauna is clearly distinguishable from the Gashatan fauna (Wang *et al.* 1998). Many researchers retained the Gashatan as a separate mammal age (Meng and McKenna 1998; Ting 1998; Wang *et al.* 1998; Bowen *et al.* 2002).

1.1.2. Correlation with North American Land Mammal Ages

Ting (1998) correlated the Shanghuan, Nongshanian and Gashatan with the North American Puercan and Torrejonian, Tiffanian and Clarkforkian, respectively. But Tong *et al.* (1995) and Wang *et al.* (1998) correlated the Shanghuan with the Puercan to middle Torrejonian based on the fossil mammals, which is supported by the palaeomagnetic results from the Nanxiong and Shanyang basins (Zhao *et al.* 1991; Xue *et al.* 1994, 1996) and a K–Ar radiometric date from Xinzhou, Hubei (Wang *et al.* 1998). Wang *et al.* (1998) further correlated the Nongshanian with the late Torrejonian to middle Tiffanian, and the Gashatan with the late Tiffanian and Clarkforkian. Such correlations were accepted and followed by Beard (1998) and Beard and Dawson (1999).

1.2. Eocene

1.2.1. Determination of Paleocene–Eocene (P–E) boundary

A carbon isotope excursion in Chron 24r has been chosen as the criterion for the P–E boundary (Magioncalda *et al.* 2004). Such a boundary is located at the base of the Wasatchian in North America (Koch *et al.* 1992; Bowen *et al.* 2001). Chemostratigraphic work at Lingcha, Hengyang Basin of Hunan Province recognized the carbon isotope excursion in the Chron 24r at the base of fossil-bearing beds (Bowen *et al.* 2002, 2005; Ting *et al.* 2003), which set an accurate reference to correlation with the international geological time scale.



Figure 1. Chinese Paleogene Land Mammal Ages and their correlation. North American Paleogene Land Mammal Ages and their correlation with International Geological Time Scale are reproduced from Woodburne (2004). The age was calibrated according to the International Stratigraphic Chart (Luterbacher *et al.* 2004).

1.2.2. Subdivision

Six land mammal ages have been recognized in the Eocene epoch. They are: Lingchan, Arshantan, Irdinmanhan, Sharamurunian, Naduan and Ulangochuan. Since some of southern China's local fauna could not be included in either the Sharamurunian or Ulangochuan, Tong (1989) proposed the Naduan as an intermediate age between the Sharamurunian and Ulangochuan. Tong *et al.* (1995) considered the Ulangochuan as an Early Oligocene land mammal age. However, this mammal age was later considered to be late Eocene, and correlated with the North American Chadronian (Wang 1997b).

1.3. Oligocene

The Oligocene has two land mammal ages: the Ulantatalian and the Tabenbulukian (Tong *et al.* 1995). Wang (1997c) used the Hsandagolian instead of the Ulantatalian. However, since the upper part of the Hsanda Gol Formation bearing the Hsandagolian fauna in Mongolia can be correlated to the deposits with the Tabenbulukian fauna in China (Wang 1997a), the Hsandagolian may overlap with the Tabenbulukian. In this paper, we follow Tong *et al.* (1995) and use the Ulantatalian as the early Oligocene land mammal age.

Studies on the Chinese Paleogene mammals can provide significant information for understanding Cenozoic mammalian history. These studies have revealed that many archaic and modern mammal groups originated in Asia (Li *et al.* 1987; Meng *et al.* 1994; Beard 1998; Wang *et al.* 1998; Beard and Dawson 1999). However, the change in the faunal composition through time and the evolution of major groups in the Paleogene have not been investigated. This paper will review the compositional changes of Chinese Paleogene faunas and discuss related issues.

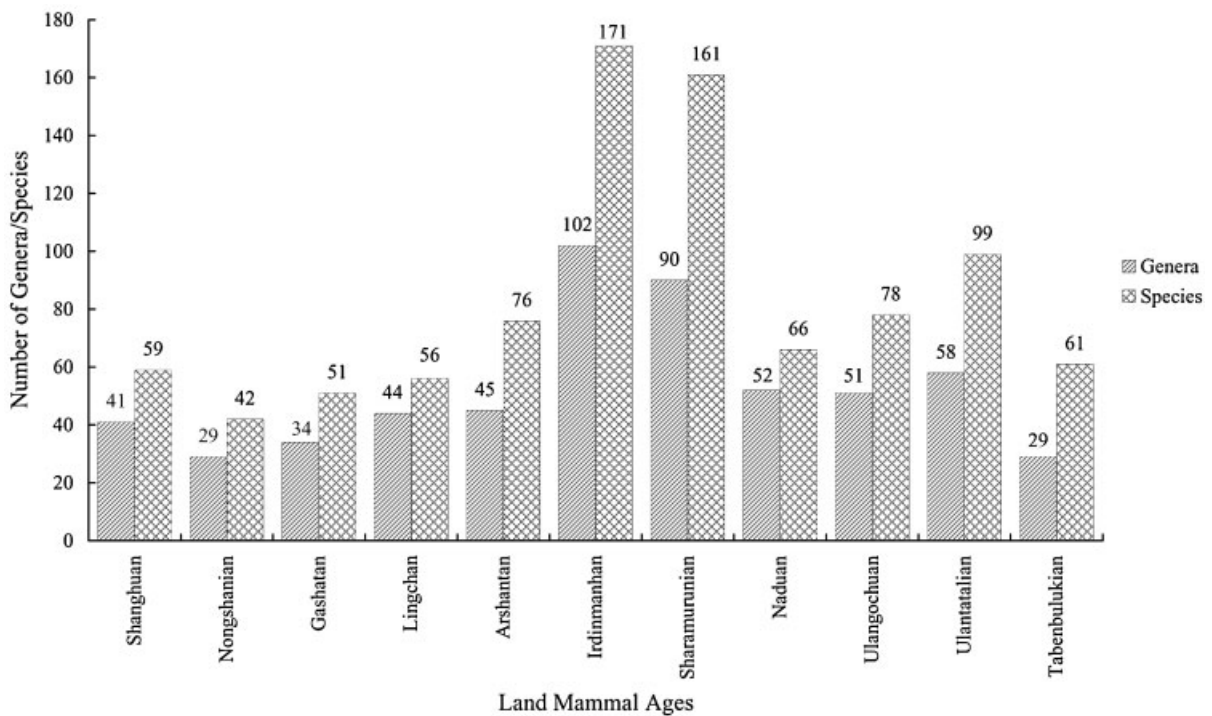


Figure 2. A histogram showing the numbers of genera and species in each land mammal age for the Chinese Paleogene.

2. COMPOSITION AND CHANGE OF MAMMALIAN FAUNAS

Li and Ting (1983) and Russell and Zhai (1987) summarized Chinese and Asian Paleogene mammal faunas. Since then, great progress has been made. So far, 758 species assigned to 386 genera have been described from the Chinese Paleogene. Figure 2 shows the number of species and genera in each land mammal age.

According to Figure 2, the Irdinmanhan and Sharamurunian have more than twice the number of genera and species than the other land mammal ages. The faunal composition of different land mammal ages is quite different (Figure 3). Among them, Primates, the insectivorous mammals, and the carnivorous mammals including Mesonychia, Creodonta and Carnivora, occupied a small proportion, while the number of herbivorous ungulates, glires and Asian endemic Anagalida varied to a great extent.

2.1. Paleocene

The Paleocene mammal fauna is characterized by the existence of many species of archaic groups. Approximately 80% of species in each land mammal age belong to the extinct orders, including Anagalida, Mixodontia and Mimotonida.

2.1.1. Shanghuan

The latest Cretaceous mammals from China (and even eastern Asia) have not been documented, and no closely related ancestral forms of the Shanghuan mammals are recognized. Nearly all of the higher level groups made their first appearance in China. Among them, Anagalida and Mimotonida are exclusively known from Asia, and the earliest and most primitive representatives of Pantodonta, Tillodontia and Mesonychia appeared in this land mammal age (Gingerich 1981; Ting and Li 1987; De Muizon and Marshall 1992; Wang and Jin 2004; Figure 3). All the families are recorded for the first time, and Astigalidae (Anagalida) and Bemalambdidae (Pantodonta) have their occurrence only in the Shanghuan (Zhou *et al.* 1977; Zhang and Tong 1981; Wang *et al.* 1998).

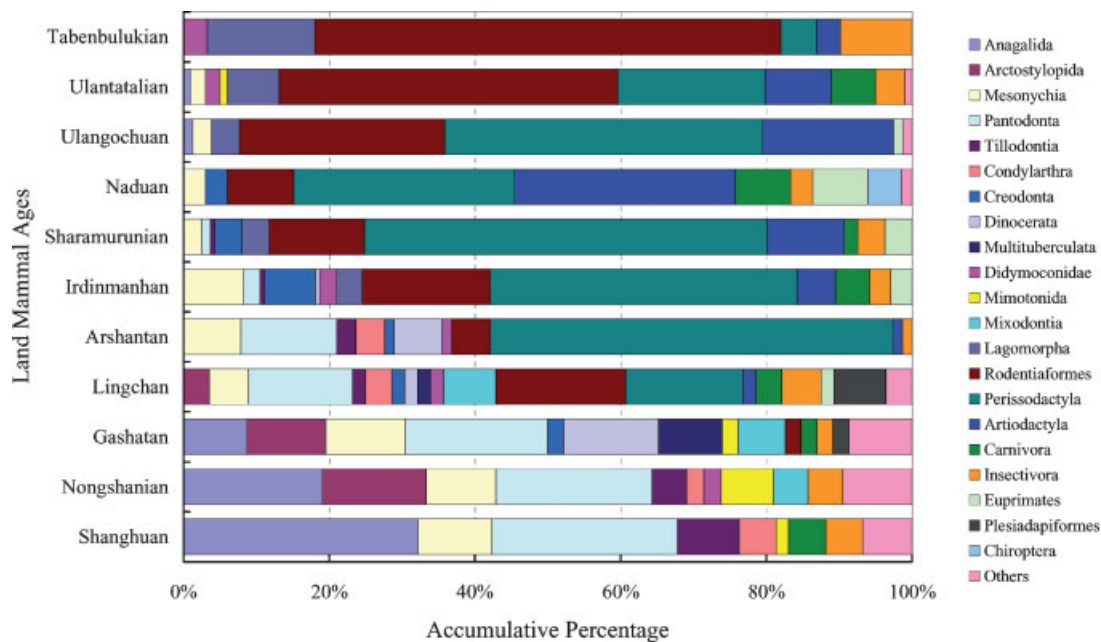


Figure 3. Faunal composition (in percentage of species) for Chinese Paleogene Land Mammal Ages.

2.1.2. Nongshanian

The representatives of Mixodontia, Didymoconidae and Arctostylopida first appeared in the Nongshanian (Li 1977; Zheng 1979a,b; Li *et al.* 1987; Cifelli *et al.* 1989; Figure 3). Most mammalian families of the Shanghuan were recorded in the Nongshanian (Figure 4), but over 85% of Shanghuan genera disappeared. Nearly 80% of the reported Nongshanian genera made their first appearance in China (Figure 5). Anagalida, Pantodonta and Tillodontia greatly decreased in species number and proportion (Figure 3). Among Pantodonta, Bemalambdidae which flourished in the Shanghuan disappeared, and both Pastoralodontidae and Pantolambdodontidae of Pantodonta became their substitute (Wang *et al.* 1998).

2.1.3. Gashatan

Archaic groups still dominated the Gashatan mammal fauna, but decreased in proportion (Figure 3). Family level taxa did not greatly change from the Nongshanian through Gashatan, but genera were replaced to a great extent (Figures 4 and 5). In the Gashatan, Hyaenodontidae (Creodonta), Coryphodontidae (Pantodonta), Dinocerata, Rodentiaformes, Carpolestidae and Nyctitheriidae made their first appearance (Tong 1978; Zhai 1978a; Meng *et al.* 1994, 1998; Smith *et al.* 2004; Missiaen and Smith 2005). Meanwhile, members of Mesonychidae (Mesonychia) and Pastoralodontidae became larger in body size (Chow and Wang 1978; Zhou and Qi 1978; Wang *et al.* 1992).

2.2. Eocene

From the Eocene, the composition of mammalian faunas has changed significantly. The proportion of archaic groups declined rapidly and further decreased later, whereas the proportion of modern mammalian groups increased prominently. Perissodactyla, Artiodactyla, Lagomorpha and Euprimates first appeared at the beginning of the Eocene.

2.2.1. Lingchan

The Lingchan mammalian fauna greatly changed from that of the Gashatan. The proportion of archaic groups decreased from nearly 80% in Gashatan to less than 45% (Figure 3). Thirty-three percent of mammal families recorded in the Gashatan had now disappeared, whereas 69% of Lingchan mammal families newly appeared

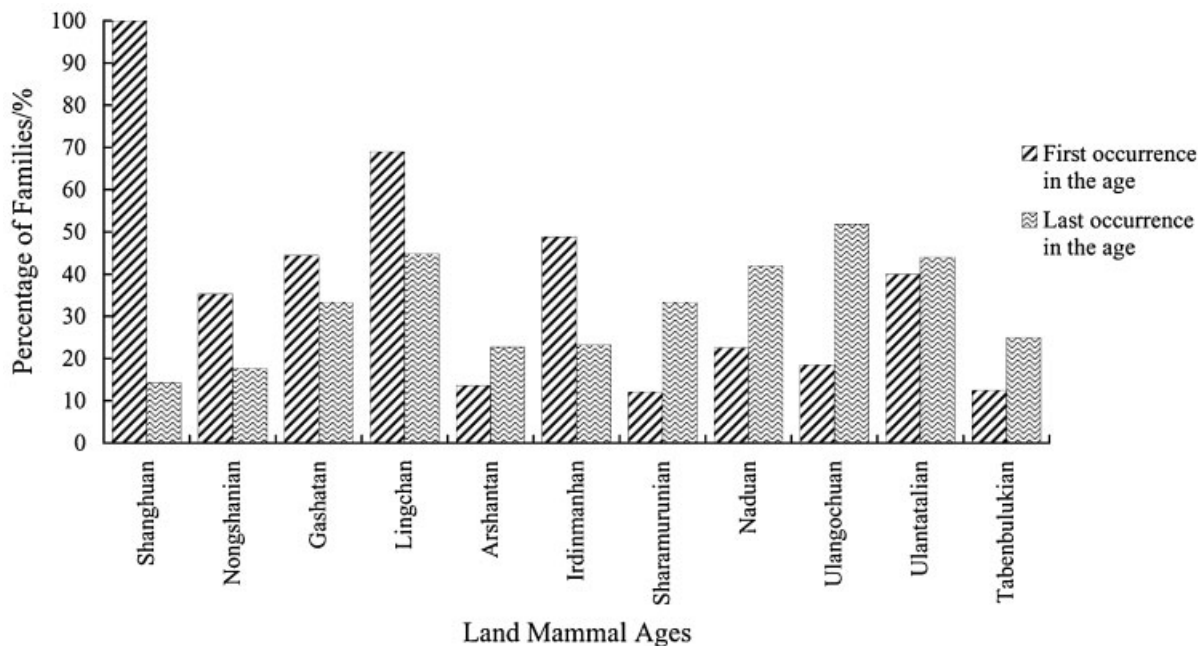


Figure 4. A histogram showing the change of faunal composition (in percentage of families) for Chinese Paleogene Land Mammal Ages.

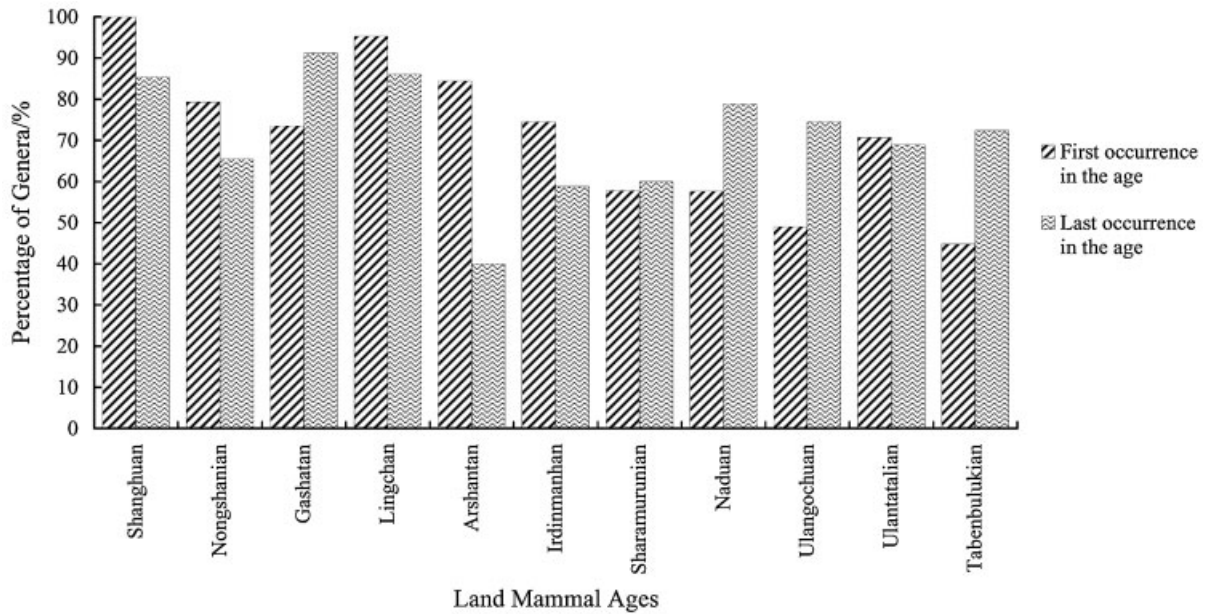


Figure 5. A histogram showing the change of faunal composition (in percentage of genera) for Chinese Paleogene Land Mammal Ages.

(Figure 4). Based on the number of genera, the mammalian fauna shows a greater change in composition: 91% of the Gashatan genera disappeared, whereas 95% of the Lingchan genera are new taxa (Figure 5). Differentiation of Rodentia and Perissodactyla and appearance of Euprimates characterized the Lingchan land mammal age (Chow and Li 1963, 1965; Li *et al.* 1979; Dawson *et al.* 1984; Ting 1993; Hu 1995; Tong and Dawson 1995; Wang and Tong 1996; Guo *et al.* 2000; Ni *et al.* 2004). In addition, Artiodactyla made its first appearance in the Lingchan (Tong and Wang 1998; Figure 3).

2.2.2. Arshantan

The proportion of archaic groups in the Arshantan mammal fauna further decreased to less than 37%. Mixodontia and Arctostylopida disappeared, but large herbivorous archaic mammals, such as Coryphodontidae and Dinocerata, still maintained a small proportion. In modern mammal groups, Perissodactyla with great diversification dominated the fauna and rose to 55% (Figure 3). The newly appeared families of perissodactyls: Brontotheriidae, Lophialetidae and Deperetellidae, greatly flourished (Li and Ting 1983; Qi 1987).

2.2.3. Irdinmanhan

Archaic groups in the Irdinmanhan mammal fauna only have a proportion of 21%. Condylarthra has disappeared from the Chinese Paleogene mammal faunas since the Irdinmanhan. Lagomorpha emerged and were differentiated to some extent (Li 1965; Tong and Lei 1987; Tong 1997; Zhang *et al.* 2001). Rodentia had a great diversity and are recorded by nine families. At species level they formed 17% of the fauna. Among perissodactyls, Brontotheriidae, Lophialetidae and Deperetellidae continued flourishing in the Irdinmanhan, while Rhinocerotidae appeared, and Amarynodontidae and Hyracodontidae began to rapidly differentiate. Eosimiidae (Euprimates) emerged (Figure 3) and began to differentiate (Beard *et al.* 1994, 1996; Beard and Wang 2004). Cricetidae and Zapodidae of Rodentia, and Helohyidae of Artiodactyla appeared in the Irdinmanhan.

2.2.4. Sharamurunian

In the Sharamurunian, only 8% of the total species are archaic mammals. Dinocerata became extinct. Artiodactyla, especially Anthracotheriidae, became more diversified and the ruminant artiodactyls appeared. Perissodactyla is

still dominant in the fauna and Amynodontidae became the most common forms in the order. Among the rodents, Eomyidae emerged, while Tamquammyidae declined. The faunal composition at family level is apparently different from that of the Irudinmanhan.

2.2.5. *Naduan*

Pantodonta and Tillodontia of the archaic groups became extinct in the Naduan. In modern mammal groups, Lophialetidae and Deperetellidae of Perissodactyla which had previously flourished began to decline. Anthracotheriidae continued to flourish in the Naduan, while Lophiomerycidae, Gelocidae and Tayassuidae appeared and initially differentiated. The earliest representative of the Suidae was also found in the Naduan (Liu 2001).

2.2.6. *Ulangochuan*

Creodonta became extinct in the Ulangochuan, whereas Lophiomerycidae and Entelodontidae flourished (Miao 1982; Li and Ting 1983; Wang and Zhang 1983). Perissodactyla continued flourishing with Amynodontidae as the dominant form. Rodentia further differentiated and Ochotonidae of Lagomorpha appeared.

2.3. *Oligocene*

Compared with the Eocene mammal faunas, the Oligocene ones greatly changed in faunal composition. Species of Rodentia and Lagomorpha form over 50% of the total species. Perissodactyla declined. Families common in the Eocene, such as Deperetellidae, Lophialetidae and Brontotheriidae, disappeared, and Amynodontidae became rare. Early members of Bovidae and Cervidae emerged (Huang 1985).

2.3.1. *Ulantatalian*

Compared with late Eocene Ulangochuan fauna, the Ulantatalian one changed significantly in composition. Fifty-five percent of families present in the Ulangochuan disappeared in the Ulantatalian, and newly emerged families comprise 40% of the Ulantatalian ones. Some common Eocene families became extinct or rare, but Chalicotheriidae and Indricotheriidae (Perissodactyla) further developed (Xu and Wang 1978; Zhai 1978c). In Lagomorpha, Ochotonidae were not represented by a large number of species, but they are widely distributed and very abundant in the number of individuals. Since the Ulantatalian, Rodentia have flourished and radiated. The species of Rodentia rises to 46% of the total species in the fauna. Among this order, Ctenodactylidae flourished well, Tsaganomyidae appeared and bloomed. Representatives of Aplodontidae also appeared (Wang *et al.* 1981; Wang 1987; Wang and Wang 1991). Bovidae and Cervidae of Artiodactyla emerged in this land mammal age (Huang 1985).

2.3.2. *Tabenbulukian*

Mesonychia, Anagalida and Mimotonida of the archaic groups disappeared in the Tabenbulukian. Perissodactyla decreased in quantity. Most artiodactyls are bovids and cervids. Lagomorpha further differentiated. Rodentia continued to flourish, and became the only dominant group, with 62% of the total species. Zapodidae and Ctenodactylidae are the richest families, whereas the previously flourishing Tsaganomyidae declined.

3. EVOLUTION OF MAJOR GROUPS

Radiation of Paleogene mammals in China was characterized by the evolution of major groups and alteration of dominant groups. It began with the fauna dominated by archaic groups, and followed by the appearance and differentiation of modern groups and eventually formed the modern group dominated faunas. Different groups had their own history, which varied notably in the time and scale of radiation.

3.1. *Anagalida*

Anagalida appeared and apparently differentiated in the Shanghuan. Anagalidae emerged earlier than Pseudictopidae and Astigalidae (Wang *et al.* 1998). In the Nongshanian, Astigalidae disappeared, and Pseudictopidae and Anagalidae decreased in the number of genera and species. In the Gashatan, only one genus in each family has been documented. They had no record later, except in the Ulangochuan and Ulantatlian (Simpson 1931; Bohlin 1951; McKenna 1963). In general, *Anagalida* were most abundant in the Early to early Late Paleocene, and began to decline in the late Late Paleocene. From the Eocene, *Anagalida* became almost extinct (Figure 6).

3.2. *Arctostylopida*

Arctostylopida first appeared and began to differentiate in the early Nongshanian in southern China (Zheng 1979b), and formed five species of three genera in the late Nongshanian (Tang and Yan 1976; Zheng and Huang 1986; Huang and Zheng 2003). This group kept flourishing in the Gashatan with five species of four genera (Tang and Yan 1976; Cifelli *et al.* 1989; Huang and Zheng 1997; Huang 2003). *Arctostylopida* began to decline in the Lingchan, and only two species of two genera have been reported (Zhai 1978b; Huang *et al.* 2001). At the end of the Lingchan, this group disappeared (Figure 6). Cifelli *et al.* (1989) separated *Arctostylopidae* from the *Notoungulata* and included it in its own order, but the origin of *arctostylopids* remains mysterious. According to the available information, it is reasonable that eastern Asia was the centre of origin and radiation of *Arctostylopida*. *Arctostylopida* emigrated to North America during the late Late Paleocene (initial Gashatan or late Tiffanian). Only one *arctostylopid* species has been named from the North American Paleogene, but this group persisted into the Early Eocene Wasatchian (Zack 2004).

3.3. *Glires*

Phylogenetic study of *Glires* suggested that the Asian endemic *Mixodontia* and *Mimotonida* are closely related to *Rodentia* and *Lagomorpha*, respectively (Li *et al.* 1987; Li and Ting 1993; Meng *et al.* 2003). The earliest record of

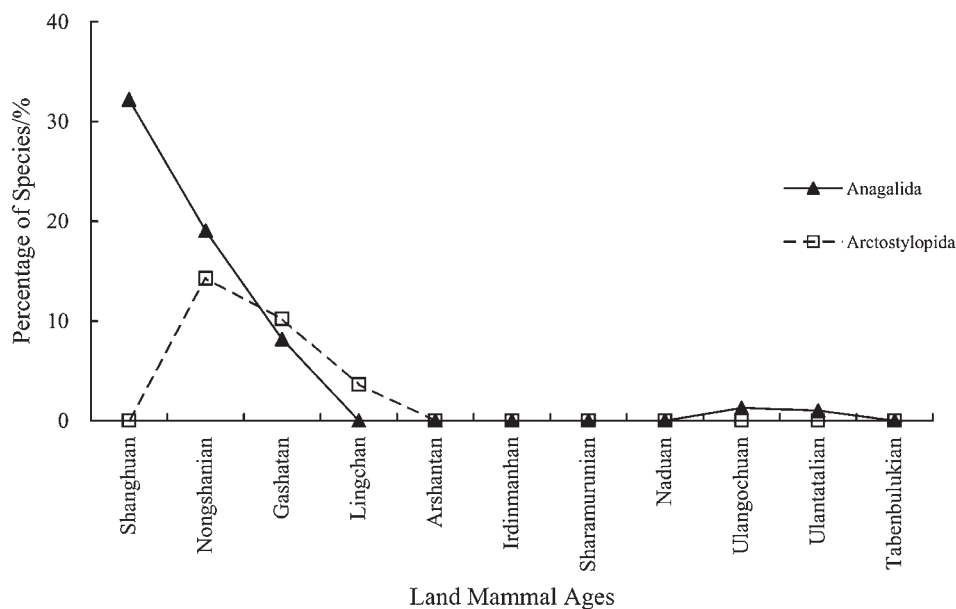


Figure 6. Changes of *Anagalida* and *Arctostylopida* faunas (in percentage of species) through the Chinese Paleogene Land Mammal Ages.

Glire is a mimotonid from the late Shanghuan. In the Nongshanian, three species of Mimotonida have been documented. The mimotonids began to decline in the Gashatan, and have virtually disappeared since the Eocene but for an exceptional latest record in the Ulantatalian (Figure 7). Mixodontia first appeared in the early Nongshanian (only one genus), and the Gashatan and Lingchan have two genera each. They disappeared in the Arshantan.

The major radiation of Glire occurred after the emergence of Rodentia. The earliest representative of Rodentiaformes is from the Gashatan, with a single species (Meng *et al.* 1994). The Lingchan Rodentia differentiated to 10 species of nine genera in four families (Russell and Zhai, 1987; Hu 1995; Tong and Dawson 1995; Guo *et al.* 2000). The proportion of rodents in the fauna did not change much in the Middle and Late Eocene, except in the Ulangochuan land mammal age. Rodentia had a great diversity in the Irdinmanhan and Sharamurunian. Fossils of nine and seven families have been found from the Irdinmanhan and Sharamurunian, respectively. Cricetidae, Tamquammyidae and Zapodidae appeared in this interval. Since the Ulangochuan, the proportion of Rodentia in the fauna has successively increased (Figure 7). With the extinction of Yuomyidae, Ischryomyidae and Gobiomyidae, major rodent families changed in the Ulantatalian. Ctenodactylidae and Tsaganomyidae flourished and Aplodontidae appeared. In the Tabenbulukian, rodents continued to flourish and Ctenodactylidae and Zapodidae became the dominant groups.

Lagomorpha first appeared in the Irdinmanhan and Leporidae had dominated the order until the end of the Eocene. However, Ochotonidae took over dominance in the Ulantatalian.

The Asian origin of Glire has been widely accepted. Two archaic groups had their history only in Asia (Carroll 1988). Soon after their appearance in the late Late Paleocene, rodents migrated into North America and differentiated there (Dawson and Beard 1995). Since the Eocene, faunal exchange in Holarctica became more frequent. Rodents migrated between Asia and North America on several occasions. For example Paramyidae might have migrated into Asia from North America at the beginning of the Eocene.

3.4. Ungulates

Ungulates usually play an important role in the mammalian faunas. From the early Paleocene, archaic ungulates appeared and began to differentiate.

Pantodonta appeared in the Shanghuan, and differentiated into four families in the late Shanghuan. Among these families, Bemalambdidae is the most common and widely distributed group in the Shanghuan. It disappeared in the Nongshanian, and Pantolambdodontidae and Pastoralodontidae flourished instead. In the Gashatan, Coryphodontidae

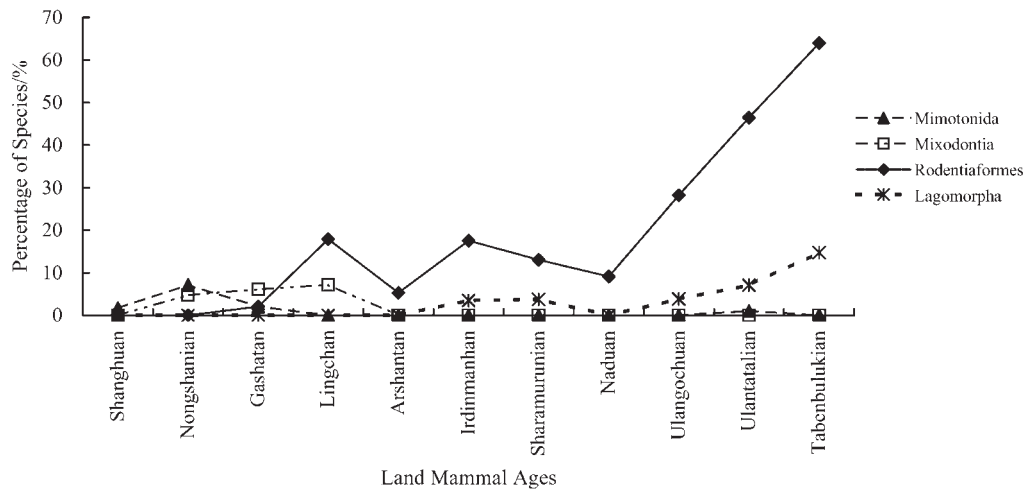


Figure 7. Changes of Glire faunas (in percentage of species) through the Chinese Paleogene Land Mammal Ages.

emerged. It became the dominant pantodont group after the extinction of Pastoralodontidae and Harpyodidae at the end of the Gashatan. This family declined in the Irдинmanhan, and completely disappeared in the Naduan (Figure 8).

Tillodontia were less abundant than Pantodonta in both number and proportion of the fauna, but had a similar history. They appeared and began to differentiate in the Shanghuan, then reduced in number and proportion in the fauna and became extinct in the Naduan (Figure 8). This group did not migrate into North America until the late Late Paleocene.

Another archaic herbivorous group, Dinocerata, had a short history on the Earth, with relatively low diversity. They appeared in the Gashatan and became extinct in the Sharamurunion (Figure 8).

Modern ungulates began their history in China in the Eocene. Both Perissodactyla and Artiodactyla appeared in the Early Eocene Lingchan. In the Paleogene mammal faunas, perissodactyls exceeded artiodactyls in both diversity and number of individuals, in contrast to the late Cenozoic faunas dominated by artiodactyls (Figure 8).

Soon after their appearance in the Lingchan, Perissodactyla began to differentiate and formed the Palaeotheriidae, Helaletidae, Isectolophidae and Lophialetidae. In the Arshantan, Perissodactyla flourished with high diversity and formed a large proportion of the fauna (Figure 8). Brontotheriidae, Deperetellidae, Hyracodontidae, Eomoropidae and Amynodontidae all appeared. The proportion of Perissodactyla in the Irдинmanhan fauna is smaller than in the Arshantan fauna, but the diversity of perissodactyls in the Irдинmanhan (72 species) is much higher than that in the Arshantan (42 species). All the families other than Palaeotheriidae flourished and the Rhinocerotidae first appeared in the Irдинmanhan. Perissodactyla in the Sharamurunion rose to 89 species. Members of Chalicotheriidae appeared, but Helaletidae and Eomoropidae became extinct. Perissodactyla decreased in both species number and proportion in the fauna in the Naduan, but the group was still dominant in the fauna. Perissodactyla kept flourishing in the Ulangochuan, but Deperetellidae and Lophialetidae declined, and Amynodontidae became the most common perissodactyl group. Since the Ulantatalian, Perissodactyla decreased greatly in both the number of genera and species and the proportion of the fauna. Deperetellidae and Lophialetidae disappeared, while Chalicotheriidae and Indricotheriidae flourished. In the Tabenbulukian, only members of Chalicotheriidae, Rhinocerotidae and Indricotheriidae remained.

After their appearance in the Lingchan, Artiodactyla did not greatly radiate until the Sharamurunion when Anthracotheriidae differentiated into nine species of six genera (Figure 8). In the Naduan, Anthracotheriidae

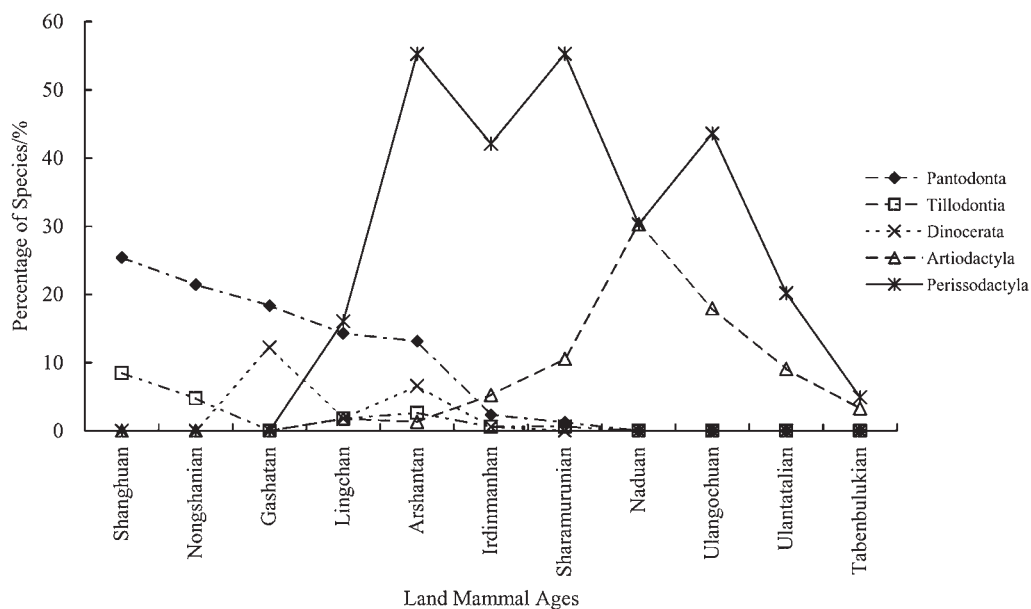


Figure 8. Changes of ungulate faunas (in percentage of species) through the Chinese Paleogene Land Mammal Ages.

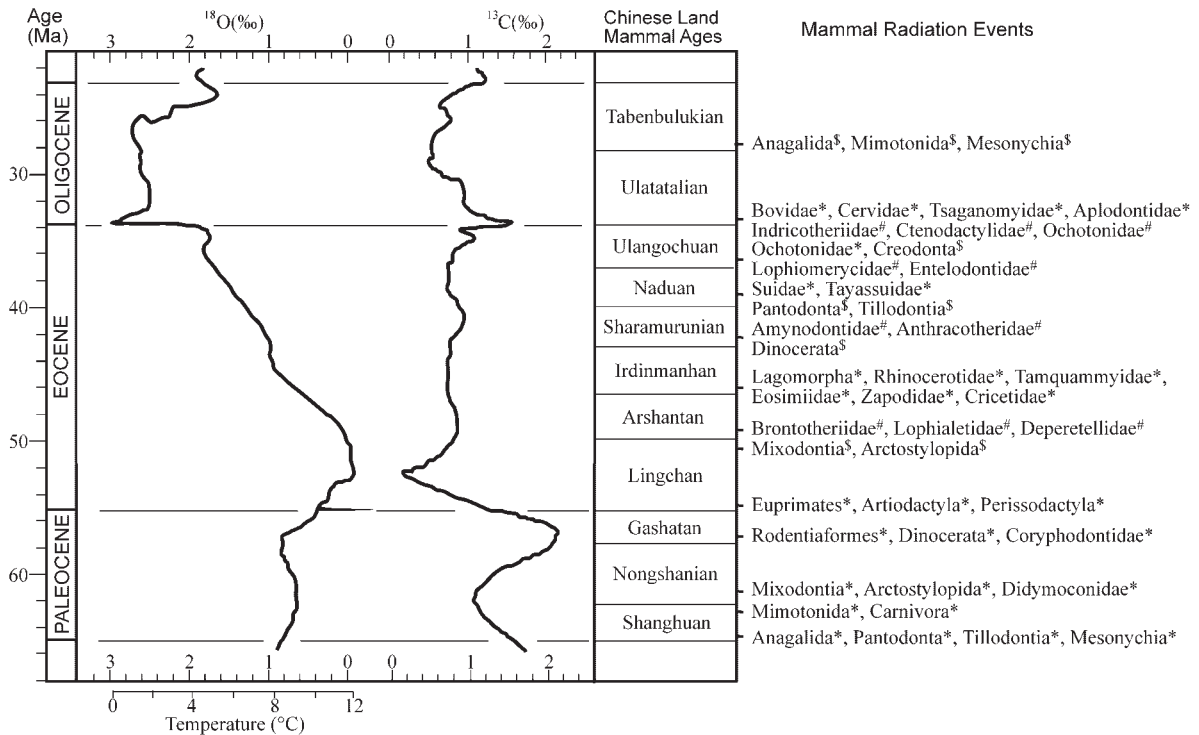


Figure 9. Major events in the radiation of Paleogene mammals in China. Deep sea oxygen and carbon isotope records are reproduced from Zachos *et al.* (2001). * = taxa first appeared; # = taxa began to flourish; \$ = taxa became extinct.

continued to flourish; Tayassuidae began to differentiate; and the earliest member of Suidae emerged. In the Ulangochuan, Anthracotheriidae declined and Tayassuidae disappeared, while Lophiomerycidae and Entelodontidae were well differentiated. Artiodactyla as a whole declined in the Ulatatalian, but the early representatives of Bovidae and Cervidae appeared. Both families began their radiation in the Neogene to become the dominant ungulates.

4. CONCLUSIONS

The radiation of Chinese Paleogene mammals is characterized by the Paleocene flourish of archaic groups, the Eocene rising and development of modern major groups and the Oligocene faunal reorganization. Figure 9 summarizes the major radiation events of Paleogene mammalian evolution in China.

At the beginning of the Paleocene, some archaic mammal groups radiated and formed a number of groups without known ancestral forms in the Mesozoic. In the early Shanghuan, Bemalambdidae and Anagalidae bloomed. In the late Shanghuan, members of Astigalidae and Pseudictopidae appeared. In the Nongshanian, Pantolambdodontidae and Pastoralodontidae replaced Bemalambdidae to become the dominant groups in the order Pantodonta. At the same time, Anagalidae and Pseudictopidae further differentiated and Mixodontia, Mimotonida and Arctostylopida emerged. In the Gashatan, the Rodentiaformes and large herbivorous Coryphodontidae and Dinocerata appeared. The high endemism of Chinese Paleocene mammalian faunas indicate that the faunal exchange with other continents was limited, especially from the Early to early Late Paleocene (Ting 1998; Wang *et al.* 1998).

During the Initial Eocene Thermal Maximum (IETM), the temperature of marine surface waters in high latitudes was over 20°C (Corfield and Norris 1998). Associated with the IETM were Benthic Foraminiferal Extinction and

the Mammalian Dispersal Event (MDE) at the basal Wasatchian Zone Wa0 (Berggren *et al.* 1998; Zachos *et al.* 2001). The Chinese mammalian fauna greatly changed at this time. Archaic groups decreased significantly. Modern groups such as Perissodactyla and Rodentia began to radiate and Artiodactyla and Euprimates appeared. From the end of the Early Eocene, the temperature of sea water dropped successively and entered the ice-house at the Eocene–Oligocene transition (Zachos *et al.* 2001). During this period, Mixodontia, Arctostylopida, Dinocerata, Pantodonta, Tillodontia and Creodonta disappeared in succession. New families of Perissodactyla, Artiodactyla, Rodentia and Lagomorpha emerged continually and flourished. The dominant groups in the fauna altered frequently at family level. Ochotonidae adapted to the grassland environment that appeared in the late Late Eocene (Figure 9). In general, Perissodactyla flourished and dominated the fauna for most of the Eocene Epoch (Figure 3).

Due to the severe cooling at the Eocene–Oligocene boundary, the Eocene perissodactyl-dominant faunas of the Eocene were abruptly replaced by rodent/lagomorph-dominant faunas of the Oligocene. Rodentia formed a large proportion of the fauna (Figure 3). Ctenodactylidae, Tsaganomyidae, Ochotonidae and Indricotheriidae became the most common groups in the Oligocene. Compared with the Eocene forms, rodents, lagomorphs and artiodactyla of the Oligocene were more hypsodont. The faunal turnover at the Eocene–Oligocene boundary was called the Mongolian Remodelling and correlated to the European Grande Coupure (Meng and McKenna 1998).

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