

Evolution of Chinese Neogene Rhinocerotidae and Its Response to Climatic Variations

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Abstract Chinese Neogene Rhinocerotidae has quite a complete record and its temporal range is the Early Miocene to Late Pliocene. The samples include 25 species in 4 tribes of 2 subfamilies. They are used as a foundation for the study of the evolution of the family and its relation to climatic changes. Taxonomic diversity, new records and extinctions are estimated for each Chinese Neogene mammal faunal unit (NMU). The diversity of Chinese Rhinocerotidae varies noticeably throughout the Neogene and is recognized within five stages: the Middle Miocene and Late Miocene are stages of high diversity and the Early Miocene, early Late Miocene and Pliocene are stages of low diversity. Rhinocerotid diversity and morphology are closely related to environmental factors and particularly sensitive to changes in ambient temperature and humidity. The interpretation of climatic variation reflected in the evolution of Rhinocerotidae corresponds precisely with the conclusions drawn from other workers and provides new evidence for research on the Neogene terrestrial ecosystem in China.

Key words: Rhinocerotidae, Neogene, climate, China

1 Introduction

Neogene Rhinocerotidae is widespread in China, as is the case with the whole Eurasian continent. Since Ringstrom (1924) initiated the study of rhinoceroses in the Baode *Hipparion* fauna, studies of Chinese Neogene rhinoceroses have increased, although these studies primarily discuss the taxonomy and rarely concern ecological implications of this important group.

Mammals are very important in the Cenozoic terrestrial ecosystem, of which ungulates are particularly very sensitive to the fluctuations in climate and environment. There has been much discussion about the relationships between artiodactyls and environment, while the literature concerning perissodactyls, particularly rhinoceroses, is lacking. The relevant work of Cerdeno et al. (1995) is exceptional in this respect. China has abundant specimens of Neogene Rhinocerotidae, which enable us to study its relationship to the environment so as to reconstruct the evolutionary process of the Neogene terrestrial ecosystem and its corresponding climatic fluctuations.

2 Material and Method

The material of this study includes the entire known fossil record of Chinese rhinoceroses represented by 25 species ranging in age from the early part of the Early Miocene to the late part of the Late Pliocene. The Neogene mammal units (NMU) of Qiu et al. (1999) are adopted for the division of the Neogene mammal faunal stages (biozones) of China. Supraspecific classification follows that of Heissig (1999).

Subfamily Aceratheriinae Dollo, 1885

Tribe Teleoceratini Hay, 1902

Aprotodon lanzhouensis Qiu et Xie, 1997

Diaceratherium aginense (Repelin, 1917)

Brachypotherium brachypus (Lartet, 1837)

Tribe Aceratheriini Dollo, 1885

Plesiaceratherium gracile Young, 1937

Acerorhinus zernowi (Borissiak, 1914)

Acerorhinus tsaidamensis (Bohlin, 1937)

Acerorhinus fuguensis Deng, 2000

Acerorhinus cornutus (Qiu et Yan, 1982)

Acerorhinus palaeosinensis (Ringstrom, 1924)

Chilotherium tanggulaense Zheng, 1980

Chilotherium hezhengensis (Qiu et al., 1987)

Chilotherium habereri (Schlosser, 1903)

Chilotherium anderssoni Ringstrom, 1924

Chilotherium xizangensis Ji et al., 1980

Subfamily Rhinocerotinae Dollo, 1885

Tribe Elasmotheriini Dollo, 1885

Hispanotherium qiu Guan et Zhang, 1992

Hispanotherium lintungensis Zhai, 1978

Caementodon tongxinensis Guan, 1988

Shennongtherium hypsodontus Huang et Yan,
1983

Tesselodon fangxianensis Yan, 1979

Ningxiatherium longirhinus Chen, 1977

Parelasmotherium simplum (Chow, 1958)

Sinotherium lagreli Ringstrom, 1924

Tribe Rhinocerotini Dollo, 1885

Dicerorhinus cixianensis Chen et Wu, 1976

Dicerorhinus ringstromi (Schlosser, 1921)

Coelodonta antiquitatis Blumenbach, 1807

Acerorhinus.

Chilotherium fenhoense from Huoxian, Shanxi, displays little difference from *Ch. anderssoni* at Baode (Tung et al., 1975). But as Heissig synonymized *Ch. habereri laticeps* and *Ch. planifrons* with *Ch. anderssoni* (Heissig, 1975), *Ch. fenhoense* should also be recognized as *Ch. anderssoni* based upon his criteria. Specimens of *Ch. tianzhuense* from Tianzhu, Gansu, are relatively fragmentary and the characters diagnosing this species are essentially indistinct from *Ch. anderssoni* from the same locality (Zheng, 1982). Therefore, *Ch. tianzhuense* is recognized as a junior synonym of *Ch. anderssoni*. Cerdeno described a new elasmothere species *Hispanotherium tungurensis* from the Tunggur fauna of Inner Mongolia (Cerdeno, 1996), but it appears to be identical to *H. lintungensis* from Lingtong, Shaanxi, and the latter holds nomenclature priority (Zhai, 1978). Therefore, the name *H. tungurensis* is hereby abandoned in favor of the former.

3 Change of Diversity

Figure 1 illustrates the chronostratigraphic distribution of the main Chinese Neogene localities with rhinoceroses. Figure 2 illustrates the diversity, new records and extinct species in different stages of the Chinese Neogene Rhinocerotidae. Diversity is expressed by the total number of species in each stage; new records represent the first occurrences of a certain species in China; extinct species denote species that appeared in a certain stage but disappeared in the next and later stage.

As there is controversy regarding the systematics of *Aprotodon* (Qiu et al., 1997), for convenience's sake, this genus is ascribed to the tribe Teleoceratini according to the classification of Prothero et al. (1989). Some localities in China have documented the presence of "*Aceratherium*" but all of these specimens are rather fragmentary. A notable distinction between *Aceratherium* and *Acerorhinus* is that the former has upper incisors while the latter's upper incisors are absent. The specimens identified as *Aceratherium* in China have neither skulls nor premaxillae; thus the status of the upper incisors is unknown. Other characters of these *Aceratherium* specimens resemble those of primitive *Acerorhinus zernowi*. Therefore, the specimens formerly assigned to *Aceratherium* from several Chinese localities are henceforth ascribed to

As illustrated in Fig. 2, there are strong changes in specific composition and diversity of the Chinese Neogene rhinoceroses. This enables us to distinguish five stages.

During the Early Miocene Xiejiaan to Shanwangian mammal ages (NMU1–5), rhinocerotid diversity is very low, with no more than two species being recognized in each mammalian age. Brachypotheres is dominant and the acerathere *Plesiaceratherium gracile* first appears slightly later. Brachypotheres includes three species: *Aprotodon lanzhouensis*, *Diaceratherium aginense* and *Brachypotherium brachypus*. The first two species become extinct at the end of the Early Miocene but *B. brachypus* continues into the Middle Miocene. *Aprotodon*, a middle Tertiary genus with autapomorphic characters, is also documented in Pakistan and Kazakhstan. In Pakistan, it may possibly coexist with either Proboscidea or indricotheres, while in Kazakhstan, its coexistence with indricotheres. *D. aginense* is reported in the MN2 in France and Germany. *B. brachypus* has a wide distribution in Europe, especially Germany and France, where it is one of the most common members of the family in the Middle Miocene (MN6–7) of Europe and replaces *Diaceratherium*. *Plesiaceratherium* appears in Europe abruptly with a range of the MN4–5. The European

Stage	NMU	Locality	①	②	③	④
Yusbeian	13	Dongyaozitou Tunliu Mazegou				○ ○ sp.
	12	Gaozhuang				○
Baodean	11	Zhongning Gyirong Xiaohu Ertemte		○	○	○
	10	Lamagou Yushe Songshan Lufeng Baode		○ ○ sp. ○	○ ○ ○ ○ ○	○ ○ ○ ○ ○
	9	Bulong Wuzhong Dashengou Bahe		○ ○	○	○
	8	Wangji caidam		○		○
	7	Qin'an Shennongjia Lingyanshan Halamagai Erlanggang Tunggur Lengshuigou	sp.	sp. sp. ○	sp. ○ ○	○ ○
	6	Guanghe Jiulongkou Dingjiaergou		sp. ○ sp.	sp. ○	○ ○
Shanwangian	5	Shanwang	sp.	○		
	4	Pupu Sihong	cf. ○			
Xiejian	3	Zhangjiaping	○			
	2	Gaolanshan Xiejia	sp. cf.			
	1	Suosuoquan	sp.			

Fig. 1. Chronostratigraphic distribution of the main Chinese Neogene localities with rhinocerotids. Tribes: ① Teleoceratini; ② Aceratheriini; ③ Elasmotheriini; ④ Rhinocerotini.

species of *Plesiaceratherium* are very similar to the Chinese type species *P. gracile*, indicating an Asian genesis for the genus.

The first major turnover of rhinoceroses occurs in the

Middle Miocene early Tunggurian (NMU6), with the appearance of five new species and a dramatic increase of diversity from two to seven species. The highlights are the increase of Aceratheriini and the appearance of

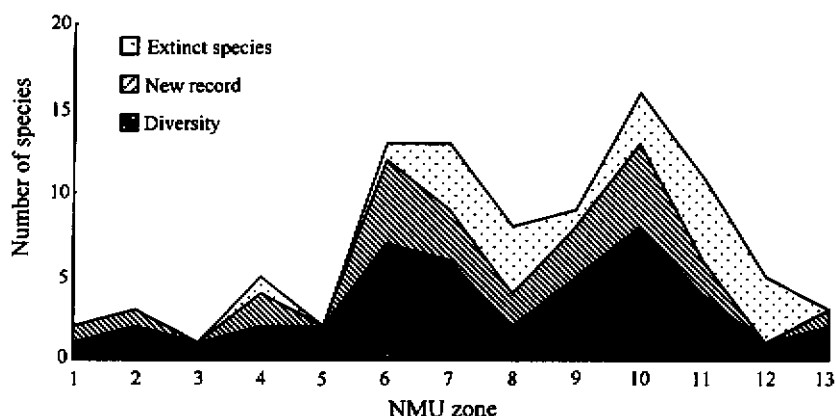


Fig. 2. Diversity, new records and extinct species of Chinese Neogene Rhinocerotidae.

Elasmotheriini and Rhinocerotini. Thus all the four tribes of Chinese Neogene Rhinocerotidae are represented in this stage. This is the first diversity peak of Chinese Neogene Rhinocerotidae, with three to four rhinocerotid species found at the same locality. On the other hand, there is difference in faunal composition between localities, which reflects a diversity of habitats. The elasmothere *Hispanotherium* appears in China, whereas its distribution in Europe is restricted to the Iberian Peninsula in the Early-Middle Miocene MN5. *Caementodon*, resembling *Hispanotherium*, is also recognized in this stage. In China, the rhinocerotine *Dicerorhinus* makes its first appearance in this stage, whereas in Europe it is first present in the Orleanian and becomes dominant in Western Europe and Turkey during the Astaracian. *Acerorhinus* and *Chilotherium*, the two important acerathere genera, also appear in this stage. In China, the flourishing trend of the rhinoceroses continues into the end of the Middle Miocene (NMU7) when diversity still reaches six species, including the three new elasmotheres *Hispanotherium lintungensis*, *Shennongtherium hypsodontus* and *Tesselodon fangxianensis*. *Shennongtherium* and *Tesselodon* are genera endemic to China, of which the latter resembles *Beliajevina* in Europe. The acerathere *Acerorhinus zernowi* also appears in the early Tunggurian of China but later in Europe, where its earliest documentation is from the Late Miocene Vallesian (MN10–11) of Turkey and Greece. The taxonomic composition of the Middle Miocene Tunggurian rhinoceroses remains consistent until the later part of this stage when the distribution of rhinoceroses becomes more wide and differences in

taxonomic composition diversity become more distinct between localities, which illustrates that the habitats of the entire Middle Miocene is very suitable for the family. Only the acerathere *Plesiaceratherium gracile* becomes extinct in this stage.

The beginning of the Late Miocene (NMU8) or the end of the Tunggurian witnessed a distinct, abrupt faunal change, characterized by a decrease in species diversity to a very low species level, i.e. only two species, the only representatives being the acerathere *Acerorhinus*

tsaidamensis and the elasmothere *Parelasmootherium simplum*. Moreover, specimens are scarce and localities are rare; they are documented only in the Qaidam and Linxia basins. Furthermore, four species of rhinoceroses become extinct in this stage, including all the brachypotheres and most elasmotheres, which represents a very significant extinction event.

In the early Late Miocene (NMU9), rhinoceroses begin to recover their high diversity by an increase of diversity to five species, including three new ones. Except one species of Rhinocerotini, *Dicerorhinus ringstromi* (which is also documented in the Near East), all the rhinoceroses are aceratheres, especially the genus *Chilotherium*, which includes three species, *Ch. tanggulaense*, *Ch. hezhengense* and *Ch. habereri*. *Chilotherium* is the most characteristic rhinoceros in the Late Miocene. Its distribution is extensive, from China to South Asia, the Middle East and Southern Europe, where it is most prolific in the Late Miocene Turolian. Prothero et al. (1989) suggested that *Chilotherium* may have had its origin in the Siwaliks of South Asia during the Middle Miocene. However, *Chilotherium* is documented in the early Middle Miocene of China, which contradicts the above hypothesis and should indicate an East Asian origin for the genus.

In the middle Late Miocene (NMU10), the diversity of rhinoceroses reaches an apex with seven species. This stage is the maximum adaptive radiation phase of Chinese Rhinocerotidae in its geological history. The two acerathere genera *Acerorhinus* and *Chilotherium* continue to be dominant, represented by *A. fuguensis*, *A. cornutus*, *A. palaeosinensis*, *Ch. habereri* and *Ch.*

anderssoni. Elasmotheriini is represented by derived *Sinotherium largeli*. The rhinocerotine *Dicerorhinus ringstromi* continues to be present in China, but declines significantly in Europe. This stage also witnesses an important turnover of Chinese Rhinocerotidae with the appearance of five new species and extinction of three species. The population of the family Rhinocerotidae declines gradually in the late Late Miocene, but species diversity is still maintained at four species with aceratheres continuing to be dominant. In addition, a new elasmothere species, *Ningxiatherium longirhinus*, appears with some morphological characters resembling *Iranotherium* and other characters resembling *Elasmotherium*. However, a mass extinction of Rhinocerotidae has been initiated with last extinction of five species. With the close of the Miocene, Chinese Rhinocerotidae is on the decline, which is consistent with the global trend. Many groups become completely extinct, including the extremely prolific aceratheres, and only Rhinocerotini survives in Eurasia, whereas in North America the entire rhinocerotid fauna disappears.

In the Early Pliocene (NMU12), the diversity of Chinese Rhinocerotidae decreases to only one species of Rhinocerotini, *Dicerorhinus ringstromi*. In the Late Pliocene (NMU 13), although the diversity again increases slightly, only two members of Rhinocerotini are present, including the woolly rhinoceros *Coelodonta antiquitatis* which firstly appears. China is the region of origin for this form, which then disperses westwards and gradually reaches Europe in the Pleistocene.

4 Significance for Climatic and Environmental Reconstruction

Within the terrestrial ecosystem, the change in mammalian diversity is closely related to climatic conditions. Temperature has great influence on diversity. The warm environment is favourable for mammalian adaptive radiation; conversely, the cold environment leads to a decrease of diversity. The rhinoceros is a typical large land mammal that has a sensitive response to the environmental or climatic fluctuations. It has been shown that a warm and moist climate supports the maximum diversity of rhinoceroses. The diversity fluctuation of different tribes of the family Rhinocerotidae through Neogene times is illustrated in Fig. 3. There are significant

differences in habitat and behaviour among various rhinocerotid species, and the specific habitat adaptation is reflected in skeletal and dental characters, from which we can judge related climatic factors, particularly temperature and humidity.

In the Early Miocene, when brachypotheres dominate the rhinocerotid fauna, diversity of the family Rhinocerotidae is very low, indicating a relatively long cold stage. The teleoceratines *Diaceratherium* and *Brachypotherium* are large to very large in body size with hypsodont dentition and hippopotamus-like gracility. Thus, it is inferred that brachypotheres should have fed on grass and inhabited the swampy or paludal environment. The mandibular symphysis of *Aprotodon* is very wide, resembling that of the hippopotamus, and as such it was initially described as a member of that family (Foster-Cooper, 1915). These taxa indicate an extensive aquatic environment and a cold and moist climate in the Early Miocene. Pollen analysis also indicates that conifers are dominant in the Early Miocene, mainly consisting of Cupressaceae, *Taxus* and *Juniperus* (Ma et al., 1998), which corresponds to the climatic characteristics reflected by Rhinocerotidae.

The Middle Miocene is an important stage of prosperity and strong adaptive radiation of the Rhinocerotidae, which indicates a warming climate. In this stage, the Chinese habitat diversity is high, as expressed by the coexistence of Teleoceratini, Aceratheriini, Elasmotheriini and Rhinocerotini, of which elasmotheres are dominant with well-developed hypsodont dentition with much cement and strong enamel plications, indicating typical steppe grazers. In addition to sharing characters with elasmotheres, *Hispanotherium* has very slender limb bones, which indicate that it is cursorial and dwells in an open steppe habitat. *Acerorhinus* represents Aceratheriini. Its closely spaced lower incisors are small with dull medial flanges and its dentition is relatively brachydont, indicating that the genus browsed mainly upon shrub leaves and was adapted to shrubby woodlands (Qiu et al., 1982). Based on the diversity and composition of Rhinocerotidae, this stage was obviously warm but semi-arid due to low humidity. The aquatic habitats were reduced while steppe and semi-shrubby woodland habitats became predominant. This conclusion coincides with the evidence from the Middle Miocene Tunggur, Xianshuihe and Tongxin faunas which indicate a temperate and semi-arid steppe interspersed

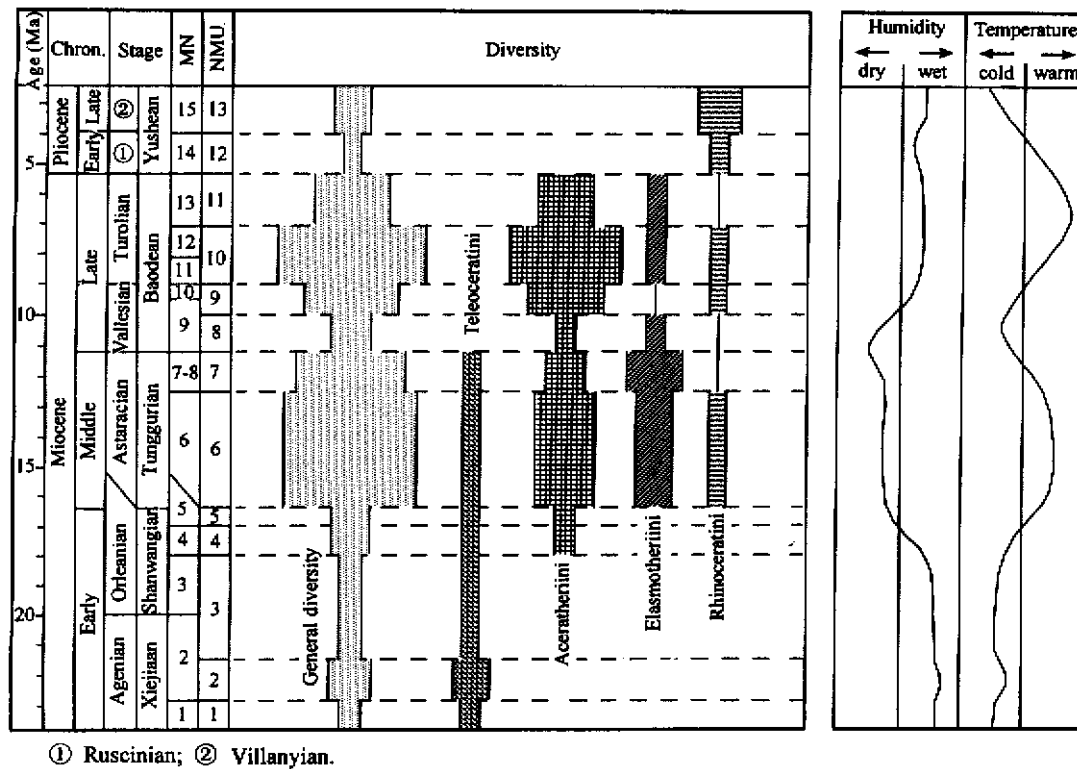


Fig. 3. Evolution of Chinese Neogene Rhinocerotidae and its correlation to palaeoclimatic curves.

with woodlands and aquatic habitats (Qiu et al., 1996).

At the beginning of the Late Miocene, a decrease in rhinocerotid diversity implies a cooling event. The acerather browser *Acerorhinus* and the elasmothere grazer *Parelasmotherium* inhabited this stage, suggesting that humidity was comparable to that of the Middle Miocene.

After the short cooling event in the Late Miocene, the rhinocerotid abundance recovered rapidly. This represents the greatest adaptive radiation stage of the family in its geological history and indicates that the climate again became warm. In this stage, the composition of the faunas differs greatly from those of the Middle Miocene: Teleoceratini disappears completely, Elasmotheriini and Rhinocerotini decline in abundance, and Aceratheriini, including *Chilotherium* and *Acerorhinus*, becomes dominant. The rostral morphology of *Chilotherium* is distinctive due to its extremely wide mandibular symphysis and huge lower incisors with upturned medial flanges. This genus is more hypsodont with relatively small well-worn premolars. These characters imply that *Chilotherium* was a grazer in temperate habitats (Ringstrom, 1924;

Qiu et al., 1982). Like brachypotheres, aceratheres have short and robust limb bones, and as such, unlike elasmotheres with slender limbs, they are not adapted to cursorial locomotion. Therefore, the habitat of aceratheres might not be quite open and they are thus regarded as woodland inhabitants. Although *Dicerorhinus* is cursorial, its body is gigantic; thus it is also considered to be a woodland dweller despite its hypsodont dentition (Guerin, 1980). Rhinocerotid fossils indicate that the environment of the Late Miocene was warm and moist.

After a serious extinct event, the diversity of Rhinocerotidae declines to its lowest level, with only the rhinocerotid species *Dicerorhinus ringstromi* being present. Though the sharp decline in diversity indicates a cooling event, the behaviour of *Dicerorhinus* indicates that the ambient temperature has not lowered to an extreme extent. In the Late Pliocene, the woolly rhinoceros *Coelodonta antiquitatis* appears, and its body is small and the tooth crown is moderately high. The woolly rhinoceros lives in a cold climate with a small torso and moderately hypsodont dentition. This form inhabited a cold climate and utilized its wide

muzzle and flat nasal horn to forage grass through snow. The appearance of the woolly rhinoceros indicates very low temperatures during the late Pliocene. According to the research of An et al. (An et al., 1999), the annual temperature fluctuation is minor in the Early Pliocene. Botanical data indicate the predominance of broadleaf trees despite the presence of abundant conifers. The Late Pliocene is the initial stage of the great ice age in the northern hemisphere. During this stage, the cryospheres increased markedly and the earliest continental mountain glaciers develop on the Tibetan Plateau. This interpretation of climatic fluctuation is consistent with the conclusions reached from the analysis of fossil rhinocerotids.

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