Cour. Forsch.-Inst. Senckenberg | 256 | 43–56 | 4 Figs, 2 Tabs | Frankfurt a. M., 15. 11. 2006

Neogene Rhinoceroses of the Linxia Basin (Gansu, China)

With 4 figs, 2 tabs

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Abstract

Ten genera and thirteen species are recognized among the rhinocerotid remains from the Miocene and Pliocene deposits of the Linxia Basin in Gansu, China. *Chilotherium anderssoni* is reported for the first time in the Linxia Basin, while *Aprotodon* sp. is found for the first time in Lower Miocene deposits of the basin. The Late Miocene corresponds to a period of highest diversity with eight species, accompanying very abundant macromammals of the *Hipparion* fauna. *Chilotherium wimani* is absolutely dominant in number and present in all sites of MN 10–11 age. Compared with other regions in Eurasia and other ages, elasmotheres are more diversified in the Linxia Basin during the Late Miocene. *Coelodonta nihowanensis* in the Linxia Basin indicates the known earliest appearance of the woolly rhino. The distribution of the Neogene rhinocerotids in the Linxia Basin can be correlated with paleoclimatic changes.

Key words: Neogene, rhinoceros, biostratigraphy, systematic paleontology, Linxia Basin, China

Introduction

The Linxia Basin is situated in the northeastern corner of the Tibetan Plateau, in the arid southeastern part of Gansu Province, China. In this basin, the Cenozoic deposits are very thick and well exposed, and produce abundant mammalian fossils from many sites, in particular rhinoceroses (Deng et al. 2004a, b). Since the 1970s, this basin has been explored and abundant mammalian fossils of the Late Cenozoic have been collected. For rhinoceroses, Qiu et al. (1987) and Qiu & Xie (1998) described the aceratheriine *Acerorhinus hezhengensis* and the elasmotheriine *Parelasmotherium simplum* from red clays, and determined the existence of Upper Miocene sediment in the Linxia Basin. Qiu et al. (1990) reported an Early Miocene mammalian fauna from the Jiaozigou Formation in the Linxia Basin, including *Dzungariotherium orgosense* and Rhinocerotidae gen. et sp. indet. However, new evidence indicates that the fauna from the Jiaozigou Formation actually belongs to the Late Oligocene, and includes more rhinoceroses, such as Hyracodontidae gen. et sp. indet., *Ardynia* sp., *A. altidentata*, *Allacerops* sp., *Dzungariotherium orgosense*, *Paraceratherium yagouense*, *Ronzotherium* sp., and *Aprotodon lanzhouensis* (Deng et al. 2004a, b, Qiu et al. 2004b). Recent expeditions to the Linxia Basin have resulted in a very fine collection with at least 5000 specimens of mammalian fossils at Hezheng Paleozoological Museum in Gansu and Institute of Vertebrate Paleontology and Paleoanthropology in Beijing.

Several hundred skulls of the Neogene rhinoceroses are known from the Linxia Basin, but most of them belong to the Late Miocene aceratheriine *Chilotherium wimani*. In addition, more abundant limb bones and isolated teeth of rhinoceroses are found in this basin, especially from the Upper Miocene red clay deposits. The studied fossil material of rhinoceroses in this paper comes from 31 localities of the Linxia Basin (fig. 1), and these localities are distributed in an area of about 2000 km^2 in Hezheng, Guanghe, Dongxiang, and Jishishan Counties, with a chronological range from the Early Miocene (MN 4, Orleanian or Shanwangian) to the Late Pliocene (MN 17, Villanyian or Nihewanian). As can be seen in table 1, the rhinoceros fossil record in the Linxia Basin has three gaps corresponding to MN 7/8, 13, and 15–16, because this basin has stratigraphical hiatuses during MN 7/8 and 13, and a thick bolder conglomerate without any fossil during MN 15–16. The European mammal units follow Steininger et al. (1996), and the Chinese mammal units are synthesized divisions of Li et al. (1984) and Qiu & Qiu (1995). Terminology and taxonomy follow Heissig (1972, 1999) and Guérin (1980). All materials discussed in this paper are preserved respectively at the following Chinese

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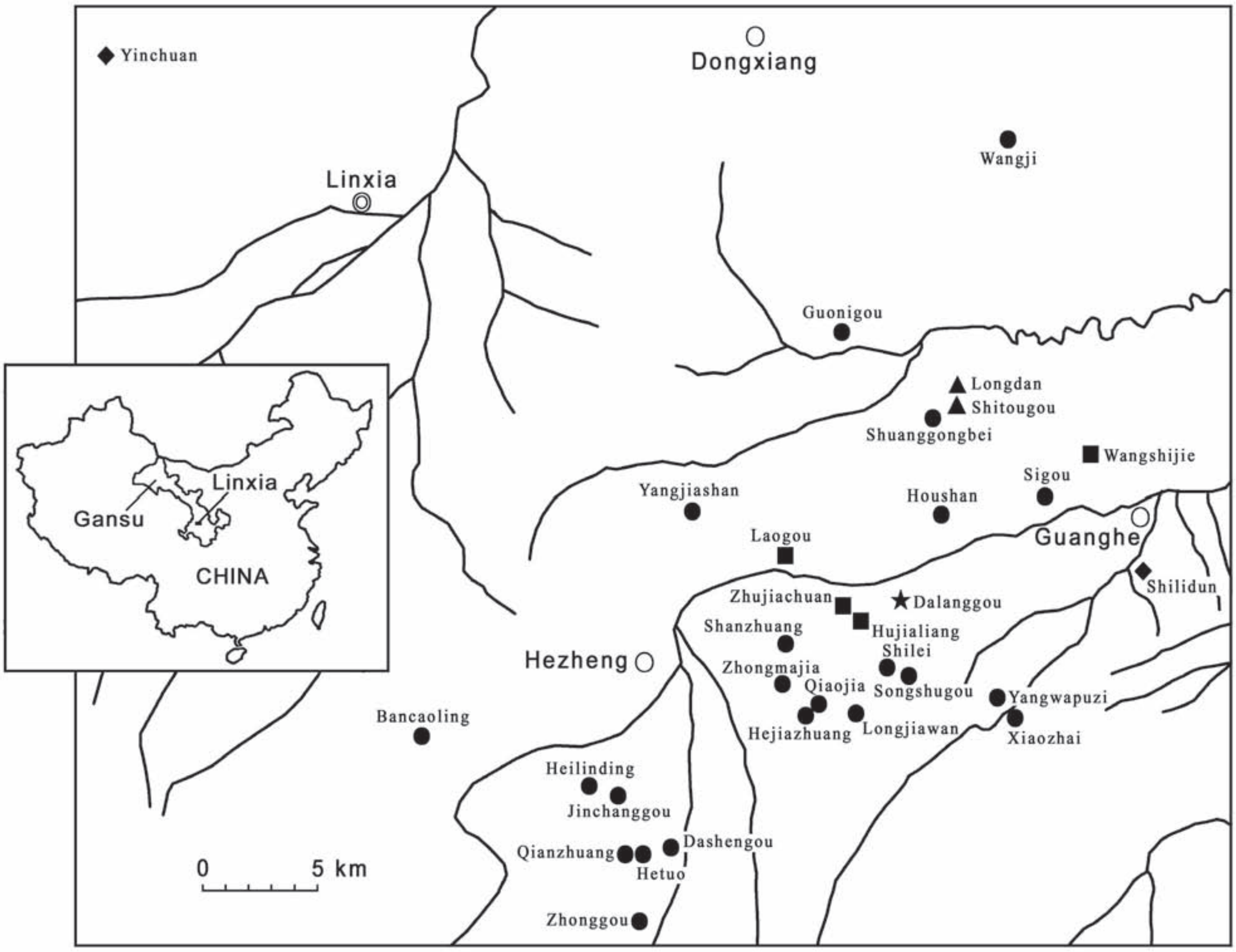

Fig. 1: Distribution of the family Rhinocerotidae in the Linxia Basin (Gansu, China) during the Neogene.

institutions: the Hezheng Paleozoological Museum in Gansu (specimen prefix: HMV), the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing (specimen prefix: IVPP V), and the Gansu Provincial Museum in Lanzhou (specimen prefix: GSMV or GVD).

Systematics

Family Rhinocerotidae Gill, 1872
Genus ***Aprotodon*** Forster-Cooper, 1915
Aprotodon sp.

The presence of a rhinocerotid in the Lower Miocene of the Linxia Basin is indicated by only several isolated lower cheek teeth whose sizes and characters are close to those of *Aprotodon lanzhouensis* from the adjacent Lanzhou Basin (Qiu & Xie 1997). At Dalanggou in Guanghe County, these isolated lower teeth were collected from a conglomerate lens in the red mudstones of the Shangzhuang Formation. In the lower premolars of *Aprotodon* sp. from Dalanggou, the paralophid is tiny, and the protolophid stretches antero-lingually; the metaconid is robust, slanting postero-lingually; the transverse part of the hypolophid is complete, but still very thin. In the lower molars, the labial valley is deep, and the anterior valley is U-shaped, with a rather right-angled posterior end.

At Dalanggou, *Aprotodon* sp. coexists with abundant fossils of *Gomphotherium* sp. In the Lanzhou Basin, *A. lanzhouensis* was found in the Lower Miocene white sandstone of the Xianshuihe Formation. *A. lanzhouensis* is found also from the Upper Oligocene yellow sandstone of the Jiaozigou Formation in the Linxia Basin, but these fossils are markedly smaller than those from Lanzhou and Dalanggou, which is considered to reflect sexual dimorphism (Qiu et al. 2004b). The mandibular symphysis of *Aprotodon* is very wide, resembling that of the hippopotamus; this taxon indicates an extensive aquatic environment and a cool and moist climate.

Subfamily Aceratheriinae Dollo, 1885
Tribe Aceratheriini Dollo, 1885
Genus ***Alicornops*** Ginsburg & Guérin, 1979
Alicornops laogouense Deng, 2004

Deng (2004) described a new species, *Alicornops laogouense* according to a skull (HMV 0982), a broken right mandible (HMV 0983), and some isolated teeth (IVPP

Table 1: Biostratigraphical distribution of the family Rhinocerotidae in the Neogene localities of the Linxia Basin (Gansu, China): a, *Aprotodon* sp.; b, *Alicornops laogouense*; c, *Hispanotherium matritense*; d, *Parelasmotherium simplum*; e, *P. linxiaense*; f, *Chilotherium* sp.; g, *C. wimani*; h, *C. anderssoni*; i, *Acerorhinus hezhengensis*; j, *Iranotherium morgani*; k, *Dicerorhinus ringstromi*; l, *Shansirhinus ringstromi*; m, *Coelodonta nihowanensis*.

Age	Stage		MN	Locality	a	b	c	d	e	f	g	h	i	j	k	l	m
	Villanyian	Nihewanian	17	Longdan													+
Late Pliocene				Shitougou													+
Middle Pliocene		Mazegouan	16														
	Ruscinian	Gaozhuangian	15														
Early Pliocene			14	Yinchuan												+	
				Shilidun												+	
	Turolian	Baodean	13														
Late Miocene			12	Qianzhuang								+			+		
				Jinchanggou											+		
				Bancaoling								+			+		
			11	Shilei							+		+				
				Xiaozhai							+						
				Heilinding							+						
				Longjiawan							+		+				
				Zhonggou							+						
				Yangwapuzi							+						
				Yangjiashan							+						
				Songshugou							+		+				
				Hetuo							+						
	Vallesian	Bahean	10	Shanzhuang							+		+	+			
				Qiaojia							+						
				Shuanggongbei							+		+	+			
				Hejiazhuang							+						
				Dashengou							+		+				
				Houshan							+		+	+			
				Sigou							+		+				
			9	Wangji				+									
				Guonigou					+								
				Zhongmajia						+							
	Astaracian	Tunggurian	7/8														
Middle Miocene			6	Laogou		+	+										
				Hujialiang			+										
				Zhujiachuan		+	+										
	Orleanian	Shanwangian	5	Wangshijie		+	+										
Early Miocene			4	Dalanggou	+												

V 12672.1–15) from Laogou in Hezheng County. This species is also found in Zhujiachuan and Wangshijie in Guanghe County, represented by several isolated teeth, carpals and tarsals. At Laogou and Zhujiachuan, *A. laogouense* coexists with *Platybelodon grangeri* and *Anchitherium gobiensis*, whereas at Wangshijie, it coexists with a smaller *Anchitherium* but without *Platybelodon*.

A. laogouense is a middle-sized rhinoceros, and skull is the largest of the genus. The nasals are narrow, and the skull is very high, with a lozenge-shaped roof. The frontal bone is narrowing posteriorly, and the surface between the parietal crests is narrow. The nasal notch is situated at the level of the middle of P^3, and the orbit is situated at the level of the anterior part of M^1. The postorbital process is comparatively weak.

There are some differences between *A. laogouense* from Laogou and *A. simorrense* from Simorre and Villefrache d'Astarac in France (Lartet 1851). The size of *A. laogouense* is much larger than that of *A. simorrense* according to the measurements of Guérin (1980) and Cerdeño & Alcalá (1989) for the mandibles and teeth of *A. simorrense* from different European localities. The lingual cingulum in P^3 and P^4 of *A. simorrense* is developed only on the protocone, but that of *A. laogouense* is better developed and continuous with the anterior and posterior cingula. The skull of *A. laogouense* differs from those of *A. simorrense* from Moraleja de Enmedio and Toril-3 in Spain (Cerdeño & Sánchez 2000). In the latter, the parietal crests are close or united into a sagittal crest, the nasal notch is at the P^4 level, and the anterior border of the orbits is above the $M^1 – M^2$ commissure or at the level of the anterior part of M^2.

Cerdeño & Alcalá (1989) described another species of *Alicornops*, *A. alfambrense* from La Roma 2 at Alfambra in Teruel, Spain, but the material includes only postcranial bones which are different from *A. simorrense* in being of larger size and having more robust limb bones. A comparison between *A. simorrense*, *A. alfambrense*, and *A. laogoense* shows that *A. alfambrense* is also smaller than *A. laogouense*. Several isolated teeth from Dorn-Dürkheim 1 in Germany were identified as *A. alfambrense* (Cerdeño 1997), and they differ from the teeth of *A. laogouense* in slightly smaller size, lower crowns, and in the absence of the labial and lingual cingula in the lower premolars.

The Middle Miocene fauna bearing *A. laogouense* in the Linxia Basin corresponds to MN 6. With the discovery of *A. laogouense* in the Linxia Basin, it appears that the genus *Alicornops* dispersed from western Europe through eastern Europe, western Asia and southern Asia, to the Far East. During MN 6 time, its distribution was relatively widespread, spanning the whole of Eurasia. In China, *A. laogouense* lived together with *Hispanotherium matritense*, which inhabited a warm environment (Deng & Downs 2002). A large number of fossils of the Amebelodontidae, which favoured habitats near water, were found with *A. laogouense* in the Linxia Basin. This shows that lakes and rivers were abundant in the environment in which this rhinocerotid species lived.

Tribe Chilotheriini Qiu, Xie & Yan, 1987

Genus ***Acerorhinus*** Kretzoi, 1942

Acerorhinus hezhengensis Qiu, Xie & Yan, 1987

Qiu et al. (1987) described a new species, *Acerorhinus hezhengensis* according to an associated skull and mandible (GSMV 8001) from Dashengou in Hezheng County. Recently, more skulls and mandibles of *A. hezhengensis* are discovered from the middle and upper red clays of the Upper Miocene Liushu Formation at many localities in the Linxia Basin. *A. hezhengensis* is relatively frequent in the Late Miocene *Hipparion* fauna of the Linxia Basin, but it is much less abundant than *Chilotherium wimani*.

A. hezhengensis is a large-sized rhinoceros. Its posttympanic process is long, strongly compressed latero-medially, and stretching downward beyond the condyles. The false external auditory meatus is not closed, or only weakly so. The sagittal crest is absent, and the area bordered by the rather straight parietal crests is wide and flat. The nasal notch is deeply incised, and the orbit is situated comparatively low. The median valleys in the upper premolars are isolated only when heavily worn. The upper molars have strong protocone constrictions and antecrochets, and their labial walls are undulating, with prominent paracone ribs and parastyle folds. The symphysis is not widened, but ascends anteriorly.

A. hezhengensis differs widely from *A. zernowi* from Sevastopol (Borissiak 1914), because the latter is comparatively brachycephalic, with short paroccipital process, its parietal crests are united into a narrow sagittal crest, and its upper cheek teeth are all primitively constructed, with weak crochet, antecrochet, crista and protocone constriction.

The difference between *A. hezhengensis* and *A. palaeosinensis* from Baode (Ringström 1924) is apparent. In the latter, the upper half of the occiput is remarkably wide; the occiput and the temporal region are comparatively heightened in lateral view; the orbit and the nasal notch both shift anteriorly, with their anterior borders above M^1 and P^4 respectively; there is a prominent postorbital process on the zygomatic arch; all the upper premolars have well-developed medifossettes; the antecrochet in the upper molars is large; the symphysis stretches mainly anteriorly.

In comparison with *A. fuguensis* from Fugu, Shaanxi (Deng 2000), *A. hezhengensis* seems to be advanced as well. *A. hezhengensis* differs from *A. fuguensis* in having wider distance between the parietal crests and flatter preorbital surface. In general the two forms are quite similar in morphology, especially in tooth structure.

Acerorhinus, *Shansirhinus* and *Chilotherium* do possess common characters, but at the same time differ greatly. The most evident difference between the three genera is that in *Acerorhinus* the symphysis is not especially wide, with a distance across the two I_2 equal to or less than that across the two P_2, while in *Shansirhinus* and *Chilotherium* the symphysis is much wider, with a distance across the two I_2 that exceeds that across the two P_2. The three genera, however, differ from all the other members of the subfamily Aceratheriinae. Qiu et al. (1987) proposed to separate them in a new tribe, the Chilotheriini.

Genus ***Shansirhinus*** Kretzoi, 1942

Shansirhinus ringstromi Kretzoi, 1942

A well-preserved skull and articulated mandible (IVPP V 13764) of *Shansirhinus ringstromi*, a horned acetherine rhinocerotid, was found in the red clay of the Lower Pliocene Hewangjia Formation at Yinchuan in Jishishan County (Deng 2005a). Its premaxillae are significantly short and have no incisors, its nasals are short and raised, with a rough horn boss on the tip. The mandibular symphysis is moderately expanded, with a concave labial surface. In its upper cheek teeth, DP^1 is very small, the protocone is strongly constricted, and the bridge and medifossette are well developed in the premolars, with elaborate enamel plications and with a continuous lingual cingulum. In its lower cheek teeth, the trigonid is squared and U-shaped.

A sister-group relationship between *Shansirhinus* and *Chilotherium* is proposed on the basis of cranial, mandibular and dental evidence. Shared derived characters that support this relationship include: an expanded mandibular symphysis with a concave ventral surface; short premaxillae without upper incisors, lost in both these genera; a robust and right-angled facial crest; a flat or somewhat concave dorsal skull profile; a weak or absent parastyle fold; and a constricted protocone in the premolars. *Shansirhinus* was probably a grazer, as suggested by the high crown, well-developed secondary folds, and many enamel plications in its teeth.

According to Kretzoi (1942) the features of *Rhinoceros brancoi* described by Schlosser (1903) are unique; he therefore suggested the creation of a new genus, *Shansirhinus*. He also created another species, *S. ringstromi*, based on the maxillary of *R.* aff. *brancoi* from Huangshigou in Yushe, Shanxi, which had been described by Ringström (1927). The skull from Yinchuan resembles *S. ringstromi* from Huangshigou in the maxillary and dental morphologies. Similarities include a narrow choana, a widely arched palate, and a relatively prominent anterior end of the zygomatic arch. The teeth are characterized by numerous enamel plications, weak parastyle folds, a relatively small DP^1, very strong crochets, and strongly constricted protocones. The premolars have well-developed lingual bridges, strong medifossettes, squared, U-shaped lingual valleys, continuous lingual cingula, and expanded, squared hypocones. The Yinchuan skull and the maxillary of *S. ringstromi* from Huangshigou are certainly not identical: in the premolars of the Huangshigou maxillary there are two or three medifossettes, the lingual bridges are strong, and the lingual pillar is absent on P^3. These differences, however, are simply due to individual variation. Hence, the Yinchuan skull is identified as *S. ringstromi*.

Qiu & Yan (1982) discussed the feeding habits of *S. ringstromi*, and concluded that it was a browser that fed on leaves and soft twigs. In contrast, the high crowned teeth with enamel plications of *Shansirhinus* imply that it may graze on tough grasses like certain rhinoceroses and horses, such as *Elasmotherium* and *Hipparion*, which have high-crowned and strongly plicate teeth. The dominant mammalian taxa accompanying *Shansirhinus* are rodents, perissodactyls and artiodactyls (Tang et al. 1974, Zheng 1982), which indicate an open and dry ecological environment.

Genus ***Chilotherium*** Ringström, 1924

Chilotherium sp.

A skull with its articulated mandible (HMV 0102) attributed to a primitive species of *Chilotherium* was found in the basal red clay of the Liushu Formation at Zhongmajia, in Hezheng County, and its age corresponds to MN 9 (Deng in press). The ventral surface of the mandibular symphysis is flat, which is different from the concave surfaces of other known species of *Chilotherium*. The parietal crests are hardly separated and form a sagittal crest, which is different from the broadly separated parietal crests of the advanced species of *Chilotherium*, and also different from other primitive species of this genus which have slightly separated parietal crests, without a sagittal crest.

All known species of *Chilotherium* have a strongly concave ventral surface of the mandibular symphysis, while *Chilotherium* sp. from Zhongmajia has a relatively flat ventral surface. *Chilotherium* sp. is relatively small, much smaller than *Chilotherium wimani*, but somewhat larger than *C. xizangensis* (Ji et al. 1980).

Chilotherium sp. from Zhongmajia shares many synapomorphies with the other species of *Chilotherium*, but not with the primitive chilothere *Acerorhinus* nor with other rhinocerotids as a whole: fused posttympanic and postglenoid processes, a low parietal crest, a narrow zygomatic arch without a posterodorsal projection, a gradual tapering of the skull behind the orbits, a strong broadening of the mandibular symphysis, well-developed secondary structures on the cheek teeth, comparatively small P^2, and upturned medial flanges of I_2. These apomorphies show that *Chilotherium* sp. from Zhongmajia is actually a member of the genus *Chilotherium*. Nonetheless, *Chilotherium* sp. lacks some apomorphic characters of other *Chilotherium* species, such as a thick posttympanic process, widely separated parietal crests, a wide nasal notch, a long diastema between I_2 and P_2, and a concave ventral surface in the mandibular symphysis.

Chilotherium sp. from Zhongmajia is the most primitive *Chilotherium* described so far; it possibly dates to the Middle Miocene. For example, doubtful remains of *Chilotherium* sp. were reported from Halamagai (Xinjiang, China) by Chow (1957) and from Jiulongkou (Hebei, China) by Chen & Wu (1976). Chow described only a right M^1 from Halamagai. This molar has a well defined parastyle fold, and its protocone is not constricted. These features are actually suggestive of *Acerorhinus*, and not of *Chilotherium* (Deng 2000, Deng & Downs 2002). Tong et al. (1990) also reported some questionable fossils of *Chilotherium*, but they did not describe them. The Jiulongkou material is constituted by two portions of two different juvenile skulls, i.e., a snout and a left maxillary bone, as well as a P^2, but these specimens are not diagnostic of *Chilotherium*. At the moment, Zhongmajia is the earliest known locality in the Linxia Basin to contain undoubted remains of the genus *Chilotherium*.

Chilotherium wimani Ringström, 1924

Chilotherium wimani is the most abundant taxon in the Linxia Basin's Late Miocene *Hipparion* fauna. Remains of *C. wimani* are in fact found practically everywhere in the middle and upper red clays of the Liushu Formation (table 1). *C. wimani* was established by Ringström (1924) on just a few specimens from Fugu, Shaanxi. Deng (2001a) described other *C. wimani* remains from Fugu, so the characters of this species are fairly well known by now. Many *C. wimani* fossils recently discovered in Linxia Basin (fig. 2) are similar to those from Fugu, but their skulls, mandibles, teeth, and limb bones show obvious individual differences (Deng 2001c, 2002b).

C. wimani is a middle-sized rhinoceros. Its occipital surface is trapezoid, and its occipital crest bears a wide median notch. The large orbit is in comparatively low position, with strong supraorbital tubercles, weak postorbital processes on the frontal and zygomatic bones, and irregular infraorbital foramina. The skull has a narrow and long rhombic dorsal outline, a concave dorsal profile, hardly separated parietal crests, and steep outer walls in the braincase. The nasals are wide and separated from the maxillary bones by a deep nasal notch. The postglenoid process is robust and fused with the thick posttympanic

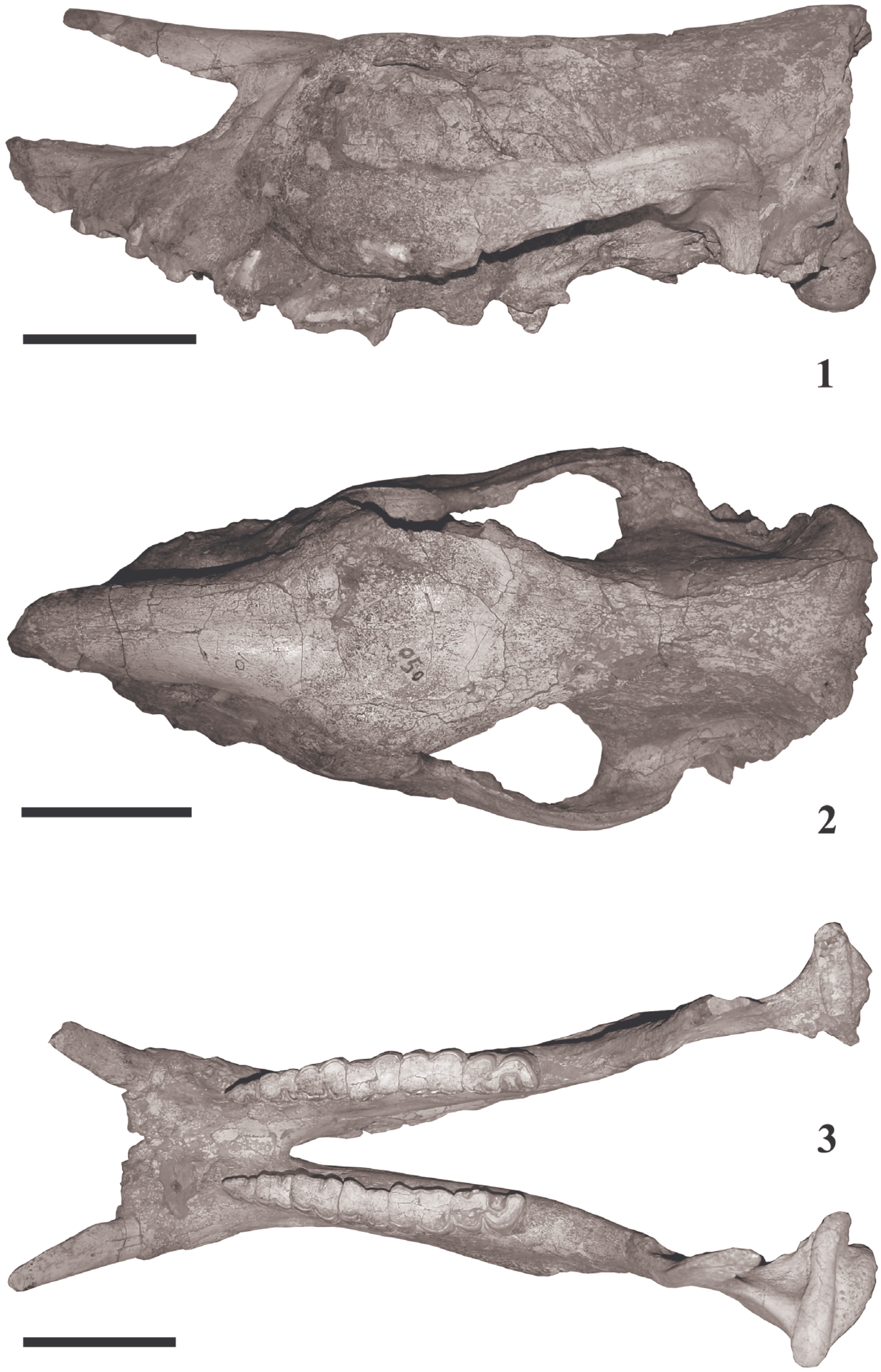

Fig. 2: Skull and mandible of *Chilotherium wimani* from Songshugou in the Linxia Basin (Gansu, China), IVPP V 14966. 1. Lateral view of skull; 2. dorsal view of skull; 3. occlusal view of mandible. Scale bars: 10 cm.

process. Its particularly wide mandibular symphysis has concave dorsal and ventral surfaces, and its huge I_2 has an upturned medial flange. The premolars have well-developed parastyle folds and paracone ribs, as well as weakly constricted protocones and hypocones. The fore and hind feet of *C. wimani* are tridactyl, and the limb bones are as short and robust as those of *C. anderssoni* from Baode.

Some cranial characters of *C. wimani* are very similar to those of the more primitive genus *Acerorhinus*. Their shared characters include: a higher than wide occipital surface with round upper corners, a comparatively slender paroccipital process, strong postglenoid processes, closely spaced parietal crests, a distinctly concave cranial dorsal profile, a high occipital elevation, weak postorbital processes, a prominent supraorbital tubercle, skull with a wide dorsal surface, a very thick orbital upper margin, wide and strong nasals vaulted in cross section and with drooping lateral margins, comparatively low cheek tooth crowns, wavy labial walls in the upper cheek teeth, well-developed parastyle folds and paracone ribs, small antecrochets, weak crochets, and a comparatively large P^2.

The skull of *C. wimani*, however, differs from that of *Acerorhinus*. *C. wimani* is a middle size rhinoceros, while *Acerorhinus* is larger. *C. wimani* has trapezoidal occipital surface instead of the bell-shaped one for *Acerorhinus*. In *C. wimani* the posttympanic process is thick, does not protrude laterally, and is fused with the postglenoid process so that it's the false exterior auditory meatus is close. In contrast, in *Acerorhinus* the two processes are partially sealed or not at all fused. The skull's dorsal outline in *C. wimani* tapers gradually behind the orbits, while the skull of *Acerorhinus* shows a sudden lateral constriction. The preorbital fossa in *C. wimani* is shallow and not well delineated, while that of *Acerorhinus* is deep and well defined. The zygomatic arch in *C. wimani* does not have a jutting posterodorsal angle and its posterior margin is straight, while in *Acerorhinus* the posterodorsal angle is robust and protruding and the posterior margin of the zygomatic arch is inclined anteroventrally. In the mandibles, the symphysis is particularly broad in *C. wimani*, while it is narrow in *Acerorhinus*, with a width not exceeding the distance across the two P_2. *C. wimani* has upturned medial flanges in I_2, while in *Acerorhinus* the medial flanges are almost leveled off.

Chilotherium anderssoni Ringström, 1924

According to Ringström (1924) a highly diagnostic character of *Chilotherium anderssoni* is its broadly separated parietal crests. However, Deng (2001a) proved that the character is most variable. The parietal crests are generally very close to one another in *C. wimani*, but they are broadly separated in old individuals. Ringström (1924) indicated that the various species of *Chilotherium* have no evident differences in their cranial and dental structures. No skull or mandible from the Linxia Basin can be reliably referred to *C. anderssoni*.

In contrast, the upper cheek teeth of *C. anderssoni* show advanced characters that distinguish them from those of *C. wimani*, such as a flat labial wall almost without paracone rib and parastyle fold, the absence of the medifossette, a strongly constricted protocone, and a robust antecrochet. In the upper premolars of *C. anderssoni*, the lingual cingulum is weak and discontinuous, while in its upper molars, the lingual cingulum and the crista are completely absent, and the antecrochet is large enough to fill in almost the whole median valley. Isolated teeth with these characters were found in Bancaoling and Jinchanggou, in Hezheng County: they therefore indicate that *C. anderssoni* may actually be present in the Linxia Basin.

In Baode, Shanxi, *Chilotherium anderssoni* was found in Loc. 30 (Daijiagou = T'ai-chia-kou) (Ringström 1924), which is the most representative faunal site in Baode. It is referred to MN 12 (Qiu & Qiu 1995, Qiu et al. 1999). Recent paleomagnetic analyses have confirmed this biochronological attribution. In fact, the fossiliferous bed at Loc. 30 is correlated with Chrons C3Ar and C3Bn, and therefore dated 6.5–7.0 Ma (Yue et al. 2004). The two localities with *C. anderssoni* mentioned above, Bancaoling and Jinchanggou, are situated in the top red clay of the Liushu Formation on the southern margin of the Linxia Basin, and their horizon is higher than that of the Yangjiashan fauna in the central part of the basin, which indicates that there has been prolonged deposition along the basin margin. *C. anderssoni* coexists with *Dicerorhinus ringstromi* in Baode, and the two species also coexist in Linxia. The age of the Linxia Basin localities with *C. anderssoni* is consistent with MN 12.

Subfamily Rhinocerotinae Gill, 1872
Tribe Elasmotheriini Dollo, 1885
Genus ***Hispanotherium*** Crusafont & Villalta, 1947
Hispanotherium matritense (Prado, 1864)

Deng (2003) first recognized the existence of *Hispanotherium matritense* in China on some isolated teeth (IVPP V 12649.1–20) from Laogou, in Hezheng County, and included several elasmotheres from the Chinese Middle Miocene in the synonymy of this species. Recently, some teeth and limb bones of *H. matritense* were found in Hujialiang, Zhujiachuan and Wangshijie, in Guanghe County. In the genus *Hispanotherium*, the earliest known species *H. beonensis* appeared in MN 4. The next early species, *H. matritense*, was distributed widely in Spain, Portugal and southern France in MN 5. *H. matritense* then dispersed to Turkey, Pakistan, China and Mongolia in MN 6. The more evolved species *H. tungurense* lived in northern China in MN 7–8. It has a more developed cement cover, stronger enamel folds, wavier ectoloph, and more constricted protocones than other species of *Hispanotherium*.

H. matritense is a small-sized rhinoceros with one nasal horn, whose sexes can sometimes be teased apart. It has subhypsodont cheek teeth, with very thick cement cover as well as deeply constricted protocones and slightly constricted metaconids. The upper premolars have a closed median valley with strong secondary enamel folds. The I_2 is a small tusk of different size in the two sexes. Its limb bones are slender; Mc V is rudimental and was not functional.

The size of the teeth of *H. matritense* from Linxia is similar to those of other European and Asian representatives of *H. matritense*. The upper cheek teeth from Linxia have more wavy ectolophs than any other rhinoceros of the region, and the most variable enamel folds in the median valleys among all the representatives of the same species. P^1 is somewhat wider than those of the Iberian specimens of *H. matritense*, while it is similar to first upper premolars of specimens from Turkey and Mongolia. The boundary between the ectoloph and metaloph in M^3 is well marked. I_2 is as wide as the second lower incisors of the male specimens and as long as those of the females of *H. matritense* from Corcoles in Spain (IÑIGO & CERDEÑO 1997). The lower cheek teeth of *H. matritense* from Linxia are the most hypsodont, and their metaconids have markedly constricted grooves. M_3 is slightly narrower than any known M_3 from other regions.

H. matritense is a characteristic species of the European MN 4–5 faunas (IÑIGO & CERDEÑO 1997). This species was considered to live in dry and warm settings because of its hypsodont teeth with thick cement cover and slender limbs (CERDEÑO & NIETO 1995, IÑIGO & CERDEÑO 1997). In the Linxia Basin, the fossils of *H. matritense* came from fluvial grey-yellowish sandstones with gravel, and its paleoenvironment in China was somewhat different from that of its European counterparts. IÑIGO & CERDEÑO (1997) indicated that *H. matritense* is distributed in the Iberian Peninsula during MN 4–5, and somewhat later in some Asian localities, for example during MN 6–8, in Turkey, Pakistan and Mongolia. The material from Linxia proves that *H. matritense* also lived in China during MN 6 (DENG 2003).

HEISSIG (1999) considered that *Hispanotherium beonenensis* from the Lower Miocene of Montréal-du-Gers in France (ANTOINE 1997, 2002) is the ancestor of the more evolved *H. matritense*, because the former has thinner cement cover, flatter ectolophs and weaker enamel folds than the latter. As a result, the origin of the *Hispanotherium* lineage may be in southwestern Europe. The discontinuous protoloph in P^3–P^4 and the non-constricted protocone in the P^1–P^3 of *H. beonensis* are primitive traits which are not shown by *H. matritense*. Although the tribe Elasmotheriini dispersed from Asia, its origin is unknown.

Genus ***Parelasmotherium*** KILLGUS, 1923

Parelasmotherium simplum (CHOW, 1958)

QIU & XIE (1998) reported three isolated upper molars (GVD 8801) of *Parelasmotherium simplum* from Wangji, in Dongxiang County, but their stratigraphic position could not be precisely established. DENG et al. (2004b) found that the Wangji fossiliferous bed is located in the basal red clay of the Liushu Formation.

Parelasmotherium was established by KILLGUS (1923) on specimens from Shanxi. Its type species is *P. schansiense*, which RINGSTRÖM (1924) considered as synonymous with *Sinotherium lagrelii* from Baode, Shanxi, or even as a subspecies of the latter, at most. QIU & XIE (1998) claimed, however, that *Parelasmotherium* is smaller than *Sinotherium*, has upper cheek teeth undifferentiated into crown and prism parts (see RINGSTRÖM 1924), and almost no enamel plications. QIU & XIE (1998) therefore suggested resuming the genus *Parelasmotherium*. They referred CHOW's (1958) *Sinotherium simplum* to the genus *Parelasmotherium*, and attributed the specimens from Wangji to *P. simplum*.

P. simplum is smaller than *P. schansiense*. Its crista in the upper molars is small and short, hardly forked at its lingual end. Its cristella and postcrista are at the initial stage of development, as they show almost no fine enamel plications.

QIU & XIE (1998) indicated that there are only three truly hypsodont elasmotheres (the crown height in M^2 is far greater than its length or width): *Elasmotherium*, *Sinotherium* and *Parelasmotherium*. Both *Elasmotherium* and *Sinotherium* are large. Their teeth are differentiated into crown and prism parts, and have particularly complex enamel plications. *Parelasmotherium* is smaller, without undifferentiated crown and prism parts in the upper cheek teeth, and with almost no fine enamel plications (KILLGUS 1923).

Parelasmotherium linxiaense DENG, 2001

Some cheek teeth (IVPP V 12650.1–6) of *Parelasmotherium linxiaense* were found in the basal red clay of the Liushu Formation at Guonigou, in Dongxiang County (DENG 2001b). The large size, relatively weak enamel plications, and marked crista and hypocone distinguish *P. linxiaense* from *P. schansiense* and *P. simplum*. The upper cheek teeth of *P. linxiaense* are not differentiated into crown and prism parts, and the enamel is scarcely wrinkled. The upper molars have well-developed crista and large hypocone, and the lower molars have trigonid and talonid of the same size, as well as well-developed anterior and posterior cingula.

The upper cheek teeth of *P. linxiaense* are wider than those of *P. schansiense* and *P. simplum*, but also of *S. lagrelli*. *Parelasmotherium* and *Sinotherium* have significantly different lower cheek teeth. As in the upper cheek teeth, the enamel plications in the lower cheek teeth of *Parelasmotherium* are minimal, whereas *Sinotherium* has highly plicate enamel. In lateral view, in the lower cheek tooth row of *Sinotherium* the premolars are inclined backward while the molars are inclined forward. Hence, the worn surface is beveled in *Sinotherium*, and orthogonal in *Parelasmotherium*. RINGSTRÖM (1924) described that the lower cheek teeth of *Sinotherium* have no well-developed cingula. In contrast, *Parelasmotherium* has well developed anterior and posterior cingula in its lower cheek teeth, and the anterior cingulum of M_3 extends to the middle of its labial wall. The trigonid and talonid of the lower cheek teeth in *Parelasmotherium* are of equal size, while the trigonid is smaller than the talonid in *Sinotherium* and *Elasmotherium*.

Parelasmotherium now counts three species, i.e., *P. schansiense*, *P. simplum* and *P. linxiaense*. Kretzoi (1942) divided the elasmotheres into two subfamilies on account of the position of the horn on the skull: the Elasmotheriinae, with a large frontal horn, and the Iranotheriinae, with a nasal horn. The Elasmotheriinae include *Sinotherium* and *Elasmotherium*. Heissig (1989) considered Chen's (1977) *Ningxiatherium longirhinus*, transitional from the Iranotheriinae to the Elasmotheriinae. Fortelius & Heissig (1989) shared this opinion. Cerdeño (1995), in contrast, placed *Ningxiatherium* and *Elasmotherium* in a monophyletic group closer to other Rhinocerotini than to the Iranotheriinae. The new material from Linxia proves that *Parelasmo therium* is closely related to *Sinotherium* and *Elasmotherium*. Cerdeño (1995) also admitted that the tooth characters of *Ningxiatherium* are similar to those of *Iranotherium* and different from those of *Elasmotherium*.

Genus ***Iranotherium*** Ringström, 1924
Iranotherium morgani (Mecquenem, 1908)

Two almost complete skulls (HMV 0979, 1098) and a mandible (HMV 1099) of the genus *Iranotherium morgani* were found in lower red clay of the Liushu Formation at Shanzhuang and Houshan, in Guanghe County (Deng 2005b). *I. morgani* is the only known rhinoceros with a rugosity for larger masseteric and temporalis musculature on each zygomatic arch of the male individual, which suggests that the sexes of this species are distinguished by dimorphic differences.

I. morgani is a large-sized rhinoceros with a huge nasal horn, and its skull is particularly elongate and dorsally concave. The parietal crests are broadly separate, and the nasals are long and wide, with a shallow nasal notch. The orbit is prominent, with an anterior margin situated at the level of M^3. The nasal horn of the male is much larger than that of the female, and a strong and rough hemispherical hypertrophy is present on the posterior part of the zygomatic arches of the male (Deng 2005b). The posterior part of the zygomatic arches is uplifted and higher than the skull roof. The paroccipital process is completely fused with the posttympanic process. The teeth are hypsodont, covered and filled with cement, and the enamel is slightly wrinkled. The premolars are significantly shortened.

The specimens from Linxia are generally similar to the skull and mandible of *Iranotherium morgani* from Maragha (Mecquenem 1908), with some differences. Because the P_2 strongly overlaps P_3, which in turn markedly overlaps P_4, the premolar row of the Linxia mandible is very short, and the premolar row/molar row ratio is 0.4. In the Maragha mandible, in contrast, the P_2 does not overlap P_3, and the premolar/molar row ratio is in fact 0.6. These are interpreted as individual or sexual differences of no taxonomic importance.

The skulls of *I. morgani* from Linxia are relatively complete; new cranial characters can thus be observed. Ringström (1924) thought that the species' upper dental formula was 0.0.3.3, but P^1 is well developed on both skulls from the Linxia Basin. Moreover, male skulls are more massive than those of females, and have larger nasal horn and stronger zygomatic arches. The cheek teeth of *I. morgani* are hypsodont and have wrinkled enamel, indicating that it was a grazer that lived in open grassland.

Iranotherium morgani was originally known only from Maragha and Kerjavol in Iran and it was biochronologically referred to MN 11–12 (Bernor et al. 1996, Antoine 2002). *I. morgani* from the Linxia Basin, instead, can be correlated to MN 10 (Deng et al. 2004a, b), and therefore appeared earlier than the Maragha representative of the species. The Elasmotheriini dispersed from Asia (Heissig 1999). *I. morgani* is likely to have first appeared in northwestern China and it later dispersed westward to central Asia (Deng 2005b).

Rhinocerotini Dollo, 1885
Genus ***Dicerorhinus*** Gloger, 1841
Dicerorhinus ringstromi Arambourg, 1959

Several skulls of *Dicerorhinus ringstromi* were discovered from the top red clay of the Liushu Formation at Qianzhuang, Jinchanggou, and Bancaoling, in Hezheng County (fig. 3). This species has a long skull with a very wide infraorbital foramen on each maxillary. The nasals are long and wide, with a huge and domed horn boss. The nasal notch is widely U-shaped in lateral view; it ends at the level of the P^3/P^4 commissure. The anterior margin of the orbit is located at the level of the middle of M^2, with a strong preorbital tubercle and a well-developed lacrimal tubercle. The postorbital process is weak, and the facial crest is strong. The skull roof is concave, but the occiput is not too raised. The frontal is very convex, but the frontal horn boss is small, and the parietal crests are broadly separated. The occipital surface is inclined anteriorly, and the occipital crest bears a wide notch at the midline. The nuchal ligament depression is shallow, and the occipital condyles are triangular, with a marked horizontally transverse crest. The vomer is thin and far from the palate. The posttympanic and the postglenoid processes are fused to form a false exterior auditory meatus.

In the upper premolars, the protocone is not constricted, the antecrochet is absent, the crochet is narrow, the parastyle is weak, and the paracone rib is weak or absent. In the upper molars, the protocone is not constricted, the parastyle is wide and projected, the antecrochet is wide and short, and the crochet is well developed. M^1 and M^2 have a marked paracone rib, and M^3 has a triangular occlusal surface.

Ringström (1924) described *Dicerorhinus orientalis* from Baode, Shanxi, but Arambourg (1959) considered

Fig. 3: Skull of *Dicerorhinus ringstromi* from Qianzhuang in the Linxia Basin (Gansu, China), HMV 1115. 1. lateral view; 2. dorsal view; 3. occlusal view. Scale bars: 10 cm.

it different from the European representatives, and renamed the Chinese species *Dicerorhinus ringstromi*. *D. ringstromi* is markedly larger than *D. orientalis* from Pikermi, Greece, but it also exceeds in size the extant *D. sumatrensis*

D. ringstromi was also discovered in the Duodaoshi Formation in Jingmen, Hubei, as well as in the Youshashan Formation in Qaidam, Qinghai, which are both referred to MN 12 (Yan 1979, Deng & Wang 2004). The body size of *D. ringstromi* is gigantic, and it has hypsodont teeth and cursorial limb bones (Guérin 1980). Its habit was very similar to that of the extant *Ceratotherium simum*, adapted for life in a steppe (Ringström 1924).

Genus ***Coelodonta*** Bronn, 1831

Coelodonta nihowanensis Kahlke, 1969

Teilhard de Chardin & Piveteau (1930) described a milk tooth row from Nihewan (Hebei, China) as *Coelodonta* cf. *antiquitatis*, which was clearly considered a primitive species of woolly rhino, and implied that the woolly rhino actually originated in Asia. A new species, *Coelodonta nihowanensis*, was later defined for the Chinese Late Pliocene *Coelodonta* specimens (Kahlke 1969). Beliaeva (1966) described a new species, *Coelodonta tologoijensis*, from Tologoj (Ulan-Ude, Transbaikalia), whose distal limb bones exhibit primitive and cursorial features different from the short-limbed *C. antiquitatis*. *C. tologoijensis*, however, is similar to *C. antiquitatis* in some respects, while it differs from *C. nihowanensis* in having very wide nasals significantly bent downward, a rounded nasal tip, a well-developed frontal horn boss, and a constricted mandibular symphysis with a posterior border at the level of the P_2/P_3 commissure. The protocone and hypocone in the upper teeth of *C. nihowanensis* are characteristically large, much larger than those of *C. tologoijensis* and *C. antiquitatis*. *C. tologoijensis* is actually very close to *C. antiquitatis* in its cranial, mandibular and dental characters. The skull, mandible, teeth, and limb bones of *C. nihowanensis* are more primitive than those of *C. tologoijensis*.

A complete adult skull with mandible (HMV 0980) and a partial juvenile skull (HMV 0981) of *Coelodonta nihowanensis* were found in the earliest loess deposits, paleomagnetically dated 2.55–2.16 Ma, at Longdan, in Dongxiang County (Deng 2002a, Qiu et al. 2004a). This material is assigned to the woolly rhino because of the diagnostic presence of the ossified nasal septum, the loss of the incisors, and the wavy labial wall of the upper and lower cheek teeth. The woolly rhino from Linxia is also characterized by its dolichocephalic skull and great occipital elevation as in the skulls of some later Eurasian representatives of *Coelodonta* (Borsuk-Białynicka 1973).

C. nihowanensis is more primitive than *C. antiquitatis* in its smaller size, weaker frontal horn, incomplete nasal septum, triangular M^3, hardly separated parietal crests, shorter nasals separated from premaxillaries by a nasal septum, uplifted posterior part of the zygomatic arches, shorter preorbital length, and larger angle between the parietal and occipital surfaces; vertical ascending rami, and anteriorly shifted mental foramina; presence of lower incisor alveoli, moderate cement on the slightly wrinkled enamel surface, weaker parastyle and posterior edge of protoconid, absence of true metalophid in P^4, wider median valley and slighter oblique protocone, and weaker antecrochet in DP^3.

Recently discovered limb bones of *C. nihowanensis* from the Linxia Basin show that it was a highly cursorial rhino with very slender limb bones. Beliaeva (1966) indicated that the limb bones of the woolly rhino discovered in Nihewan by Teilhard de Chardin & Piveteau (1930) were more slender not only than those of the Late Pleistocene *C. antiquitatis*, but also of *C. tologoijensis*, in particular their humeri, radii, and femora. The slenderness of the limbs of *C. nihowanensis* from Longdan (fig. 4, tab. 2) is readily apparent if we compare the measurements of its metacarpals with those of *C. antiquitatis*. *C. nihowanensis* can thus be considered the earliest known woolly rhino.

We can therefore assert that the woolly rhino, which was distributed widely in north Eurasia during the Late

Fig. 4: Right carpals and metacarpals of *Coelodonta nihowanensis* from Longdan in the Linxia Basin (Gansu, China), IVPP V 14967. 1. mesial view; 2. anterior view; 3. lateral view. Scale bars: 5 cm.

Table 2: Measurements (mm) and comparison of metacarpals of *Coelodonta nihowanensis* from the Linxia Basin (Gansu, China) and *C. antiquitatis*

Measures	*C. nihowanensis* IVPP V 14967			*C. antiquitatis* Mean (Guerin, 1980)		
	Mc II	Mc III	Mc IV	Mc II	Mc III	Mc IV
1. Length	164.5	-	154.4	164.2	189	151.1
2. Proximal transverse diameter	46	50.4	43.4	52.9	68.2	53.3
3. Middle transverse diameter	31.5	40	35.4	42.4	56.4	37.6
4. Distal maximal transverse diameter	42	-	-	48.8	65.8	47.9
5. Distal articular transverse diameter	30	-	35	43.5	56.1	45.2
6. Distal anteroposterior diameter	35.4	-	32.5	43.1	50.8	42.3
Proportion: 2/1 (%)	28	-	28.1	32.2	36.1	35.3
Proportion: 3/1 (%)	19.1	-	22.9	25.8	29.8	24.9
Proportion: 5/1 (%)	18.2	-	22.7	26.5	29.7	29.9

Pleistocene, first appeared in northern China at 2.55 Ma. In the Late Pliocene of northern China *Coelodonta* was represented by only one species, *C. nihowanensis*. The genus then underwent an adaptive radiation during the Pliocene, which originated the multitude of species described in the literature (Guérin 1980). The cranial and dental features of the Eurasian *Coelodonta* indicate that derived varieties of *Coelodonta* already existed in northern China by the end of the Pliocene, and that they dispersed to North Asia and Europe giving rise to several different forms during the Middle Pleistocene and later time.

Conclusions

Ten genera and thirteen species of Rhinocerotidae have been found in Neogene deposits in the Linxia Basin (Gansu, China). *Chilotherium anderssoni* is reported for the first time in the Linxia Basin, while *Aprotodon* sp. is found for the first time in the Lower Miocene of the basin. A very primitive species of *Chilotherium* appears in the Lower Miocene basal red clay: this suggests that the genus originated in East Asia. The Miocene and Pliocene history of the Linxia Basin rhinoceroses is quite well documented, but there are three biozone gaps in the local mammalian sequence from MN 4 on. Not only rhinoceroses, but also other macromammals are not represented in the local MN 7/8, MN 13, and MN 15–16 biochronologic units.

The history of the Linxia Basin rhinocerotids can be divided into several stages which can be grouped as follows:

1. Early Miocene (MN 4). *Aprotodon* sp. is the only rhinoceros known in the Linxia Basin during this age, where it lived alongside the well represented proboscidean *Gomphotherium*, as indicated by the Dalanggou fossil record.

2. Middle Miocene (MN 5–6). This time period is characterized by the abundant presence of *Hispanotherium matritense* and *Alicornops laogouense*. They also accompany the equid *Anchitherium* and different proboscideans, such as *Gomphotherium* sp., which was found at Wangshijie, and *Gomphotherium* sp., *Zygolophodon* sp., and *Platybelodon grangeri*, encountered at Zhujiachuan, Hujialiang and Laogou.

3. Late Miocene (MN 9–12). This is the period when rhinoceroses reached the highest diversity. In fact, eight species are represented at this time, although no more than three occur at each site, i.e., Houshan, Shuanggongbei and Shanzhuang. They are associated with very abundant macromammals of the *Hipparion* fauna, and *Chilotherium wimani* is absolutely dominant in number, and present in all the sites of MN 10-11 age. Elasmotheres are more diversified in the Linxia Basin during the Late Miocene than in any other Eurasian region of any age.

4. Early Pliocene (MN 14). At this time there is the rare presence of *Shansirhinus ringstromi*, attested to at Yinchuan and Shilidun. In the Linxia Basin, the diversity and number not only of the rhinoceroses, but also of other mammals dramatically dropped during this age. Because *Shansirhinus* is phylogenetically intermediate between *Acerorhinus* and *Chilotherium*, it likely appeared earlier, during the Miocene.

5. Late Pliocene (MN 17). Rhinoceroses are rare. They are only represented by *Coelodonta nihowanenis*, as attested to by the finds from Longdan and Shitougu. In contrast, other large mammals in the accompanying *Equus* fauna grew in diversity and number, especially carnivores, reaching a taxonomic composition similar to that of the alpine mammalian fauna of modern Himalayas.

Rhinocerotid diversity and physical morphology are most sensitive to environmental factors and particularly to changes in temperature and humidity. The different stages described above can be compared with the major event in the history of the equids. Rhinoceroses' greatest diversity in the Linxia Basin is reached when *Hipparion* arrives and radiates in the area. The opposite occurred in Spain, where the arrival of *Hipparion* occurs when rhinocerotids begin to decline (Cerdeño 1992). The distribution of the Neogene rhinocerotids in China can be correlated with paleoclimatic changes (Deng & Downs 2002), and their distribution in the Linxia Basin reflects the same trend.

Acknowledgements

I thank Prof. Z. X. Qiu, Prof. B. Y. Wang, Dr. X. M. Wang, and Dr. X. J. Ni for their support in the fieldwork and discussion on the manuscript. I am grateful to Dr. L. Flynn for his improvement to the manuscript in English. CFS reviewers, Dr. C. Guérin and an anonym are thanked for their helpful suggestions and constructive comments. This work is supported by the National Natural Science Foundation of China (40232023), and the Major Basic Research Projects of MST of China (2006CB806400).

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Manuscript submitted 2005–10–04
Revised manuscript accepted 2006–08–14