Linxia Basin: An Ancient Paradise for Late Cenozoic Rhinoceroses in North China

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The Linxia Basin is located on the triple-junction of the northeastern Tibetan Plateau, western Qinling Mountains and the Loess Plateau. The basin is filled with 700−2000 m of late Cenozoic deposits, mainly red in color and dominated by lacustrine siltstones and mudstones, and the Linxia sequence represents the most complete and successive late Cenozoic section in China. The localities in the Linxia Basin are notable for abundant, relatively complete, well-preserved, and sometimes partially articulated bones of large mammals, which often occur in dense concentrations. Many new species of the Late Oligocene *Dzungariotherium* fauna, the Middle Miocene *Platybelodon* fauna, the Late Miocene *Hipparion* fauna, and the Early Pleistocene *Equus* fauna have been described from the Linxia Basin since 2000, including rodents, lagomorphs, primates, carnivores, proboscideans, perissodactyls and artiodactyls.

Among these mammalian fossils, several hundred skulls of the late Cenozoic rhinoceroses are known from the Linxia Basin. In addition, more abundant limb bones and isolated teeth of rhinoceroses are found in this basin, especially from the Late Miocene red clay deposits. Rhinoceroses were over 70% in diversity during the Late Oligocene, and they were dominant in population during the Late Miocene. In the Middle Miocene and Early Pleistocene faunas, rhinoceroses were important members.

Late Oligocene

The Late Oligocene fauna of the Linxia Basin comes from the sandstones of the Jiaozigou Formation. At least eight species of rhinoceroses were found from this fauna, including two forms of giant rhinos. The giant rhinos, the largest land mammals, are an endemic group almost exclusively to Asia, with only sparse findings in Europe (Qiu and Wang, 2007). Their giant size and some features so distinctive from the living rhinoceroses have attracted much attention not only from specialists, but also from the public. According to the fossil specimens from the Linxia Basin, the body weight of the giant rhino *Dzungariotherium orgosense* is estimated at 24 tons, and another species *Paraceratherium yagouense* at 22 tons (Deng, 2009). In this fauna, other rhinoceroses include Hyracodontidae gen. et sp. indet., *Ardynia* sp., *A. altidentata*, *Allacerops* sp., *Ronzotherium* sp., and *Aprotodon lanzhouensis*. Rhinoceroses dominated the Late Oligocene fauna in the Linxia

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Basin, where predators were relatively primitive, with creodonts represented by *Megalopterodon* (Fig. 1) only rarely seen.

In the Siwalik area on the southern border of the Tibetan Plateau, there was also distribution of giant rhinos in the Late Oligocene. In the global range, a great regression took place at 30 Ma, with nearly simultaneous disappearance of the Turgai Strait. The first uplift of the "Tibetan Plateau" might have occurred in a large area at the latest Early Oligocene. On the other hand, the discoveries of giant rhinos on the south and north sides of the Tibetan Plateau indicate that the uplift of the plateau had no enough height to prevent dispersals of huge mammals, therefore giant rhinos, aprotodons and chalicotheres were free to migrate between the south and north sides of the "Tibetan Plateau."

Fig.1 A habitat of giant rhinos during the Late Oligocene. In the foreground, a creodont (*Megalopterodon* sp.) is attacking a giant rhino calf (*Dzungariotherium orgosense*). The top right corner shows the comparison of the upper second molars between *D. orgosense* (left) and *Ardynia altidentata* (right) to the same scale.

Middle Miocene

The Middle Miocene mammals of the Linxia Basin were collected from the sandstones or conglomerates of the Dongxiang and Hujialiang formations. The fossils of this fauna are represented by the shovel-tusked elephant *Platybelodon*, and the rhinoceroses *Hispanotherium matritense* and *Alicornops laogouense* are important members. In Eurasia, *H. matritense* was found in Spain, Portugal, and France in Europe, and Turkey, Pakistan, Mongolia, and China in Asia. *H. matritense* is small-sized, with one nasal horn, and it has subhypsodont cheek teeth with very thick cement cover. *Alicornops* is distributed widespread in Europe during MN 6-10, and it was found from the Middle Miocene strata in Turkey. *Alicornops laogouense* is a middle-sized acerathere, and its skull is the largest of the genus. The origins of the *Hispanotherium* and *Alicornops* lineages may be in southwestern Europe. With the discovery of *H. matritense* and *A. laogouense* in the Linxia Basin, it appears that they dispersed from western Europe through eastern Europe, western Asia

and southern Asia, to the Far East.

H. matritense in Europe was considered to live in dry and warm settings because of its hypsodont teeth with thick cement cover and slender limbs. 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. A large number of fossils of *Platybelodon*, which favored habitats near water, were found with *H. matritense* and *A. laogouense* in the Linxia Basin. This shows that lakes and rivers were abundant in the environment in which these rhinoceroses lived (Deng, 2003, 2004). In the Middle Miocene, *Platybelodon* was found from many localities on the north side of the Tibetan Plateau, while this proboscidean form has no trace in the Indian subcontinent on the south, which suggested that the uplift of the Tibetan Plateau by this period was high enough to baffle interchanges of large mammals.

Late Miocene

The Late Miocene fauna of the Linxia Basin was found from the red clays of the Liushu Formation and characterized by the three-toed horse *Hipparion*. In this fauna, the rhinoceros *Chilotherium* was dominant in population, and other rhinoceroses showed the largest diversity of this group during the geological history of the Linxia Basin, including *Acerorhinus hezhengensis, Shansirhinus ringstroemi, Chilotherium primigenius, C. wimani, C. anderssoni, Iranotherium morgani, Parelasmotherium simplym, P. linxiaense, Ningxiatherium euryrhinus, Dicerorhinus ringstroemi,* and *Diceros gansuensis.*

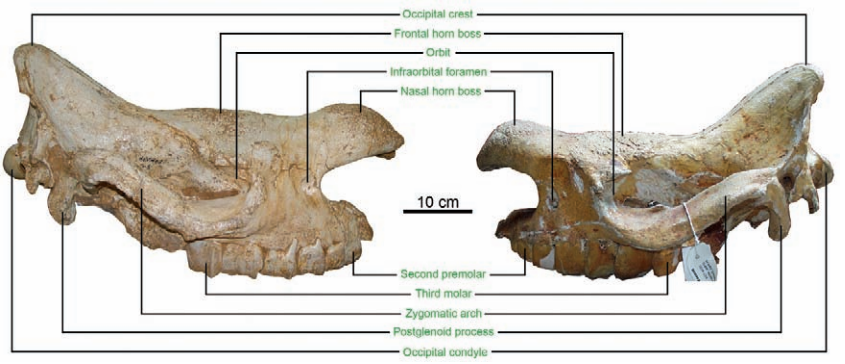

Fig.2 The fossil black rhino (*Diceros gansuensis*) from the Linxia Basin, the first discovery of this lineage from East Asia, is the ancestor form of the extant African black rhino (*D. bicornis*). Two skulls (left: *D. gansuensis;* right: *D. bicornis*) are shown herein to exhibit the morphological similarities and differences between them.

Chilotherium wimani is the most abundant taxon in the Linxia Basin. Remains of *C. wimani* are in fact found practically everywhere in the middle and upper parts of the Liushu Formation. *C. wimani* is a middle-sized rhinoceros without any horn, and its particularly wide mandibular symphysis has two huge tusk-like incisors. *Iranotherium 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 this species was sexually dimorphic. *I. morgani* has a large size with a huge nasal horn and hypsodont teeth, and its skull is particularly elongate and dorsally concave. The sexually dimorphic characters of the male and female skulls of *I. morgani* show that the male skull is more massive, with stronger zygomatic arches. These features, especially the huge nasal horn, could be used for defense or competition for mates. *I. morgani* was a polygynous grazer lived in an open steppe. It is likely to have first appeared in northwestern China, later dispersing westward to central Asia (Deng, 2005). The skull, mandible and teeth of *Diceros gansuensis* from the Linxia Basin are distinct from those of the African living black rhino *D. bicornis* (Fig. 2). Lacking fossils, the early evolutionary history of the African rhinoceroses remained poorly known until quite recently. *Diceros gansuensis* is the first fossil species of the *Diceros* lineage ever found in East Asia, and this discovery supports that the African rhinoceroses were split up into its two living genera already at the beginning of the Late Miocene (Deng and Qiu, 2007). In the Late Miocene, the Tibetan Plateau became a more sufficient barrier for animal dispersals. Components of the *Hipparion* fauna at high-level taxa were similar to those of the modern mammalian fauna.

Early Pleistocene

The Early Pleistocene fauna of the Linxia Basin comes from the Wucheng Loess. In this fauna, the number of carnivore species is high, and their specimens are particularly numerous, even outnumbering the total of herbivores. The representative *Equus eisenmannae* is a giant true horse, and its size implies that it inhabited a cold

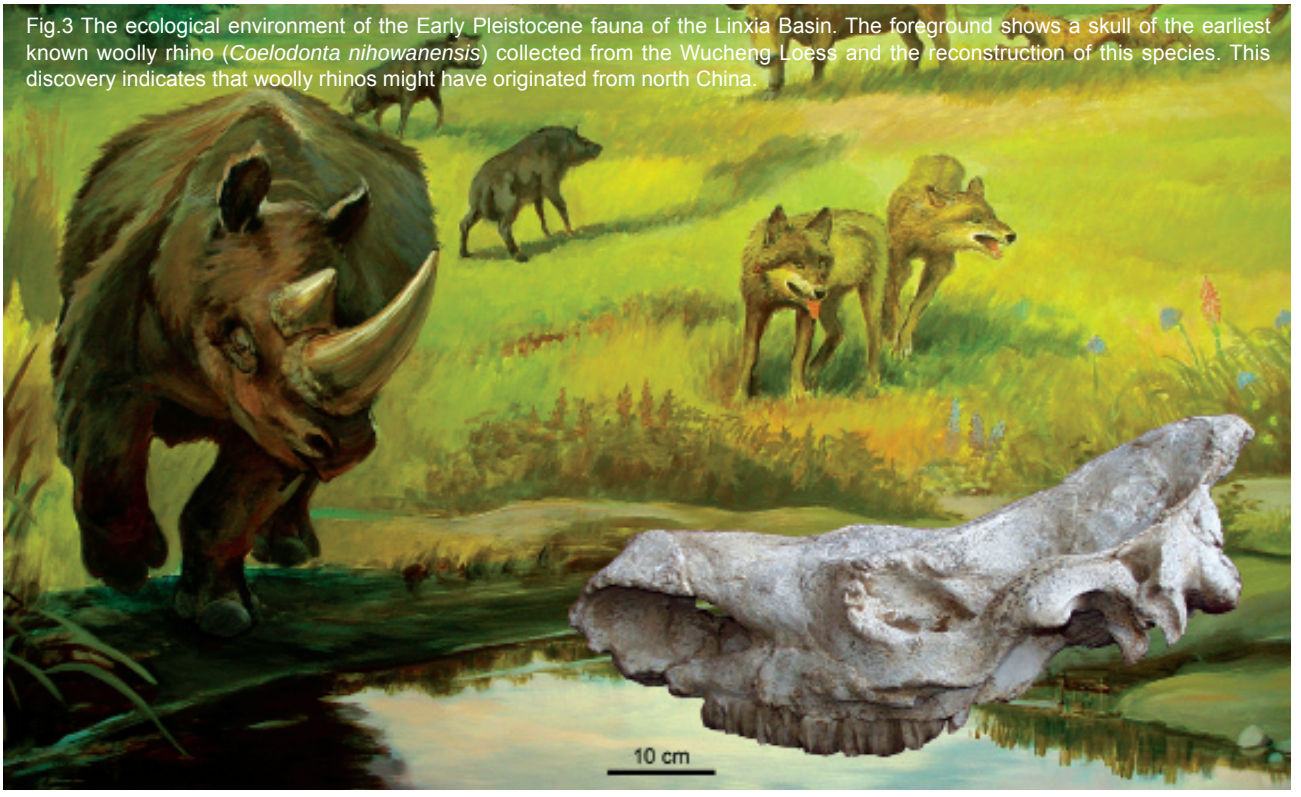

Fig.3 The ecological environment of the Early Pleistocene fauna of the Linxia Basin. The foreground shows a skull of the earliest known woolly rhino (*Coelodonta nihowanensis*) collected from the Wucheng Loess and the reconstruction of this species. This discovery indicates that woolly rhinos might have originated from north China.

environment with a vegetation of tough grasses. This habitat was suitable for the ancestor of the woolly rhino, *Coelodonta nihowanensis*, which was first found from Nihewan, Hebei, but its material included only a milk tooth row. A complete adult skull with mandible and a partial juvenile skull of *C. nihowanensis* were found from the earliest loess deposits in the Linxia Basin. It was clearly considered a primitive species of woolly rhino, and implied that the woolly rhino actually originated in Asia. They are by far the earliest remains of the woolly rhino in the world, and the origination of the woolly rhino, which was distributed widely in north Eurasia during the Late Pleistocene, is affirmed from northern China at the beginning of the Quaternary (Deng, 2008).

Since the beginning of the Quaternary, the climate had become cold and dry, and the diversity of mammals had reduced in the Linxia basin. Taken as a whole, the Linxia Basin should have been predominantly an area of steppe, mixed with shrub and bush areas, occasionally with small patches of forest and woodland (Fig. 3). Loess might have just started to deposit, covering only small tops of the low mountains in this area. In the Early Pleistocene, the Tibetan Plateau was already uplifted considerably. The strong uplift of the Tibetan Plateau must have caused great environmental changes in the Linxia Basin. A stronger winter monsoon system and a higher continental desiccation occurred during this time span. The deteriorated climatic conditions in this area, such as lower temperature and less precipitation, are also reflected in the loess deposits, which are thick, but without marked paleosols.

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