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Incisor fossils of *Aprotodon* (Perissodactyla, Rhinocerotidae) from the Early Miocene Shangzhuang Formation of the Linxia Basin in Gansu, China

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Abstract　Lower incisor fossils of *Aprotodon lanzhouensis* collected from the Early Miocene deposits in the Linxia Basin, are described in this paper. Characteristically, they are relatively robust and strongly curved. The discovery of the new specimens causes the occurrence of *Aprotodon* across the Oligo-Miocene boundary in the Linxia Basin to be completely confirmed. The chronological and geographical distribution of *Aprotodon* was essentially coincident with that of giant rhinos, but the localities and numbers of individuals recording *Aprotodon* were relatively rare. The mandibular morphological function of *Aprotodon* suggests that this form lived in sparse riparian mosaics within the arid part of northwestern China, and South and Central Asia from the Late Eocene to the Early Miocene. *Aprotodon* experienced total extinction before the Middle Miocene, which possibly resulted from climatic changes. The pattern of occurrence of *Aprotodon* also indicates that the climatic and environmental conditions of the Linxia Basin during the Early Miocene were similar to relatively open woodlands of the Late Oligocene, in contrast to dense forests of the Middle Miocene.

Key words　Linxia Basin, Gansu, China; Early Miocene; Rhinocerotidae; *Aprotodon*

1　Introduction

Aprotodon is a large-sized primitive rhinocerotid form, and its distinct features include the specialized wide mandibular symphysis, which is similar to that of the hippopotamus, and the relatively robust and strongly curved lower incisors. Although *Aprotodon* has an enormous size, the previously found material included only some fragmental mandibular symphyses with huge tusks from South and Central Asia (Forster-Cooper, 1915; Beliajeva, 1954). Not until Qiu and Xie (1997) reported a skull and several mandibles from the Lanzhou Basin, were the characters of *Aprotodon* clearly recognized. After that, Qiu et al. (2004) reported a skull and mandible of *Aprotodon lanzhouensis* discovered from the Late Oligocene deposits in

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the Linxia Basin, Gansu, and Wang et al. (2009) described the lower incisors and cheek teeth of this species from the Late Eocene Houldjin Formation near Erenhot, Nei Mongol (Inner Mongolia). Previously, due to the lack of materials, the taxonomic position of *Aprotodon* was a highly disputed issue, and the genus had been considered to belong to brachypotheres (Pilgrim, 1912; Heissig, 1989; Prothero et al., 1989), elasmotheres (Kretzoi, 1942, 1943), aceratheres (Borissiak, 1954), or teleoceratines (McKenna and Bell, 1997). Qiu and Xie (1997) thought that all of the above-mentioned taxonomic positions were incorrect, and that *Aprotodon* would be an early specialized primitive true rhinoceros (family Rhinocerotidae).

Aprotodon was considered to be closest to the genus *Symphysorrachis*, which was created by Beliajeva (1954). The mandibular symphysis of the latter has begun to enlarge, and its dorsal surface is deeply concave between incisors; the i2 is robust and long, with very thin enamel; the lower dentition is complete, with flat but antero-labially oblique labial wall of the protolophid, sharp postero-labial corner, and relatively oblique labial cingulum at the anterior and posterior ends. Qiu and Xie (1997) indicated that some characters of *Aprotodon* are similar to those of the European *Ronzotherium*. Forster-Cooper (1915) considered that *Aprotodon* was similar to the hippopotamus in morphology, and its habitat and behavior indicated an extensive aquatic environment and a moist climate (Deng and Downs, 2002). The cheek teeth of *Aprotodon* are subhypsodont (Qiu and Xie, 1997), so it ate mainly leaves and soft twigs.

The fossils of *Aprotodon lanzhouensis* from the Lanzhou Basin have an age from the Early Oligocene to the Early Miocene (Qiu and Xie, 1997). The Late Oligocene Jiaozigou Fauna of the Linxia Basin also contained *A. lanzhouensis* (Qiu et al., 2004), but the Early Miocene deposits of this basin produced only a few lower cheek teeth of *Aprotodon* sp. (Deng, 2006). In May 2008, we collected six huge tusk-like incisors of *Aprotodon* from the Shangzhuang Formation in the Linxia Basin, which not only showed that *Aprotodon* survived surely into the Early Miocene in the Linxia Basin, but also proved that the climate in the Linxia Basin during the Early Miocene was similar to that of the Late Oligocene, and unlike that of the Middle Miocene.

Institutional abbreviations EMM, mammalian fossils of Eren Dinosaur Museum, Erenhot, Nei Mongol Autonomous Region; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; LX, prefix of IVPP vertebrate localities of Linxia Basin; V, vertebrate collection of IVPP.

2 Locality information

The incisors described in this paper were collected at Bianzike (LX 0801, 35°19′06.8″N, 103°17′06.7″E, elevation 2444 m) in Xinying Township, Hezheng County, Gansu Province. The fossiliferous bed is in the upper part of the Shangzhuang Formation, corresponding to the early Shanwangian Age of the Early Miocene. The fossil locality is situated at half way up a hill, and the lower part of this hill exposes the brownish-red mudstones of the Shangzhuang Formation with a stratigraphic attitude of 215°∠23°. This locality is near the deep grand fault in the south margin of the Linxia Basin, so the strata are obviously inclined. The studied fossils were excavated from about 10 m underground by a vertical shaft.

In the Linxia Basin, the late Cenozoic sedimentary sequence is very rich in mammalian fossils. Until now, a faunal sequence from the Late Oligocene to the Early Pleistocene has been established (Deng et al., 2004). On the other hand, Early Miocene fossils have been sparsely found. Previously, only some small mammalian fossils were found from the red mudstones of the Shangzhuang Formation at Sigou (LX 0051) in Alimatu Township, Guanghe County, including *Mioechinus* sp., *Amphechinus* sp., *Sinolagomys ulunguensis*, *Atlantoxerus* sp., *Paracricetulus*? sp., *Heterosminthus* sp., *Protalactaga* sp., *Litodonomys* sp., *Sayimys* sp., and *Tachyoryctoides* sp. (Deng et al., 2013), and a few large mammalian fossils were collected from the conglomerate and sandstone lenses of the Shangzhuang Formation at Dalanggou (LX 0001) in Maijiaxiang Township, Guanghe County, including *Choerolophodon guangheensis*, *Archaeobelodon* cf. *A. tobieni*, *Turcocerus* sp., and several isolated lower cheek teeth of *Aprotodon* sp. (Deng, 2006; Wang and Deng, 2011).

3 Description and measurements

The studied specimens are six in all (IVPP V 18191-18193). All of them preserve crowns and roots, but V 18193.1 (arc length: 248 mm at midline, Table 1) and V 18193.2 (Fig. 1B, arc length: 245 mm) lack most of their crowns. V 18191.1 is a left i2, without its tip and the end of the root, and its preserved part has an arc length of 320 mm. V 18191.2 (Fig. 1A) is the right i2 of the same individual as V 18191.1, and it is preserved the most completely, having lost only a little of the end of the root, with a remaining arc length of 424 mm. Each incisor was broken into many fragments, but they had been restored. Four specimens can be easily distinguished as two pairs, representing two individuals, and V 18192.1 (Fig. 1C) and V 18192.2 should be the crown and the root of the same incisor, with arc lengths of 249 mm and 201 mm, respectively. All incisors have a distinct wear facet that is narrowly oval in outline (Fig. 1, A1 and B1). The root surface develops dense and slightly undulating rings, with a frequency of one ring each millimeter and a more marked white ring every 5 rings (Fig. 2A).

Table 1 Measurements of incisors of *Aprotodon lanzhouensis* from Bianzike in the Linxia Basin (mm)

Catalogue No.	Arc length	Chord length	Base width	Base thickness
V 18191.1 (left)	320	292	43.5	31
V 18191.2 *(right)	424	347	42.5	34.3
V 18192.1 (crown)	249	215	52	36
V 18192.2 (root)	201	201	52	41.5
V 18193.1 (left)	248	219	49.1	37.8
V 18193.2 (right)	245	218	46	38.4

* This specimen is nearly complete, and others are incomplete in different degrees.

Fig. 1 Right lower incisors of *Aprotodon lanzhouensis* from the Lower Miocene in the Linxia Basin
A. IVPP V 18191.2; B. V 18193.2; 1. lingual view; 2. labial view; C. V 18192.1, crown in anterior view

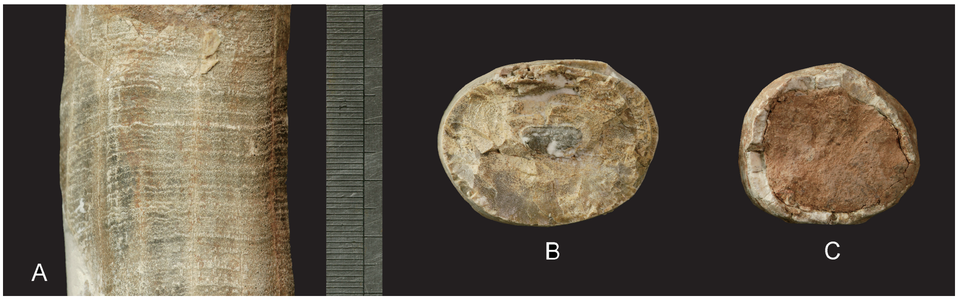

Fig. 2 Lower incisors of *Aprotodon lanzhouensis* from the Lower Miocene in the Linxia Basin
A. growth rings on the root, IVPP V 18191.1; B. cross section of the crown, V 18193.1; C. pulp cavity, V 18192.2; scale is in mm

The incisors are long and strongly curved, and their cross sections become oval at the crown base from triangular at the upper part of the crown. Thin enamel covers the labial and anterior surfaces. Both the crown and the root have similar lengths. The most completely preserved V 18191.2 has the crown length of 199 mm and the root length of 188 mm. The lingual margin is flange-like. The labial margin is a flange on the upper 2/3 of the crown, and gradually becomes rounded on the lower 1/3; the anterior margin is angular but rounded, and becomes an obtuse ridge near the tip. The lingual surface is a flat wear facet without any enamel from the tip to the crown base (Fig. 1, A1). The anterior surface is obviously narrower than the lingual and labial surfaces, and slightly concave (deeply concave to form a wide groove on V 18192.1, see Fig. 1C). The labial surface is smooth and slightly arched, with a width two times that of the anterior surface (Fig. 1, A2 and B2). The angle between the lingual and labial surfaces is acute, the angle between the lingual and anterior surfaces is slightly less than a right angle, and the angle between the anterior and labial surfaces is perpendicular. The dentine of the crown forms concentric circles, with a thickness in cross section of 2.5 mm for each layer (Fig. 2B).

The cross section of the root is oval in outline, and slowly becomes smaller toward the terminus, so the entire root is relatively robust. On the root surface, there are irregular longitudinal ridges and wide, shallow grooves. The pulp cavity is large, and filling of the red mudstone can be seen in the fractures of V 18191.2 (Fig. 2C) and V 18192.2. In V 18192.2, the pulp cavity has a major diameter of 26 mm and a minor diameter of 22 mm, with a wall 2.5 mm thick. The pulp cavity disappears at the break near the root end of V 18191.1, so it is not very deep. The complete root of V 18193.2 indicates that the pulp cavity is closed. The crown has a gradual transition to the root, without a clear boundary. The base of the wear facet has a large transverse groove on the anterior and labial surfaces, which corresponds to the alveolus margin.

The complete root of V 18193.2 is only 140 mm long, distinctly shorter than the 215 mm of V 18191.2. Therefore, the pair of incisors, V 18193.1 and V 18193.2, is interpreted to represent a female individual, and the other three incisors would represent male individuals. Their wear facets on the lingual surface are very long and stretch toward the crown base, with a length of 209 mm on V 18191.2. In other rhinocerotid forms, however, the lingual wear facet is always much shorter than the root.

4 Comparison

The Bianzike lower incisors (i2) are identical with those of *Aprotodon* in shape and size, clearly distinguishing this genus from other rhinoceroses. Among the known four species of *Aprotodon*, *A. lanzhouensis*, *A. smith-woodwardi*, *A. fatehjangensis*, and *A. aralensis*, the Bianzike specimens are closest to the lower incisors of *A. lanzhouensis*, but differ from the other three species in robustness, curvature, and cross section.

The lower incisors of *A. aralensis* are slender, with a maximum chord length of 237 mm and a smaller curvature (see Beliajeva, 1954:fig. 4). Among the Bianzike specimens, the chord length of V 18191.2 is 347 mm, much longer than that of *A. aralensis*, and the reconstructed full lengths of other lower incisors from Bianzike are also obviously longer than that of *A. aralensis*. The largest diameters of the lower incisors in *A. aralensis* are 33 mm × 35 mm, whereas 42.5–52 mm × 31–41.5 mm characterizes the Bianzike specimens. The crown in *A. aralensis* lacks a very prominent antero-labial edge, but this is very marked in the Bianzhike specimens, and is identical with that seen in *A. lanzhouensis* from Lanzhou.

According to the report of Beliajeva (1954), the lower incisors of *A. smith-woodwardi* have a relatively compressed and wide section, with an antero-posterior diameter of 24 mm and a lingual-labial diameter of 52–60 mm, features that differ greatly in the Bianzike specimens (Table 1).

A. fatehjangensis has no record of lower incisors, but it is an extremely specialized species with a large size (Qiu and Xie, 1997), greater than that of the Bianzike material.

The Bianzike specimens are identical in morphology to the lower incisors of *A. lanzhouensis* discovered from the Lanzhou Basin, and all measurements of the Bianzike specimens (Table 1) fall in the variation range of the specimens of *Aprotodon lanzhouensis* from the Lanzhou Basin (Qiu and Xie, 1997). They have almost the same diameters at the crown base: 42.5–52 mm × 31–41.5 mm for the Bianzike specimens, and 40–50.5 mm × 35–44.3 mm for the Lanzhou specimens (Qiu and Xie, 1997). In morphology, the Lanzhou and Bianzike lower incisors have a strong curvature and an enamel-free wear facet that is longer than the root, and their roots have a laterally compressed and inferiorly rounded cross section. Very thin enamel covers their anterior and labial surfaces with a lot of black longitudinal cracks. The cross section of their crowns is triangular, with sharp antero-lingual and postero-labial angles, a rounded antero-labial angle, a smooth or slightly concave anterior surface, and a slightly convex labial surface.

The shape and size of the Bianzike specimens are very similar to those of lower incisors of *Aprotondon lanzhouensis* from the Jiaozigou Formation in the Linxia Basin, especially a male incisor (IVPP V 13853)(Qiu et al., 2004). On the other hand, the Jiaozigou specimens have some minor differences from the Bianzike specimens. In the Jiaozigou incisors, for example, the lingual flange slightly exceeds the root in width, and the labial surface is slightly concave near the lingual surface to form a vertical groove (Qiu et al., 2004).

The specimens of *Aprotodon lanzhouensis* from the Houldjin Formation in Erenhot, Nei Mongol include a complete left i2 (EMM 0082), and three fragmentary lower incisors (Wang et al., 2009). EMM 0082 is robust and arched, with a chord length of 295 mm, an inner arc length of 305 mm, and an outer arc length of 355 mm, which are identical with those of V 18191.2. The thin enamel, triangular crown cross section, long wear facet, sharp lingual and labial margins, rounded anterior margin, marked longitudinal grooves on the anterior crown and lingual root surfaces, and weak longitudinal grooves and ridges on the labial surface are present in both Houldjin and Bianzike specimens. The Houldjin incisors have some features different from the Bianzike ones, such as a tongue-like facet under the wear facet and a transverse major axis of the root.

Among mammals with huge lower tusks, forms to compare with the Bianzike specimens include aceratheres, giant rhinos, and hippos.

The Bianzike specimens are different from lower incisors of the acerathere *Acerorhinus*. With *Acerorhinus lufengensis* as an example, its i2 is a huge tusk, with arched curvature from the crown to the root, and the lingual wear facet on the crown is a curved concave surface with a much shorter length than the root, the lower end of which extends onto the root. The crown base is the widest of the tooth and projecting lingually. The cross section is narrowly triangular, with a sharp lingual angle and rounded antero- and postero-labial angles. Its anterior and labial surfaces are smooth. The cross section of the root is narrowly oval, with a robust end, decorated by fine and dense longitudinal and transverse grooves on the surface to form a grid pattern (Deng and Qi, 2009). Qiu and Xie (1997) indicated that the lower incisors of *Aprotodon* are different from those of *Chilotherium*. The lower incisors of the latter are weakly curved, with rapidly narrowing roots and thick enamel. The i2 measurements of 70 *Chilotherium wimani* individuals show that the maximum crown length is 118.4 mm, the crown base width is 57.7 mm, and the crown base thickness is 30.5 mm (Chen et al., 2010), which indicate that the i2 crown of *Ch*. *wimani* is obviously shorter than that of the Bianzike specimens, and the base of the former is wider and more compressed.

Among giant rhinos, the lower tusks of *Paraceratherium* or *Aralotherium* are paired huge i1, but they are clearly different from the Bianzike specimens. The root of the former is robust, and the crown is a long cone with a circular cross section and a lingual cingulum, but lacking a wear facet (Ye et al., 2003; Qiu and Wang, 2007). On the other hand, the crown cross section in the Bianzike specimens is triangular, with a well-developed wear facet, but lacking a cingulum. The Bianzike specimens are much longer than the lower tusks of giant rhinos in both crown and root lengths. The i1 of *Paraceratherium lepidum* is 45 mm long for the crown and 33.5 wide at its base (Qiu and Wang, 2007). The i1 of *Aralotherium sui* is ca. 73 mm long for the crown and ca. 55 mm wide at the base (Ye et al., 2003). The i1 of *Turpanotherium elegans* is robust and long, and its root is slightly thicker than the crown base. Both crown and base have oval cross sections. The crown is coniform, with thin enamel and weak lingual cingulum at the base. The crown is 60 mm long, with a long diameter of 58 mm and a short diameter of 40 mm at the base (Qiu and Wang, 2007).

The incisors of the hippopotamus are very large, but they are straight and cylindrical, different from the compressed and strongly curved Bianzike incisors. The lower canines of the hippopotamus are strongly curved indeed, and they have thick enamel, strong longitudinal ridges and wide grooves on the surface, and a small wear facet at the upper half of the crown, which faces the center of the tooth arch. The pulp cavity of the root is large and open, and the diameter of the root is constant, not constricting toward its end. The crown has symmetrical lingual and labial surfaces. The arc length of the lower canine of the hippopotamus can reach 535 mm, and the chord length can reach 361 mm (Tripati and Godfrey, 2007), which are similar to the size of the Bianzike specimens. The canines of the modern hippopotamus have strong convergent ridges on the enamel (Boisserie, 2004). In hippopotamus fossils, the lower canines of *Hexaprotodon lothagamensis* are compressed from side to side and taper lingually, with a flattened lingual border, but they have a kidney-shaped section and enamel adorned with fine parallel ridges (Weston, 2000, 2003). Obviously, these features are different from those of the Bianzike specimens.

5 Paleoecology

The Houldjin fossils indicate that *Aprotodon lanzhouensis* first appeared in the Late Eocene (Wang et al., 2009). During the Oligocene and Early Miocene, *Aprotodon* apparently was rare, and it was distributed in the Lanzhou and Linxia basins as well as Pakistan and Kazakhstan, and was totally extinct before the Middle Miocene. It is significant to note that the chronological and geographical distribution of *Aprotodon* was essentially coincident with that of giant rhinos (Qiu and Wang, 2007). But the fossil localities of the former are much fewer than those of the latter. For example, *Aprotodon* has not been found in eastern Yunnan of southwestern China, in which there are several fossil localities with giant rhinos.

The Late Eocene-Early Oligocene transition was characterized by a major shift in global climate towards generally lower mean annual temperatures (by about 10℃), increased aridity, greater seasonal temperature fluctuations, and contraction of the tropical/temperate belts across the earth (MacFadden, 1992). The global climate gradually cooled with the formation of major Antarctic continental ice-sheets at ~36 Ma (Wang et al., 2003). Based on a compilation of paleobotanical and lithological data over China, the Paleogene saw a broad belt of aridity stretching across China from west to east, and during the Neogene this arid zone retreated to northwestern China (Sun and Wang, 2005). *Aprotodon* was distributed in the arid zone where most giant rhinos were found (Qiu and Wang, 2007). Because the mandibular symphysis of *Aprotodon* is very wide, resembling that of the hippopotamus (Foster-Cooper, 1915), this taxon may reflect an extensive aquatic environment (Deng, 2006). As a result, *Aprotodon* lived in rivers that crossed the otherwise open and dry woodland with low diversity under arid or semiarid conditions, so that *Aprotodon* has a limited distribution and number of individuals. The extinction of *Aprotodon* possibly resulted from climatic changes, because the climatic and environmental characteristics during the Early Miocene were similar to those in the Late Oligocene, but different from the dense and humid forests with high diversity of the Middle Miocene.

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临夏盆地早中新世上庄组的巨獠犀门齿化石

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摘要：记述了在临夏盆地早中新世地层中发现的兰州巨獠犀(*Aprotodon lanzhouensis*)的下门齿化石，其特点为非常粗壮并强烈弯曲。新材料的发现使巨獠犀在临夏盆地的延续时代跨越渐新世/中新世界线的推测得到完全证实。巨獠犀分布的地质时代和地理范围与巨犀重合，但巨獠犀的化石地点和个体数量都相当稀少。巨獠犀的下颌形态功能特点指示其生活于晚始新世至早中新世中国西北、南亚和中亚干旱环境地带中镶嵌分布的少量近水环境。巨獠犀在中中新世之前彻底绝灭，其原因可能是气候变化的结果，也说明临夏盆地早中新世的环境特征与晚渐新世的疏林系统相似，而不同于中中新世的茂密森林。

关键词：甘肃临夏盆地，早中新世，犀科，巨獠犀

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