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New material of *Aprotodon lanzhouensis* (Perissodactyla, Rhinocerotidae) from the Early Miocene in Northwest China

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Aprotodon is an extinct genus of the family Rhinocerotidae with a peculiar morphology that is mainly embodied in the wide mandibular symphysis and a pair of prominent second low incisors. The genus once lived on the vast grasslands of Asia, from Pakistan, and Kazakhstan to China, during the Late Eocene to the Early Miocene. The scarcity and incompleteness of the record, however, make the morphological characteristics of *Aprotodon* rather perplexing. Here, we report on a better mandible fossil with an intact second right incisor from the Xianshuihe Formation from the Early Miocene age (approximately 21–20 Ma) in the Lanzhou Basin, Gansu Province, China. Several important features, notably the elongated strongly curved tusk-like incisors and mandibular symphysis, which widens sharply in the anterior part of the mandible, support attribution to *A. lanzhouensis*. Compared with previous specimens, the material described here is distinct in the lack of p1, horizontal ramus, and the ventral morphology of the mandible symphysis. Based on the new fossil specimen, we provide new material for the understanding of this extinct peculiar rhinoceros.

KEYWORDS

Aprotodon lanzhouensis, Lanzhou Basin, new material, Rhinocerotidae, the Early Miocene

1 | INTRODUCTION

Aprotodon has already been found in Pakistan (Forster-Cooper, 1915; Pilgrim, 1912), Kazakhstan (Beliajeva, 1954; Borissiak, 1954; Heissig, 1972), and the Linxia Basin and Lanzhou Basin of Gansu Province in Northwest China, as well as in Erenhot in Inner Mongolia (Qiu et al., 1997, 2004; Wang, Qiu, Zhang, Wu, & Ning, 2009; Deng, 2013) from the Late Eocene to the Early Miocene. We know little about the overall appearance of this peculiar rhino despite the number of localities with fragmentary remains. To date, four species of *Aprotodon* have been established, including *A. smith-woodwardi* (Forster-Cooper, 1915), *A. fatehjangensis* (Pilgrim, 1912), *A. aralensis* (Heissig, 1989), and *A. lanzhouensis* (Qiu et al., 1997). The rhino's particularities not only include a mandibular symphysis that widens transversely and has a rather thin anterior border, but also a long and strongly curved set of lower second incisors. The materials of the genus are quite rare, but recently, relatively more materials of

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ing areas of China. The new fossil material was excavated from the Early Miocene

Aprotodon have been unearthed in Gansu Province and its surround-

Huangyangtou locality of Lanzhou Basin. It is similar to A. *lanzhouensis* in mandible symphysis and second incisor morphology, so it should belong to the same species. The mandible has an intact right incisor that is described here and contributes to a better understanding of this peculiar primitive rhinoceros.

Institutional Abbreviations - NWUV, vertebrate specimen of Northwest University.

2 | GEOLOGIC SETTING

As a sub-basin of the Longzhong Basin, the Lanzhou Basin is located in the transitional region between the Tibet Plateau and the Loess Plateau and in the conjunction of the Tibet Plateau cold region, the Eastern monsoon region, and the arid region of Northwest China (Dmitrienko et al., 2018; Zhang, 2015). Geographically, the basin contains important information related to the uplift of the Tibet Plateau, the formation and evolution of Asian monsoon, and drought event of Northwest China.

The Lanzhou Basin preserves continuous continental strata from the Tertiary (Figure 1), in which several widely disparate mammalian faunas are produced (including Perissodactyla, Artiodactyla, and Proboscidea, as well as small mammals such as Lagomorpha, Rodentia, and Eulipotyphla), providing an excellent window into the mammalian composition of the Cenozoic. The Tertiary of Lanzhou Basin has been divided into the Xiliugou Formation, Yehucheng Formation, Xianshuihe Formation, and Linxia Formation, from the Palaeocene to Pliocene. The Xianshuihe Formation, which has a stratigraphic chronology from the late Early Oligocene to the Miocene, consists of fluvial-lacustrine deposits (Yue et al., 2003). Qiu et al. (1997) divided it into three sedimentary cycles from the bottom to top layer, corresponding to the lower, middle, and upper portions, respectively (Figure 2). More specifically, the lower segment of the Xianshuihe Formation is composed of yellow sandstone at the bottom and dark red mudstone in the lower section and contains Nanpoping fauna and Xiagou fauna, that date from the late Early Oligocene to the Late Oligocene. The middle member belonging to the Early Miocene consists of white sandstone and yellow mudstone and contains Zhangjiaping fauna and Duitinggou fauna. The upper section is mainly composed of the intermixed beds of yellow-pebbled sandstone and dark brown mudstone and contains Quantougou fauna and Xingjiawan fauna, from the middle to Late Miocene (Qiu et al., 1997, 2001; Xie, 2004; Li, Li, Zhang, Li, & Xie, 2016).

In 1986, Qiu and other researchers from the Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences collected several *Aprotodon* fragments from Zhangjiaping, a village approximately 10 km northwest of Lanzhou. Two years later, they collected a relatively complete left mandible with symphysis near Duitinggou, approximately 10 km east of Zhangjiaping. Except for one specimen produced from the yellow sandstone in the lower member of the Xianshuihe Formation, the remains were unearthed from the white sandstone of the middle member of the formation (E. Miocene). Based on these new materials, a new species, *A. lanzhouensis*, (Qiu & Xie, 1997) had been established.

The new fossil material described here was excavated from the upper section of the white sandstone layer in the middle member of Xianshuihe Formation in Huangyangtou of the north bank of the Yellow River (Figure 1). The palaeomagnetic age of this member is 24–18 Ma (Yue et al., 2001; Zhang, 2015), which contains the fossiliferous bed of the Zhangjiaping fauna (approximately, 21–20 Ma). Therefore, the new material belongs to the Zhangjiaping fauna and can be compared with the Xiejia period in China, which are MN2 and Ar3 in the European and North American geochronology respectively.

3 | SYSTEMATIC PALAEONTOLOGY

Order Perissodactyla, Owen, 1785 Family Rhinocerotidae, Gray, 1821 Genus Aprotodon, Forster-Cooper, 1915 Aprotodon lanzhouensis, Oiu & Xie, 1997

Material-NWUV1541 is a relatively complete mandible to which a complete right incisor robustly is attached. The sample lacks a mandibular angle and vertical ramus, and only p4 and m1 are present on the broken left horizontal ramus.



FIGURE 1 Maps of Tertiary strata and localites of *Aprotodon* in Lanzhou Basin, Gansu Province, China (modified from Qiu et al., 1997; China map after China National Bureau of Surveying and Mapping Geographical Information, Ministry of Natural Resources of the P.R.C.)

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FIGURE 2 Stratigraphic column of the Oligocene-Early Miocene of Huangyangtou and Duitinggou in the Lanzhou Basin (modified from Zhang, 2015; Yue et al., 2001; Li et al., 2019)

Locality and Horizon: The upper section of the first white sandstone layer of the Xianshuihe Formation from the Early Miocene, north trench of Huangyangtou, Lanzhou Basin, Gansu Province.

Diagnosis: According to Qiu et al. (1997), the mandibular symphysis widens abruptly from p4, and the front border is rather thin; ventral surface of the mandibular symphysis is flat or bears a prominent middle ridge (the new specimen); the lower incisors are long and strongly curved; a robust mandible with high horizontal ramus bears the mandibular foramen below the third premolar (p3), without an alveolar trace on the diastema anterior to the second premolar (p2) while p1 is very small or absent (the new specimen).

Description and measurement: The fossil described here is likely the best-preserved mandible and incisor of *A. lanzhouensis* discovered to date, although it lacks a mandibular angle (Figure 3). Due to the nonpreservation of a left horizontal ramus posterior to the first molar (m1), only half of the horizontal ramus is preserved with a remnant of i2, while the right i2 remains complete. From the lateral view, the horizontal ramus is robust and tall, at approximately four to six times the size of the crowns of the cheek teeth. Except for slightly bending ventrally, the inferior margin of horizontal branch and alveolar borders both stay horizontal so that the height of the preserved portion of the right ramus is constant. The extremely thin, blade-shaped anterior border is merely 8 mm in thickness, bearing a pair of first lower incisor alveoli. The width of each alveolus is just 8 mm, and the distance between the alveoli is 13.95 mm. There exists a longitudinal ridge in the middle of the ventral surface, with irregular nutrient foramina on both sides. The second pair of lower incisors is long and strongly curved, with the crown turning upright and even slightly inwards. In the occlusal view, the symphysis starts widening rapidly from p4 ventrally at a width of 108.5 mm, expanding to 211.45 mm at the front border, presenting a prominent inverted triangle. The existence of robust mandibular incisors leads to thick cylindrical bulges of two sides of the symphysis, while the middle section invaginates, forming a longitudinal, anteverted concavity consequently, deepening gradually from p2 ventrally.

The right i2 is complete. The elongate incisors are one of most prominent features, with a complete outer arc length of 525.32 mm,



FIGURE 3 Lower mandible of *A. lanzhouensis* from Huangyangtou of Lanzhou Basin. (a) labial view; (b) anterior view; and (c) occlusal view. Scale bar equals 5 cm

inner arc of 427.38 mm, and chord length of 374.65 mm. These are so long that they can be clearly distinguished from those of other genera, such as the cone-shaped incisor of Indricotherium and shorter, daggershaped incisors of Chilotherium (Li, Zhang, Li, Li, & Xie, 2017; Qiu et al., 2007). With the help of computed tomography (CT) scanning technology, we observed that the proximal end of the incisor extends anteriorly to the p4 (Figure 4). In the lateral view, the root is wrapped in the tooth-socket and lifts slightly, before bending obliquely upwards. The tooth crown is almost perpendicular to the horizontal ramus, with the tip of the crown turning inwards. The lingual surface is flat and wide, without an enamel layer but with dense, tiny lines extending from the top to the root of the incisor, indicating the wear facet of i2. The anterior surface is obviously narrower and is concave, forming a vertical groove. The labial surface has a similar width as the lingual surface. A ring-like protrusion separates the crown base and root of the incisor. The cross section of the crown is nearly triangular, with a length of 216.9 mm. Only a thin layer of enamel covers the anterior and labial surfaces. The side between the lingual surface and anterior surface is relatively sharp, opposite to the obtuse ridge edges between the lingual and labial surfaces, as well as the anterior and labial surfaces. As a result, the lingual and anterior surfaces bear an acute angle. The intersection angle between the lingual and anterior surfaces is two times that of the former and is at approximately a right angle. The cross-section of the incisor root assumes an oval shape with the major axis extending forward but coarsens downwards gradually and tapers beneath p3. The incisor root growing outside the alveolus is 107 mm and lacks an enamel layer. The length and width of the crosssection at the alveolus of the left incisor is 49.14×37.32 mm, which is appreciably larger than the right incisor. The pulp cavity is very small and disappears near the end of the root.

There are no signs of p1 or its alveoli on the mandible of the fossil described here. Both p2 and p3 were lost, but the morphological



FIGURE 4 Computed tomography (CT)-based scanning technology of the A. *lanzhouensis* mandible symphysis. (a) Labial view, bone-made semitranspatent for observation of incisor's morphology; (b) occlusal view; and (c) cross-section of mandible on CT images. Scale bar equals 5 cm

features of the alveoli indicate that the teeth possess strong double roots. All the check teeth, from p4-m1, tilt forward obviously. The upper portion of roots of the teeth was exposed above the gum line, with minimum heights for p4-m3 of 10.66, 12.87, 9.82, and 8.61 mm, respectively. However, the crowns of the lingual side are relatively low, for example, the maximum height of m1 is just 7.4 mm. Suffering from severe abrasion, the white dentin of the teeth has been broadly exposed on the chewing surface.

The p4 is molarized. The labial and lingual surfaces are covered with enamel, except for the anterior and posterior sides. Only a small remnant of the trigonid basin remains, and the talonid basin has become a shallow V-shaped pit. The protolophid, metalophid, and hypolophid are actually wide, whereas the ectolophid narrows towards the lingual side.

The m1 suffered such severe abrasion that almost the crests have been worn away and the dentin is exposed across the entire width of the flat chewing surface. We can observe that the anterior and posterior dentine of m1 are tightly attached to those of p4 and m2 and lack enamel. The lingual side seems to be worn more heavily than the labial side. The trigonid and talonid basins are worn down.

The m2 is less worn than m1 and has an intact tooth crown. The protolophid's ectotheca bulges outwards and shows an obtuse angle.

The paralophid presents a finer ridge, that narrows towards the lingual side. The straight ectotheca of the hypolophid stretches obliquely forward until the lower one-third of the metalophid. The posteroexternal corner approximates a right angle. Both the trigonid basin and talonid basin are V-shaped, but the latter seems apparently wider and deeper.

The exposed dentine between the cusps of m3 is joined together. The chewing surface of the trigonid tilts forward. Its paralophid is like a slender ridge forming an acute angle on the lingual side. Trigonid basin develops into a V-shaped valley, which is much larger than that of m2, while the talonid basin is wide and deeply U-shaped, reaching the base of the crown. The complete metalophid, ectolophid, and hypolophid are clear. We can also observe an obtuse postero-external corner and a faint cingulum on the labial surface, which obliquely rises to the top of the crown.

Comparison and discussion: The genus *Aprotodon* was first established by Forster-Cooper based on two mandibular symphyses from Baluchistan, Pakistan. The name *Aprotodon smith-woodwardi* originated from the misidentification of this new species as the earliest hippopotamus without incisors. Since then, similar mandibular symphyses, skulls, and scattered upper teeth have intermittently been found in other places of Pakistan and Kazakhstan (Beliajeva, 1954; Forster-Cooper, 1934; Heissig, 1972; Pilgrim, 1912), which were successively classified as *Teleoceras*, *Chilotherium*, *Aceratherium*, and Aprotodon aralense. Then, Qiu established A. lanzhouensis based on a skull and a mandible with symphysis and combined the species *Teleoceras fatehjangense* created by Pilgrim into the genus *Aprotodon*. It was not until then that the features of *Aprotodon* began to become clearer. Since then, materials of *Aprotodon*, such as skulls, mandibles with symphysis, and lower incisors from Linxia Basin in Gansu Province and Erenhot in Inner Mongolia, have been reported, confirming that this genus survived from the Late Eocene to the Early Miocene. According to the previous studies, the fossils of *Aprotodon* include four species: A. *smith-woodwardi*, A. *fatehjangensis*, A. *aralensis*, and A. *lanzhouensis*. Compared with the other three species, the Huangyangtou specimen has its own unique features (Table 1).

First, the dental formula is different. P1 does not erupt in Huangyangtou specimen, and the dental formula should be $2 \cdot 0 \cdot 3 \cdot 3$. The CT cross-sectional images also show no sign of p1 or alveolar remnants. A. *smith-woodwardi* and A. *aralensis* possess p1, although the presence of p1 in A. *fatehjangensis* still remains controversial due to the lack of mandible materials. Regarding the absence of p1 in our fossil material, there are two possibilities: one is that the specimen from Huangyangtou did not develop dp1 after birth as a result of intraspecific variation, which is different from other mandible materials of A. *lanzhouensis*. Except for the first possibility, the lack of p1 may also be related with tooth replacement at different stages of dental development. According to extensive research, as the most

TABLE 1 Comparison of Huangyangtou specimen and other species of Aprotodon

	A. lanzhouensis			
Species	Huangyangtou specimen	Duitinggou specimen (holotype)	A. aralensis	A. smith-woodwardi
p1	Non-existent	Existent	Existent	Existent
i1	Existent	Existent	Existent	Non-existent
i2	Long, strongly curved	Long, strongly curved	Short, lessly curved	_
Outer arc of i2 L(mm)	525.32	350	237	-
Cross-section of root L \times W(mm)	$\textbf{51.73}\times\textbf{30.8}$	$40\sim 50.5\times 34$	33 imes 35	-
Major axis of incisor cross-section	Longitudinal	Longitudinal	Transversal	Transversal
Antero-external edge of incisor crown	Apparent	Apparent	Inapparent	-
Top surface of symphysis	Deeply concave	Deeply concave	Lessly concave	Deeply concave
Ventral surface of symphysis	Uneven, with apparent middle ridge	Flat, middle ridge inapparent	Flat, middle ridge apparent	Flat, without middle ridge
Thickness of symphysis front border	Extremely thin, about 8–9 mm	Extremely thin, about 10 mm	Slightly thick, about 18 mm	Extremely thin
Width of symphysis front border	211.45	220 ^a	205 ^a	200
Horizontal ramus width of posterior border of symphysis	57.45-60.79	45	-	55
Morphology of horizontal ramus	High and horizontal	Low and curved	-	_
Morphology of check teeth alveolar border	Horizontal	Curved	-	-
Cingulum	Very little	Visible	Visible	-

^aThe data from the illustrations of articles of Qiu et al., 1997; Beliajeva, 1954; Forster-Cooper, 1915. A. *fatehjangensis* is not listed for this species only has a P4 and M2.

variable character among all teeth, dp1 usually erupts after dp2 and dp3 and sometimes later than dp4 (Hitchins, 1978; Player & Feely, 1960; Tong, 2001). However, as an individual grows up, dp1 is not replaced by a permanent premolar, which is different from what occurs in dp2-dp4 (Forster, 1965; Goddard, 1970). Considering that the mandible of a male *A. lanzhouensis* individual from Duitinggou of Lanzhou Basin still bears a dp1 and that the mandible of a female individual from Yagou also preserves a tiny alveolus of dp1, it is reasonable that the Huangyangtou specimen could have developed a dp1 at a younger age and later lost it without replacement of the permanent premolar. Later, the small alveolus healed and gradually closed up.

Furthermore, there are significant discrepancies in the morphology of the mandible symphysis, horizontal ramus, and lower i2 between the new fossil material and others.

The transverse width of A.smith-woodwardi's mandibular symphysis is approximately 200 mm, and the horizontal ramus of the posterior border of symphysis is 55 mm wide, which resembles with the measurements of the new material from Huangyangtou (211.45 mm and 57.45-60.79 mm, respectively). Furthermore, both species have a symphysis with extremely thin front borders. The incisor alveoli of A. smith-woodwardi present a longitudinally compressed ellipse, of which the transverse width (52–60 mm) is larger than the thickness (24 mm; Beliajeva, 1954). We can observe the opposite situation in the Huangyangtou specimen. The incisor cross-section is a lengthwise oval with a larger thickness (51.73 mm) than width (42.5 mm). In addition, according to the description of Forster-Cooper (1915), there is no sign of the first incisor socket on the front border of symphysis. and he excluded the possibility of closure from extremely old age. One fragment of the mandibular symphysis still maintains the stump of the first premolar. However, we cannot observe any sign of dp1 (or p1) on the mandible of A. lanzhouensis from Huangyangtou but a pair of tiny first incisor alveoli on the front border of the symphysis.

The incisors of A. *aralensis* look much finer and shorter, curving slightly; the diameter of the thickest section is only 33×35 mm, and the maximum chord length is just 280 mm. The Huangyangtou specimen has much longer, stouter, and more strongly curved incisors. In addition, the antero-external side of *A. aralensis* incisor crown is inapparent, while that of the latter approximates a typical triangular pyramid with clear sides. Finally, the thickness of symphysis front border of *A. aralensis* is up to 18 mm with a less-concave top surface, but

concerning the Huangyangtou specimen, the thickness of the front border of symphysis is just half that of *A. aralensis*, and has a deeper concave surface.

The materials of *A. fatehjangensis* only include P4 and M2 for comparison. Judged by the measurements, the length and width of P4 are 43×55 mm which is larger than that of the *A. lanzhouensis* holotype, so Qiu et al. (1997) inferred that this species was probably bulkier than *A. lanzhouensis*. However, the scarcity of fossil materials makes objective description of *A. fatehjangensis* rather difficult.

As the earliest Aprotodon individual found in China, the holotype of A. *lanzhouensis* was also collected from the white sandstone of the Xianshuihe Formation in Duitinggou of the Lanzhou Basin. Our new material actually shares common features with the Duitinggou specimen: the rapid widening of the mandibular symphysis with a thin front border, the concave top surface, and the pair of very small incisor alveoli. The shapes and measurements of the lower incisors also align well (Table 2), such as those of the long and strongly curved i2 and cross-sectional shape of the crown and root. Consequently, the new material from Huangyangtou is most similar to A. *lanzhouensis* and can be assigned to this species.

On the other hand, the Huangyangtou specimen has some characteristics that differ from the Duitinggou material (Figure 5). There is a middle ridge on the ventral side of the Huangyangtou specimen symphysis, both sides protruding upwards while Duitinggou specimen has a flat ventral surface and an inapparent middle ridge. Its horizontal ramus is higher, with much longer incisors than the counterparts from Duitinggou (Table 2). The lower edge of horizontal ramus of the Huangvangtou specimen is subparallel with gum lines, showing an approximately straight line, which is markedly different from the Duitinggou specimen, which is arcuate, lifting forward slightly. The high horizontal ramus shrinks obliguely forward from the mandibular angle to the posterior edge of p4 and then widens sharply, while the horizontal ramus of the Duitinggou material is relatively low. More importantly, the dental formula of cheek teeth of the Huangyangtou specimen is incomplete, with few cingula but the Duitinggou specimen bear single-rooted dp1 and well-developed antero-external cingula.

The wear of cheek teeth is certainly caused by chewing food, which results in marked changes in the shape and appearance of the grinding surface, and should be proportional to the individual's age as well as teeth replacement (Morris, 1972). In view of this correlation,

TABLE 2 Measurements and comparison of i2 among A. lanzhouensis from different sites (mm)

Locality ^a	Duitinggou of Lanzhou ¹	Erenhot ²	Bianzike of Linxia ³	Huangyangtou of Lanzhou
Length of outer arc	350	355	424	525.32
Chord length	280	295	347	374.65
Length of crown base ^b	43	42.5 ; 47.7 ; 51.4	40.3 ; 43.6	47.6
Width of crown base ^b	34	32.9 ; 41.7 ; 43	29.5;32.7	30.8
Length of root base ^b	$40\sim 50.5$	40.3 ; 43.6	42.5 ; 47.7 ; 51.4	51.73
Width of root base ^b	$35 \sim 44.3$	29.5;32.7	32.9 ; 41.7 ; 43	42.5

^aBased on: (1) Qiu et al. (1997), Qiu, Wang, and Deng (2004); (2) Wang et al. (2009); (3) Deng (2013). ^bThe bases of crown and root represent the thickest part of incisors. **FIGURE 5** Morphological comparison of horizontal rami between A. *lanzhouensis* from Huangyangtou and Duitinggou. Scale bar equals 5 cm. (a) Specimen from Huangyangtou and (b) specimen from Duitinggou (Qiu et al., 1997)



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TABLE 3 Relative age classes and chronological ages of extant African black rhinoceros (Hillman-Smith et al., 1986)

Age classes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Chronological ages	0	0.5	1	1.5	2	3	4	5	6	7	8	9	10	12	14	17	21	25	30	35

TABLE 4 Lower check teeth measurements of A. lanzhouensis (mm)

Locality ^a	Duitinggou of Lanzhou ¹	Yagou of Linxia ²	Erenhot ³	Huangyangtou of Lanzhou
dp1	9.8 × 9	_	_	Nonexistent
p2 L \times W	18.2×14	23.8 × 13.1	-	-
p3 L \times W	$\textbf{23.6-30.8}\times\textbf{19}\sim\textbf{21}$	28 imes 20	$\textbf{26.5} \times \textbf{19.8}$	-
p4 L \times W	26.2×21.8	32.3 × 23	$\textbf{30.4} \times \textbf{21.8}$	28.83 × 23.79
m1 L \times W	$31.3-35.4 \times 24.1-24.2$	31 imes 24.3	35.5 imes 23.4	$\textbf{29.1} \times \textbf{23.82}$
m2 L \times W	36.2-42.8 imes 22.5-24.2	40.7 × 25	$\textbf{42.3} \times \textbf{25.3}$	$\textbf{38.97} \times \textbf{25.67}$
m3 L \times W	39 × 24.4	45 imes 23	-	$\textbf{43.81} \times \textbf{26.85}$
p2-p4L	66	84.4	-	71.86
m1-m3L	109	116.2	-	108.36
dp1-m3L	183	195	-	-
p2-m3L	175	-	_	181.21

^aBased on: 1 Qiu et al. (1997); (2) Qiu et al. (2004); (3) Wang et al. (2009).

we can estimate the relative age of the rhinoceros by comparing with tooth eruption and wear stages of well-established age-classes based on extant rhinoceroses (Goddard, 1970; Hitchins, 1978; Hillman-Smith, Owen-Smith, Anderson, Hillman-Smith, & Selaladi, 1986; Tong, 2001; Wilson, Grigson, & Payne, 1982). According to Goddard's research (Goddard, 1970), the age criteria of extant black rhinoceros can be divided into 20 relative age classes (Table 3). The fossil described here is undoubtedly an adult due to the deciduous teeth that have already been replaced by permanent teeth and an erupted m3. Furthermore, the exposed dentine between the cusps of cheek teeth is joined together, and all cusps of m1 are worn away, just leaving a flat chewing surface, p2 and 3 missing. Comparing these characters with age classes built by Goddard (1970), the age of the rhinoceros we excavated from Huangyangtou could be assigned to class 15-16, which corresponds to a mean chronological age of 14-17 years. We know that the highest life expectancy of extant adult rhinoceros is about 30 years, however, only approximately 23% of investigated samples can live up to 23 years (Goddard, 1970; Zhang &

Xue, 1994). It means that rhinoceros of 14–17 years likely represents a relatively older individual in the rhino fauna. In addition, other changes also occur in teeth, for example, the pulp cavity can serve as an index of mammalian relative age because young teeth always have large pulp cavities, while older teeth have smaller space inside (Morris, 1972). Through CT scanning technology, we found that the pulp cavity became occluded by hard dentine except for a tiny space at the end of the incisors. Based on the above analyses, the specimen described here may represent an older individual. It is possible that the two rhinoceros individuals from Huangyangtou and Duitinggou died at different ages and that the Huangyangtou specimen should be older than the latter. As a result, the cingula had already been worn away, while that of the Duitinggou fossil material suffered lighter abrasion and the dp1 had not yet fallen out.

Except for Lanzhou Basin, skulls and mandibles of A. *lanzhouensis* were also found in Yagou Late Oligocene brown sandstone and sandy conglomerate in Linxia Basin (Qiu et al., 2004). The position of the mandible foramen and incisor shape are similar to those of the Huangyangtou

fossil. Qiu et al. (2004) considered that specimen to be a female individual, which bears a much narrower mandibular symphysis and the lower edge of the horizontal ramus is curved, and the second incisors are much shorter and thinner than those of the male individual from Huangyangtou.

Wang et al. (2009) reported a right mandible and left i2 of *A. lanzhouensis* from the Late Eocene Huerjing Formation of the Erlian Basin (Tables 3 and 4). It provides fossil evidence for the earliest emergence of the genus *Aprotodon* in China. The similarities between this specimen and the material from Huangyangtou lie in the long and curved i2, thin enamel layer, cross-section morphology, sharp ridge between the lingual and anterior surfaces and ridge between labial and anterior surfaces. But the left i2 from Erlian Basin is shorter, and the lingual surface seems smoother without longitudinal grooves.

Deng (2013) described the incisors of A. *lanzhouensis* from the Early Miocene deposits of the Shangzhuang Formation from Bianzike in Linxia Basin (Tables 3 and 4), which resembled the specimen of Huangyangtou to a large extent, such as the stout and curved i2 and the cross-sections of crown and root, but the former is shorter than Huangyangtou specimen.

Considering its peculiar morphology and surface feature, it can be speculated reasonably the long incisors can serve as defensive weapons for interspecific interactions with predators (Hyaenodonts) or may be used as intraspecific signalling just like the tusks of hippos. However, the long incisors should not possess the function of chewing food.

Overall, based on the living environment of the extant or closely related species, Zhangjiaping fauna to which our material belongs can be roughly divided into two categories: grassland animals and forest animals (Zhang, 2015). The grassland mammals accounted for more than 60% of the total species (Zhang, 2015), which indicates that temperate grassland expanded in the Early Miocene. Sporopollen analysis also suggests that herbs (mainly Chenopodiaceae, Compositae, and Gramineae) increased greatly, while trees decreased compared with in the Oligocene. Typical indexes of dry environment (Ephedripties and Nitrariadites) appeared; Pteridophyte, which favours warm, moist environments of the lower layer of forest was obviously reduced (Geng, Tao, & Xie, 2000; Ma, 1992; Song, Wang, & Mao, 2008; Wang & Qiu, 2000a, 2000b). The palaeoenvironment of the Lanzhou Basin in the Early Miocene evolved into a temperate semidry grassland characterized by the Chenopodipollis-Ephedripites-Compositae assemblage and sparse forest steppe. In addition, from the perspective of sedimentary environment, the greyish-white medium-coarse sandstone bearing the Huangyangtou specimen develops tabular cross-bedding and trough cross-bedding, which indicates a rather strong water dynamic condition; besides, as the markers of fluvial channel sedimentary microfacies, fine-grained conglomerates and mud gravel can also be observed at the bottom of the thick sandstone. From above sedimentary characteristics, we consider the Huangyangtou area was mainly influenced by fluvial sedimentary environment, and there should be river(s) flowing through the region. Therefore, we can speculate A. lanzhouensis lived on riparian mosaics near rivers flowing across the semiarid open bush-grassland of the Lanzhou Basin during the Early Miocene (Deng, 2015). It also reflects the climate of the

Early Miocene might be slightly warmer and wetter than current environment of Lanzhou area.

4 | CONCLUSIONS

The new material of primitive rhinoceros occurred from the Early Miocene Xianshuihe Formation of Northwest China should be attributed to A. *lanzhouensis* for elongated strongly curved tusk-like incisors and wide mandibular symphysis. Besides, combined with its morphological characteristics, especially the wear of cheek teeth, it probably represents an old male individual. The earliest *Aprotodon* materials in Asia were excavated from the Late Eocene Huerjing Formation of the Erlian Basin, Inner Mongolia; then, it survived from the Oligocene to the Early Miocene and experienced the final extinction in the middle Miocene. About 21 million years ago, this kind of peculiar rhinoceros, as well as other mammals, once habitated on the semiarid open bush-grassland of Lanzhou Basin, which also indicates warmer and moister environment than today.

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CONFLICT OF INTEREST

The authors declare there is no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data openly available in a public repository that issues datasets with DOIs.

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REFERENCES

- Beliajeva, E. I. (1954). New material of Tertiary rhinocerotids. *Trans Paleont Inst Acad Sci USSR*, 47, 24–54.
- Borissiak, A. A. (1954). The oldest Aceratherium from Kazakhstan. *Trans Paleont Inst Acad Sci USSR*, 47, 5–23.
- Deng, T. (2013). Incisor fossils of Aprotodon (Perissodactyla, Rhinocerotidae) from the Early Miocene Shangzhuang Formation of the Linxia Basin in Gansu, China. Vertebrata Palasiatica, 51(2), 131–140.
- Deng, T. (2015). Chinese Neogene Rhinoceroses, Shanghai, China: Shanghai Science & Technology Press.
- Dmitrienko, L. V., Wang, P. C., Li, S. Z., Cao, X. Z., Ian, S., Zhou, Z. Z., ... Zhu, J. J. (2018). Meso-Cenozoic evolution of Earth surface system under the East Asian tectonic superconvergence. *Acta Geologica Sinica (English Edition)*, 92 (2), 814–849.

Forster, J. B. (1965). Mortality and ageing of black rhinoceros in east Tsavo Park, Kenya. *East African Wildlife Journal*, 3(1), 118–119.

- Forster-Cooper, C. (1915). New genera and species of mammals from the Miocene deposits of Baluchistan: preliminary notice. *The Annals and Magzine of Natural history(including Zoology, Botany and Geology), 8,* 404–410.
- Forster-Cooper, C. (1934). The extinct Rhinoceroses of Baluchistan. Philosophical Transactions of the Royal Society of London, 223, 569–616.
- Geng, B. Y., Tao, J. R., & Xie, G. P. (2000). Early Tertiary fossil plants and paleoclimate of Lanzhou Basin. Acta Phytotaxonomica Sinica, 39(2), 105–115.
- Goddard, J. (1970). Age criteria and vital statistics of a black rhinoceros population. *African Journal of Ecology*, *8*, 105–121.
- Heissig, K. (1972). Palaontologische und geologische Untersuchungen im Tertiar von Pakistan. 5. Rhinocerotidae (mamm.) aus den unteren und mittleren Siwalik-Schichten. Abhandlungen der Bayerischen Akademie der Wissenschaften, 152, 1–112.
- Heissig, K. (1989). The Rhinocerotidae. In D. R. Prothero & R. M. Schoch (Eds.), *The evolution of Perissodactyla* (pp. 399–417). New York, NY: Oxford University Press.
- Hillman-Smith, A. K. K., Owen-Smith, N., Anderson, J. L., Hillman-Smith, A. J., & Selaladi, J. P. (1986). Age estimation of the white rhinoceros (*Ceratotherium simum*). Journal of Zoology, 210, 355–377.
- Hitchins, P. M. (1978). Age determination of the black rhinoceros (Diceros bicornis Linn.) in Zululand. South African Journal of Wildlife Research, 8, 71–80.
- Li, Y. X., Zhang, Y. X., Li, J., Li, Z. C., & Xie, K. (2017). New fossils of paraceratheres (Perissodactyla, Mammalia) from the Early Oligocene of the Lanzhou Basin, Gansu Province, China. Vertebrata Palasiatica, 56(4), 367–381.
- Li, Z. C., Li, Y. X., Xue, X. X., Li, W. H., Zhang, Y. X., & Yang, F. (2019). A new fossil Erinaceidae from the Shajingyi Area in the Lanzhou Basin, China. Acta Geologica Sinica, 93(4), 789–798.
- Li, Z. C., Li, Y. X., Zhang, Y. X., Li, W. H., & Xie, K. (2016). Nanpoping fauna of the Lanzhou Basin and its environmental significance. *Science China Earth Sciences*, 46(6), 824–833.
- Ma, Y. Z. (1992). Abundant sporopollen from the Tertiary red deposits in the northeastern edge of Tibetan plateau and its significance. *Chinese Science Bulletin*, 13, 1245–1246.
- Morris, P. (1972). A review of mammalian age determination methods. Mammal Review, 2(3), 69-104.
- Pilgrim, G. E. (1912). The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. *Palaeontologia India*, 4, 1–83.
- Player, I. J., & Feely, M. A. (1960). Preliminary report on the square-lipped rhinoceros Ceratotherium simum simum. Lammergeyer, 1, 3–22.
- Qiu, Z. X., Wang, B. Y., & Deng, T. (2004). Mammal fossils from Yagou, Linxia Basin, Gansu, and related stratigraphic problems. *Vertebrata Pal-Asiatica*, 42(4), 276–296.
- Qiu, Z. X., Wang, B. Y., Qiu, Z. D., Heller, F., Yue, L. P., Xie, G. P., ... Engesser, B. (2001). Land mammal geochronology and magnetostratigraphy of mid-Tertiary deposits in the Lanzhou Basin, Gansu Province, China. *Eclogae Geologicae Helvetiae*, 94, 373–385.
- Qiu, Z. X. & Wang, B. Y. (2007). Paracerathere fossils of China. Paleontologica Sinica 193(29), 1–396.

- Qiu, Z. X., Wang, B. Y., Qiu, Z. D., Xie, G. P., Xie, J. Y., & Wang, X. M. (1997). Recent advances in study of the Xianshuihe Formation in Lanzhou Basin. In Y. S. Tong, Y. Y. Zhang, W. Y. Wu, J. L. Lim, & L. Q. Shi (Eds.), Evidence for evolution: Essays in honor of Prof. Chung chien Young on the Hundredth anniversary of his birth (pp. 177–192). Beijing, China: China Ocean Press.
- Qiu, Z. X., & Xie, J. Y. (1997). A new species of Aprotodon (Perissodactyla, Rhinocerotidae) from Lanzhou Basin, Gansu, China. Vertebrata Pal-Asiatica, 35(4), 250–267.
- Song, Z. C., Wang, W. M., & Mao, F. Y. (2008). Palynological implications for relationship between aridification and monsoon climate in the Tertiary of NW China. Acta Palaeontologica Sinica, 47(3), 265–272.
- Tong, H. W. (2001). Age profiles of rhino fauna from the middle pleistocene nanjing man site, south China-explained by the rhino specimens of living species. *International Journal of Osteoarchaeology*, 11, 231–237.
- Wang, B. Y., & Qiu, Z. X. (2000a). Dipodidae (Rodentia, Mammalia) from the lower member of Xianshuihe Formation in Lanzhou Basin, Gansu, China. Vertebrata PalAsiatica, 38(1), 10–35.
- Wang, B. Y., & Qiu, Z. X. (2000b). Micromammal fossils from red mudstone of lower member of Xianshuihe Formation in Lanzhou Basin, China. *Vertebrata PalAsiatica*, 38(4), 255–273.
- Wang, B. Y., Qiu, Z. X., Zhang, Q. Z., Wu, J. L., & Ning, P. J. (2009). Large mammals found from Houldjin Formation near Erenhot, Nei Mongol, China. Vertebrata PalAsiatica, 47(2), 85–110.
- Wilson, B., Grigson, C., & Payne, S. (1982). Ageing and sexing animal bones from archaeological sites. British Archaeological Reports, 109, 1–268.
- Xie, G. P. (2004). The Tertiary and local mammalian faunas in Lanzhou Basin, Gansu. *Journal of Stratigraphy*, 28(1), 67–80.
- Yue, L. P., Heller, F., Qiu, Z. X., Zhang, L., Xie, G. P., Qiu, Z. D., & Zhang, Y. X. (2001). Magnetostratigraphy and paleoenvironmental record of Tertiary deposits of Lanzhou Basin. *Chinese Science Bulletin*, 46(1), 770–773.
- Yue, L. P., Qiu, Z. X., Xie, G. P., Qiu, Z. D., Zhang, L., Zhang, Y. X., & Heller, F. (2003). Sedimentary environment of Tertiary recorded in the Yongdeng Section of Lanzhou Basin. Acta Sedimentologica Sinica, 21 (4), 683–694.
- Zhang, P. (2015). Magnetostratigraphy and paleoenvironmental evolution of the Middle Eocene-Early Miocene deposits in the Lanzhou Basin, northwest China (PhD dissertation). Institute of Earth Environment, Xi'an, China.
- Zhang, Y. X., & Xue, X. X. (1994). Taphonomy of Longjiagou Hipparionine Fauna (Turolian, Miocene) Wudu County, Gansu Province, China. Beijing, China: Geological Publishing House.

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