

New fossils of paraceratheres (Perissodactyla, Mammalia) from the Early Oligocene of the Lanzhou Basin, Gansu Province, China post-print

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Abstract

This study describes a newly discovered paraceratherium fossil from the yellow sandstone layer at the base of the Oligocene Hanjiajing Formation in the Lanzhou Basin: *Paraceratherium huangheense* sp. nov. (new species). The paleomagnetic age of the fossil-bearing horizon is 31.5 Ma. Diagnostic features of the new species include: absence of alveolar trace anterior to P2; a pair of robust lower incisors that are closely appressed, extending horizontally forward and slightly upward; mandibular mental foramen positioned below p3; inferior border of the horizontal ramus straight; diastema anterior to p2 partially elevated; mandibular angle rounded and blunt; posterior border of the ascending ramus inclined posterodorsally; dental formula: $? \cdot ? \cdot 3 \cdot 3 / 1 \cdot 0 \cdot 3 \cdot 3$. Except for its larger size and differences in the posterior mandibular border, the overall mandibular morphology most closely resembles that of *Paraceratherium bugtiense* from Pakistan, suggesting a close phylogenetic relationship. The discovery of this new specimen provides new evidence for constraining the age of the giant paraceratherium-bearing strata at the classic Dera Bugti locality, and furnishes new mammalian fossil data for discussions concerning the uplift of the Tibetan Plateau.

Full Text

Preamble

New Fossils of Paraceratheres (Perissodactyla, Mammalia) from the Early Oligocene of the Lanzhou Basin, Gansu Province, China

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Summary

This paper describes a new species of paraceratheres: *Paraceratherium huangheense* sp. nov., excavated from the yellow sand layers at the bottom of the Early Oligocene Hanjiajing Formation in the Lanzhou Basin, Gansu, China. The paleomagnetic age of the strata is approximately 31.5 Ma. The new species is characterized by: absence of tooth socket traces before P2; a pair of robust lower incisors that are close together, extending forward and slightly upward; the mental foramen positioned below p3; a straight ventral border of the mandibular horizontal ramus; an upward concavity beneath the diastema anterior to p2; an angular mandibular angle; and a posterior border of the ascending ramus that slopes posterodorsally. The dental formula is $? \cdot ? \cdot 3 \cdot 3/1 \cdot 0 \cdot 3 \cdot 3$. Except for its larger size and differences in the posterior mandible, its overall mandibular characteristics are most similar to *Paraceratherium bugtiense* from Pakistan, indicating a close phylogenetic relationship. The discovery provides new evidence for determining the age of the classic Dera Bugti locality and offers new mammalian fossil evidence for discussions of Tibetan Plateau uplift.

Introduction

The Cenozoic stratigraphy of the Lanzhou Basin has undergone various revisions. The basin' s Cenozoic deposits were initially designated the "Gansu Formation," comprising the Changchuanzi, Xianshuihe, Guanyinsi, and Wuquanshan series (Young and Bien, 1937). The Xianshuihe Series was originally considered Miocene in age. Based on field investigations and related research, Qiu et al. (1997; Qiu et al., 2001) divided the Xianshuihe Formation into lower, middle, and upper members, with the lower member being Oligocene and the middle and

upper members representing early and middle Miocene, respectively. The lower member includes the Nanpoping and Xiagou faunas, the middle member includes the Zhangjiaping and Duitinggou faunas, and the upper member includes the Quantougou and Xingjiawan faunas. Subsequently, Xie (2004) further subdivided the Tertiary strata in the Lanzhou Basin, establishing numerous new formations. The strata containing the Nanpoping and Xiagou faunas were assigned to the Early Oligocene Hanjiajing Formation and Late Oligocene Ganjia Formation, respectively. The Hanjiajing Formation consists primarily of gray-white and gray-yellow sandstones with abundant red mud-gravel and trough cross-bedding. Paraceratheres and some rodent fossils have been discovered at its base. The Ganjia Formation is dominated by brown-red claystones and sandy mudstones. Sedimentary facies analysis indicates that the early Oligocene in this region was characterized by lacustrine deposits, which later transitioned to fluvial environments before returning to lacustrine deposition.

Historical Discoveries of Paraceratheres Fossils in the Lanzhou Basin

In 1964, the Fourth Regional Survey Team of the Gansu Provincial Geological Bureau first collected an incomplete paraceratheres mandible from the yellow sandstone (producing the Nanpoping fauna) at Limashagou in Gaolan County, Lanzhou Basin, initially identified as *Paraceratherium* sp. and dated to the Early Oligocene. Later, a joint expedition team composed of the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, and the Gansu Provincial Museum collected some paraceratheres teeth near Zhangjiaping and Yantonggou in 1987 and 1995. According to the collectors, these fossils came from the first white sandstone layer (Zhangjiaping fauna). The joint expedition also discovered some paraceratheres limb bones in the first white sandstone layer at Taowangou (1995), which were named *Turfantherium elegans* and dated to the early Early Miocene (Qiu and Wang, 2007). In 2013, a collection of paraceratheres fossils was recovered from the basal strata of the Oligocene Hanjiajing Formation near Huangyangtou Village, north of the Yellow River in Lanzhou City (Li et al., 2016). These specimens primarily include a fragmentary left maxilla with P2-P4, three incomplete mandibles, and some postcranial elements, representing a new species of *Paraceratherium*. Paleomagnetic analysis indicates that the basal Hanjiajing Formation is approximately 31.5 Ma (Yue et al., 2001; Zhang, 2015).

Systematic Paleontology

Order Perissodactyla Owen, 1785

Superfamily Rhinoceroidea Owen, 1845

Family Paraceratheriidae Osborn, 1923

Subfamily Paraceratheriinae Osborn, 1923

Genus *Paraceratherium* Forster-Cooper, 1911

Paraceratherium huangheense sp. nov. (Figs. 1-3; Tables 1-3)

Holotype: NWUV 1479, a relatively complete right mandible preserving the symphyseal region and complete right dentition; the mandibular angle and ascending ramus are partially missing.

Referred specimens: Left maxilla with P2-P4, NWUV 1480; left M2, NWUV 1481; right M3, NWUV 1482; right mandible with m1-m3, NWUV 1483; two left mandibles with m1-m3, NWUV 1484-1485 (NWUV 1484 is fragmentary and may belong to the same individual as NWUV 1479-1480); left lower incisor, NWUV 1486.

Etymology: The specific name derives from the Chinese pinyin “Huanghe,” meaning Yellow River, near which the fossils were discovered.

Locality and horizon: Lanzhou Basin, Gansu Province; Lower Oligocene Hanjiajing Formation.

Diagnosis: A large paracerather. No trace of tooth sockets anterior to P2; the diastema anterior to P2 is distinctly convex. A pair of first lower incisors (i1) with asymmetrically conical crowns, separated by a short diastema, extending slightly forward and upward. No tooth trace on the diastema before P2. The ventral border of the mandibular horizontal ramus is straight below the molars but pronouncedly concave below the diastema. Mandibular angle is angular, and the posterior border of the ascending ramus slopes posterodorsally. The mental foramen is located below p3. Dental formula: $? \cdot ? \cdot 3 \cdot 3 / 1 \cdot 0 \cdot 3 \cdot 3$.

Description

Upper Dentition

The fragmentary maxilla (Fig. 1A [Figure 1: see original paper], NWUV 1480) measures 210 mm in length with a maximum height of 160 mm. The teeth are heavily worn, indicating an elderly individual. The labial side of the tooth crowns is relatively well-preserved, while the lingual side is poorly preserved. The central portion of the crowns is nearly worn flat; P2 retains only enamel outlines, while P3 and P4 retain remnants of enamel fossettes. In labial view, the three premolars have robust, clearly visible roots that are largely exposed except near the apices. Teeth increase in size from anterior to posterior. No tooth socket traces are present anterior to P2, and the maxillary diastema is distinctly concave upward. The labial cingulum is well-developed, elevated at the anterior and posterior ends but low and flat in the middle, weaker anteriorly and more robust posteriorly.

P2 has two roots of similar size, while P3-P4 have anterior roots that are significantly more robust than posterior roots. From P2 to P4, the anterior roots tend to enlarge while posterior roots become weaker. The lateral surface of the preserved maxilla is markedly uneven due to root influence, forming an overall outwardly convex arc. In lingual view, the tooth crowns are very low: the high-

est point of the P2 crown is 5 mm, while the central portion of P4 reaches 18 mm. The roots are extensively exposed: P2–P4 measure 21 mm, 32 mm, and 38 mm respectively. Except for P2, no anterior-posterior bifurcation of lingual roots is observed in P3–P4.

The P2 occlusal outline is nearly an isosceles triangle, wider labially than lingually. The anterior border extends posteromedially, while the posterior border contacts P3 closely but with an irregular contact edge lacking enamel. Thin but distinct enamel layers line the labial and lingual margins, while the occlusal surface is almost completely worn flat, showing only slight undulations in the posterior middle portion. The P3 crown is an irregular quadrilateral, wider than long, with the labial border longer than the lingual border. The parastyle is prominent forward. Enamel is well-preserved on both labial and lingual sides, with a small enamel fossette remnant in the crown center and irregular cingulum remnants visible on the posterior lingual side. The crown is high on both labial and lingual sides, with a distinctly concave middle portion.

P4 is closely appressed to P3 and similar in morphology but larger, with a more prominent parastyle and no cingulum remnant on the posterior lingual side.

M2 (NWUV 1481, Fig. 1B) shows slightly less wear than NWUV 1482 and also represents an elderly individual. The specimen is narrower posteriorly than anteriorly, with roughly equal labial and lingual lengths. The anterior and posterior borders are slightly arched forward in the middle, giving an overall curved trapezoidal outline. The parastyle extends forward with a shallow parastyle fold. The buccal wall is strongly convex at the metacone. The protoloph is long, expanding lingually; due to heavy wear, it connects with the metaloph at the lingual base. The antecrochet is large and broadly V-shaped, extending distally to the mesial wall of the metaloph and dividing the medifossette into lingual and buccal parts. The metaloph is slightly wider and shorter than the protoloph, and the hypocone is smaller than the protocone. The crochet is low. The labial cingulum is low at the paracone base but highly ridged at the metacone base.

M3 (NWUV 1482, Figs. 1C, 2 [Figure 2: see original paper]) has a triangular occlusal outline with a vestigial, highly reduced posterior end of the ectoloph. The parastyle and lingual ends of the protoloph and metaloph are damaged. The ectoloph and metaloph are fused into a posteroexternal ridge with a rounded, non-angular posterolateral wall that is slightly inflated in the middle. Beneath the middle of the protoloph, a broad, gentle uplift extends toward the mesinus and meets an uplift extending forward from the base of the metaloph. The anterior cingulum is highly ridged, gradually decreasing from lingual to labial sides, reaching 26 mm high at the protocone and reducing to 14 mm at the paracone. The posterior cingulum is developed distal to the hypocone base, lowest at the metacone base and rising labially. The main cusps—including protocone, hypocone, paracone, metacone, and parastyle—bear robust roots. The roots beneath the paracone and parastyle, and those beneath the protocone and hypocone, are respectively connected or even fused into near-plate-like structures, while only the root beneath the metacone remains an independent

column.

No M1 is preserved in the available upper dental material, suggesting the upper dental formula may be: $1(?) \cdot 0(?) \cdot 3 \cdot 3$. The three specimens show varying degrees of wear: the three premolars are extremely worn, M2 less so, indicating an elderly individual, while M3 (Fig. 2 [Figure 2: see original paper]) shows lighter wear, with maximum crown height of approximately 66 mm at the metacone (including the cingulum). These three upper dental specimens may represent three different-aged individuals. Morphologically, P2 is semi-molariform, while P3-P4 are molariform.

Lower Dentition

The right mandible (NWUV 1479, Fig. 1D) is broken at the mandibular angle, with the ascending ramus missing, but preserves the complete right dentition; the symphyseal region and incisors are retained on the left side. In lateral view, the incisors are conical with upturned lower margins. The diastema anterior to p2 is overall elevated upward, with the symphyseal ventral border curving upward here, while the horizontal ramus ventral border is essentially straight from below p2 posteriorly, concave upward in the diastema region. The mental foramen is situated in the middle of the jawbone below the p3 root. Most cheek tooth roots are exposed, with wear gradually increasing from posterior to anterior, becoming nearly flat at p2. In occlusal view, the bilateral lower incisors extend slightly outward and forward. The symphysis narrows anterior to p2, with a longitudinal groove on its top surface whose posterior border aligns with the anterior edge of m1. The lower dental formula is $1 \cdot 0 \cdot 3 \cdot 3$. The mandibular angle is angular (NWUV 1483, Fig. 1F), and the posterior border of the ascending ramus slopes posterodorsally.

The unworn morphology of the left lower incisor resembles that of *Dzungariotherium orgosense* described by Qiu et al. (2004) but is slightly smaller. The crown cross-section is elliptical, slightly concave lingually and convex labially. In lateral view, the upper margin is slightly concave near the crown, while the lower margin is distinctly convex at the root due to cingulum development. Because the upper margin is concave near the crown while the lower margin is straight, the crown is distinctly upturned forward, with a straight root. The boundary between crown and root slopes from posterosuperior to anteroinferior. The distal ridge is sharp, while the mesial ridge is indistinct (NWUV 1486, Fig. 3 [Figure 3: see original paper]). In heavily worn elderly specimens, the wear facet is a bilaterally inward-sloping long ellipse with a weakly developed mesial ridge. The crown measures 33 mm anteroposteriorly, 39 mm in maximum height, and 25.5 mm in maximum lateral width (thickness) (NWUV 1479, Fig. 1D).

p2 (NWUV 1479, Fig. 1D) is small and single-rooted. Due to heavy wear, the occlusal surface shows no loph traces except for enamel outlines on anterior, posterior, and labial walls, with the lingual side worn to dentine. The occlusal

outline is nearly elongated. The labial cingulum is well-developed.

p3 (Fig. 1D) has a roughly trapezoidal outline, wider anteriorly than posteriorly. Due to deep wear, only a remnant of the lingual talonid basin is visible, and the ectoflexid appears as a faint depression. Both labial and lingual cingula are developed, though the anterior portion of the lingual cingulum has been worn away, leaving only the posterior portion.

p4 (Fig. 1D) is heavily worn, with the talonid basin appearing as a shallow U-shape. The protolophid, hypolophid, and metalophid are very wide, while the entolophid tapers toward the lingual side. The ectoflexid is a broad, shallow valley. Cingula are developed on both labial and lingual sides.

m1 (Fig. 1D) shows deep wear, with the trigonid basin reduced to a faint trace on the lingual side and the talonid basin forming a shallow V-shaped valley. The ectoflexid is a flat, wide V-shaped concavity. The protoconid and metaconid are expanded, while the paraconid is minimal. Both the external hypoconid and internal endoconid are heavily worn down to the root. The labial cingulum is strongly developed in the ectoflexid.

m2 (Fig. 1D) shows moderate wear with the crown surface well-preserved. The paralophid is very thin, while the metalophid and entolophid are thick. Both trigonid and talonid basins are U-shaped, though the former is shallow and the latter relatively deep. The ectoflexid is shallowly V-shaped. The labial cingulum is high anteriorly and low posteriorly.

m3 (Fig. 1D) shows the lightest wear, with crown morphology similar to m2. However, its talonid basin is wider, the ectoflexid deeper, and the loph slightly narrower than in m2. The labial cingulum is developed only at the anterolabial corner and on the posterior wall of the entolophid.

Specimens NWUV 1480, NWUV 1484, and the holotype (NWUV 1479) show similar degrees of wear, and their anatomical portions are complementary, suggesting they may belong to the same individual.

Comparison and Discussion

Since the early 20th century, numerous paraceratheres fossils of varying preservation have been reported from across China (Teilhard de Chardin, 1926; Young and Chow, 1956; Chow, 1958; Chow and Xu, 1959; Chiu, 1962; Chow and Chiu, 1963, 1964; Chiu, 1973; Chow et al., 1974; Wang, 1976; Xu and Wang, 1978; Qi and Zhou, 1989; Ye et al., 2003; Qiu et al., 2004). Qiu and Wang (2007) provided a systematic summary of paraceratheres fossils discovered in China.

The Paraceratheriinae includes seven genera (Qiu and Wang, 2007). Except for *Benaratherium*, which remains poorly understood, the others are divided into six genera based primarily on distinct differences in snout structure: *Juxia* (complete dentition, $3 \cdot 1 \cdot 4 \cdot 3$, i1 slightly larger than other incisors); *Urtinotherium*

(complete lower dentition, $3 \cdot 1 \cdot 4 \cdot 3$, i1 much larger than other incisors); *Paraceratherium* (only the first pair of incisors retained and specially developed, i1 extending forward, ventral border of mandibular horizontal ramus concave upward beneath diastema, lower dental formula $1 \cdot 0 \cdot 3 \cdot 3$); *Dzungariotherium* (highly degenerate rostrum in both upper and lower jaws, first pair of incisors retained but reduced, other incisors and canines lost, ventral border of horizontal ramus arcing upward from beneath premolars, not sloping anteroventrally at the anterior end, dental formula $1 \cdot 0 \cdot 3 \cdot 3/1 \cdot 0 \cdot 3 \cdot 3$); *Aralotherium* (long snout, lower incisors and mandibular symphysis strongly downturned); and *Turpanotherium* (mandibular symphysis and lower incisor i1 extending forward, wide diastema between left and right lower incisors) (Qiu and Wang, 2007). Among these, *Paraceratherium* was established by Forster-Cooper in 1911 based on a mandible from Oligocene deposits in Dera Bugti, Baluchistan, with the type species being *P. bugtiense*, distinguished by its uniquely enlarged first pair of lower incisors that are closely appressed and extend forward (slightly downward) (Forster-Cooper, 1911).

The newly discovered paraceratherian mandible from the Lanzhou Basin (Figs. 1, 4A) is morphologically most similar to *Paraceratherium*, particularly in its rostral portion (Fig. 4A). Features such as the upward-curved diastema, forward-extending incisors, and straight ventral border of the horizontal ramus closely resemble the type species *P. bugtiense* (Forster-Cooper, 1911) (Fig. 4B) and differ markedly from other genera. Therefore, the new specimens should be assigned to *Paraceratherium*.

Previous research recognized four species within *Paraceratherium*: the type species *P. bugtiense*, *P. asiaticum*, *P. grangeri*, and *P. lepidum* (Figs. 4B-E) (Qiu and Wang, 2007). *Paraceratherium huangheense* shares certain similarities with these species, including forward-extending incisors, a single mental foramen positioned anteroinferior to the tooth row, a straight ventral border of the horizontal ramus, a distinct mandibular angle, and large size (Tables 1-3). However, clear differences also exist (Fig. 4; Table 4).

P. huangheense resembles *P. bugtiense* (Fig. 4B) in: loss of P1; triangular P2 outline; concave contour below the diastema between p2-i1; single-rooted p2; and angular mandibular angle. However, *P. huangheense* differs from *P. bugtiense* (contrasting features in brackets) by its larger size, mental foramen underlying p3 (versus p2), posterior border of ascending ramus sloping posteriorly (versus vertical), and a short diastema between the bases of i1 (versus closely appressed) (Forster-Cooper, 1911; Gromova, 1959).

P. huangheense shares only two features with *P. asiaticum* (Fig. 4C): loss of P1 and the presence of a single stout incisor in each ramus extending forward. However, their differences are more substantial. *P. huangheense* differs from *P. asiaticum* (contrasting features in brackets) by its larger size (p2-m3 length is 77% that of *P. huangheense*; Gromova, 1959:89), concave contour below the diastema between p2-i1 (versus not concave), mental foramen underlying p3 (versus p2), angular mandibular angle (versus rounded), posterior border of

ascending ramus sloping posterodorsally (versus anteriorly slanted), and roughly triangular P2 crown outline (versus trapezoidal) (Borissiak, 1923; Gromova, 1959; Qiu and Wang, 2007).

P. huangheense resembles *P. grangeri* (Fig. 4D) in: similar size, loss of P1, and presence of a single stout incisor in each ramus extending forward. However, they differ in: mandibular angle being angular (versus rounded), posterior border of ascending ramus sloping posteriorly (versus convex posteriorly), P2 crown outline triangular (versus trapezoidal), p2 single-rooted (versus double-rooted), concave diastema between p2-i1 (versus absent or weakly concave), and dental formula $? \cdot ? \cdot 3 \cdot 3 / 1 \cdot 0 \cdot 3 \cdot 3$ (versus $1 \cdot 1 \cdot 4 \cdot 3 / 1 \cdot 0 \cdot 3 \cdot 3$) (Osborn, 1923; Granger and Gregory, 1936).

P. huangheense shares with *P. lepidum* (Fig. 4E): similar size, loss of P1, triangular P2 outline, concave diastema between p2-i1, single-rooted p2, and forward-extending single stout incisor in each ramus. However, *P. lepidum* is distinctly different from *P. huangheense* in possessing a wide and deep notch (incisura vasorum) anterior to the mandibular angle on the ventral border of the horizontal ramus (Fig. 4E) (Qiu and Wang, 2007).

In recent years, giant rhinocerotoid fossils have been reported from the Late Oligocene of north-central Anatolia (Antoine et al., 2008) and from Oligocene and Middle Miocene deposits of the Kagizman-Tuzluca Basin in eastern Turkey (Sen et al., 2011). These fragmentary limb elements were identified as *Paraceratherium* sp.; however, without any dental material, comparison with *P. huangheense* is difficult.

Morphological comparison clearly demonstrates that *P. huangheense* from Lanzhou is most similar to the type species *P. bugtiense* from Dera Bugti, Baluchistan, indicating a close phylogenetic relationship. Furthermore, the paleomagnetic age of the *P. huangheense*-bearing layer in the Lanzhou Basin is 31.5 Ma (Yue et al., 2001; Zhang, 2015), allowing reasonable inference about the age of the *P. bugtiense*-bearing beds in Baluchistan. The long-assumed Miocene age of the Dera Bugti strata (Qiu and Wang, 2007) has been debated, with proposed ages ranging from older than 21–22 Ma, to 21–18.3 Ma, to approximately 16.5 Ma. French paleontologists collaborating with the University of Baluchistan conducted extensive investigations, discovering abundant small mammal fossils such as the European Oligocene hamsters *Pseudocricetodon* and *Atavocricetodon* from the same *Paraceratherium*-bearing layer (Marivaux et al., 1999), suggesting the Bugti Member should be assigned to the Lower Oligocene. The Early Oligocene age of 31.5 Ma for *P. huangheense* from the Hanjiajing Formation provides indirect evidence supporting an Early Oligocene age for the Bugti Member.

Paraceratherium fossils from the Lanzhou Basin provide key evidence that during the Oligocene, giant rhinos inhabited northwestern China north of the Tibetan Plateau while also being distributed in the Indo-Pakistan subcontinent to the south. This distribution indicates that the Tibetan Plateau had not yet risen

to an elevation sufficient to prevent large mammal exchange. Giant rhinos, the rhinocerotid *Aprotodon*, and chalicotheres still dispersed across the “Tibetan Plateau” region (Qiu et al., 2001; Deng and Ding, 2015). The results of this study provide clearer evidence confirming the existence of *P. huangheense* in the Lanzhou Basin of China during the Early Oligocene at approximately 31.5 Ma, with fossils very similar to *P. bugtiense* from Dera Bugti, Baluchistan.

Conclusions

The discovery of *Paraceratherium huangheense* sp. nov. from the yellow sandstone near the base of the Hanjiajing Formation in the Lanzhou Basin represents a new species dating to the late Early Oligocene, with a paleomagnetic age of 31.5 Ma. Its rostrum is similar to those of *P. bugtiense* and *P. lepidum*, but the mandibular angle shows variation. Paraceratherium morphology may be more complex than previously recognized, with different species exhibiting similar rostral morphology but substantially different mandibular angles. The Lanzhou Basin *P. huangheense* shows considerable similarity in mandibular morphology to the Pakistani *P. bugtiense*, suggesting a close phylogenetic relationship. This discovery further clarifies that during the Early Oligocene, the Tibetan Plateau had not yet risen to an elevation that could affect the free migration of large mammals.

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Note: Figure translations are in progress. See original paper for figures.

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