A restudy of Rhinocerotini fossils from the Miocene Jiulongkou Fauna of China

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Abstract

All the extant rhino species belong to Rhinocerotini and either have one horn (a nasal horn) or two horns (a nasal horn and frontal horn). So far, the earliest Rhinocerotini to have been identified in China is the "Dicerorhinus" cixianensis, which was based on a juvenile skull with an associated mandible from the Middle Miocene locality of Jiulongkou in Cixian County, Hebei Province of northern China. Our analyses suggest that there are similarities between this specimen and the modern genus, Dicerorhinus, but it differs in several cranial traits and therefore cannot be assigned to the modern genus. Instead, it is closer to the Middle Miocene Lartetotherium from Europe, especially the specimen from La Retama in Spain and should be assigned to that genus, indicating the presence of intracontinental dispersal at this time. The Jiulongkou fauna is the only Middle Miocene fauna with Rhinocerotini in China, and, together with the faunal composition, this implies a more humid and closed environment, in contrast to those found in western China. We suggest that the position of the posterior border of the nasal notch is a good indication of the specimen' s evolutionary level in Rhinocerotini. The anterior position of the nasal notch as seen in modern Dicerorhinus, together with its certain similarities to L. cixianensis as well as its differences with more specialized species of the Dihoplus-Pliorhinus-Stephanorhinus -Coelodonta lineage, supports the conclusion that Dicerorhinus experienced little change during a nearly 10 Myr evolutionary history, possibly due to the low selection pressure seen in the tropical/subtropical forests in southeastern Asia.

Full Text

Preamble

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A Restudy of Rhinocerotini Fossils from the Miocene Jiulongkou Fauna of China

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Abstract All extant rhino species belong to the tribe Rhinocerotini and possess either one horn (a nasal horn) or two horns (a nasal horn and frontal horn). To date, the earliest Rhinocerotini identified in China is "Dicerorhinus" cixianensis, described from a juvenile skull with associated mandible from the Middle Miocene Jiulongkou locality in Cixian County, Hebei Province, northern China. Our analyses reveal similarities between this specimen and the modern genus Dicerorhinus, but several cranial differences preclude its assignment to the modern genus. Instead, it shows closer affinities to Middle Miocene Lartetotherium from Europe, particularly the specimen from La Retama, Spain, and should be reassigned to that genus. This reassignment indicates intracontinental dispersal between Europe and Asia during this period. The Jiulongkou fauna represents the only Middle Miocene fauna in China containing Rhinocerotini, and its faunal composition suggests a more humid, closed environment compared to contemporaneous sites in western China. We propose that the position of the posterior border of the nasal notch serves as a reliable indicator of evolutionary level within Rhinocerotini. The anteriorly positioned nasal notch in modern Dicerorhinus, combined with its overall similarity to L. cixianensis and differences from more specialized members of the Dihoplus-Pliorhinus-Stephanorhinus-Coelodonta lineage, suggests that Dicerorhinus underwent minimal morphological change during its nearly 10 Myr evolutionary history. This evolutionary stasis may reflect low selection pressure in the tropical/subtropical forests of southeastern Asia.

Key words: Jiulongkou, Middle Miocene, Lartetotherium cixianensis, Rhinocerotini

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1. Introduction

All modern rhinos possess either one or two horns on their noses and frontals. The Rhinocerotini tribe likely originated in Africa, with the earliest known species, *Rusingaceros leakeyi*, discovered in Rusinga, eastern Africa (Hooijer, 1966; Werdelin and Sanders, 2010). *Rusingaceros leakeyi* occurs in the Wayando Formation (Rusinga) of Kenya, dated to 18 Ma (early Kisingirian) (Van Couvering and Delson, 2020), equivalent to MN3 in Europe (Mein, 1999). The earliest Eurasian record of Rhinocerotini comes from Bezian, La Romieu, France (MN4b), represented by several isolated teeth assigned to *Lartetotherium sansaniense* (Ginsburg and Bulot, 1984). *Lartetotherium sansaniense* was the most common Rhinocerotini in the Middle Miocene of Europe. First discovered at the classical MN6 locality of Sansan, France, and identified as *Rhinoceros sansaniense* (Lartet, 1851), it was later erected as a separate genus *Lartetotherium* by Ginsburg (1974). It ranges from MN4 to MN9 in Europe—a rather long time span—but as Heissig (1999) noted, poor preservation of most materials masks interspecific differences. Another Middle Miocene Rhinocerotini species, *Gaindatherium browni*, was discovered at Chinji Rest House, Salt Range, Attock District, Punjab (Colbert, 1934, 1935). Both *L. sansaniense* and *G. browni* are well-known and have been included in recent phylogenetic analyses (Pandolfi et al., 2021; Antoine et al., 2022).

In contrast to these well-known species, the early Rhinocerotini record in eastern Asia is very poor. To date, the only record is from Jiulongkou in Cixian County, Hebei Province, North China (Chen and Wu, 1976). This fauna contains abundant fossil remains and is considered early Tunggurian, equivalent to MN6 of Europe (Deng, 2006). Chen and Wu (1976) erected a new species, *Dicerorhinus cixianensis*, based on a partial cranium and mandible of a juvenile individual. Some postcranial bones from this locality were assigned to *Dicerorhinus* sp., and a premaxilla fragment was assigned to Rhinocerotidae gen. et sp. indet. (Chen and Wu, 1976). This species has received little attention from most researchers (Qiu, 1990; Tong, 2012). However, as the only pre-Late Miocene Rhinocerotini discovered in East Asia, it holds potential importance for understanding the early evolution of Rhinocerotini, which flourished since the Late Miocene. This study provides a redescription and analysis of the *D. cixianensis* specimens.

2. Materials and Methods

The materials described in this study—a juvenile skull with mandible (IVPP V4833) and a premaxilla (IVPP V4841)—are housed at the IVPP. Cranial measurements and anatomical terminology follow Deng (2004), Antoine and Saraç (2005), and Qiu and Wang (2007). Measurements were taken either with calipers (for dentition) or from 3D models (for crania and mandibles). Measurements are provided in Table 1 .

Abbreviations: AMNH, American Museum of Natural History, New York, USA; HMV, Hezheng Paleozoological Museum, Hezheng, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMNH, Muséum national d’ Histoire naturelle, Paris, France; AW, anterior width of the cheek teeth; L, length; M/m, upper/lower molar; P/p, upper/lower premolar; PW, posterior width of the cheek teeth; W, width.

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3. Systematic Paleontology

Order Perissodactyla Owen, 1848
Superfamily Rhinocerotoidea Gray, 1821
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae (Gray, 1821)
Tribe Rhinocerotini Gray, 1821
Genus *Lartetotherium* Ginsburg, 1974
Lartetotherium cixianensis (Chen and Wu, 1976)

Synonymy:
Dicerorhinus cixianensis Chen and Wu, 1976, p. 8
Dicerorhinus cixianensis Qiu, 1990, p. 540
Dicerorhinus cixianensis Cerdeño, 1996a, p. 29
Dicerorhinus cixianensis Tong, 2012, p. 557
Dicerorhinus cixianensis Deng, 2015, p. 133
Dicerorhinus cixianensis Pandolfi, 2018, p. 28

Holotype: Partial cranium and associated mandible of a juvenile individual (IVPP V4833).

Type locality and horizon: Jiulongkou, Cixian County, Hebei Province; Middle Miocene, early Tunggurian, equivalent to MN 6 of Europe (Deng, 2006).

Description: The type skull IVPP V4833 represents a juvenile individual, with DP1–4 present, M1 half erupted, and the tip of the M2 cusp just breaking the alveolus.

The skull appears dolichocephalic (Fig. 1B [Figure 1: see original paper]) and relatively low. The dorsal profile of the preserved portion is mostly straight, with only the anterior part of the nasal turning downward. The nasal septum is not ossified, and the nasal bone is relatively narrow with a slightly domed horn base. The nasal notch reaches the level of the anterior border of DP1 and is V-shaped. The surface bears an indistinct rough vascular print. The anterior part of the nasal bones is not fully fused and exhibits a distinct median groove extending from the nasal tip to the top of the horn dome.

The infraorbital foramen opens at the level of DP2, while the anterior border of the orbit lies above the posterior part of DP4. Both the lacrimal process and preorbital process are absent. The postorbital processes of the frontal are weak and indistinct, and the forehead has a smooth surface without vascular prints.

The premaxilla is thin and rather elongated (Fig. 2A [Figure 2: see original paper]). No premaxillary notch is present in the preserved portion, suggesting a shallow notch in this species. No incisor alveolus is visible in the preserved part. The cheek tooth rows diverge posteriorly, and the anterior border of the bony choana reaches the level of DP4.

The mandible belongs to the same individual as the skull (Fig. 3 [Figure 3: see original paper]). The left side is largely complete, whereas the right side lacks the ascending ramus. The horizontal ramus is shallow, with its anterior part markedly shallower than the main body, and the ventral profile is convex. The symphysis is narrow and long, with its posterior border reaching the level of p3. The mental foramen lies below dp1. The ascending ramus is not particularly massive, with a posteriorly inclined anterior border. The mandibular condyle is slightly transversely convex, and the coronoid process is small with a hook-like posterior border.

The premaxilla of IVPP V4841, tentatively assigned to the same species, contains a single large incisor alveolus for I1. The alveolus is elongated and oval, with no alveolus for I2 present. A distinct lateral groove occurs in the maxilla, and the premaxillary notch is shallow centrally.

The upper deciduous teeth (Fig. 1B2) are low-crowned, lacking lingual and labial cingula, though anterior and posterior cingula are developed. DP1 is roughly triangular and wider posteriorly, with a weak paracone fold. The protocone and hypocone are conjoined lingually, the protoloph is present, the protocone is small, the hypocone connects to the metacone, and the postfossette is closed. A weak crest between the protocone and the front end of the ectoloph forms a closed shallow valley in the left DP1. DP2 has an apparent mesostyle, weak and spear-like crochet and crista, and simple, backward-inclined protoloph and metaloph. DP3 is similar to DP2 but has a metacone fold instead of a mesostyle. In DP4 and M1, the crochet is well developed and simple, and the paracone shows weak constriction. M2 is not fully erupted but displays a well-developed crochet similar to that of M1.

Table 1 provides measurements of *Lartetotherium cixianensis* from Jiulongkou (mm). Note that I1 length and width come from V4841, while all other measurements derive from V4833.

The lower deciduous teeth (Fig. 3) are low-crowned and lack a cingulum. The dp1 is structurally simple, with a small protoconid close to the ectolophid. The dp2 is heavily worn and partly broken but shows a developed paraconid. The paralophid of dp3 is wide, and a shallow valley likely existed in front of the paralophid before wear, as seen in *Pliorhinus ringstroemi* (from personal observation). The trigonid of dp3 and dp4 is angular—an obtuse dihedron in dp3 and a right dihedron in dp4. The m1 is similar to dp4 but has more rounded trigonid and talonid.

4. Comparison

“Dicerorhinus”cixianensis was initially assigned to *Dicerorhinus* based on similarities to *Pliorhinus ringstroemi* (= *Dicerorhinus ringstroemi*) and *Lartetotherium sansaniense* (= *D. sansaniensis*) (Chen and Wu, 1976). However, as *D. kirchbergersis*, *D. choukoutienensis*, and *D. yunchuensis* have been removed from *Dicerorhinus*, the genus definition has become more restricted, making placement of “D.” cixianensis in *Dicerorhinus* inappropriate. Compared to “D.” cixianensis, both juvenile and adult specimens of *D. sumatrensis* exhibit a large palatine fissure beginning at the front of DP1, with unfused premaxillae (Tong and Guérin, 2009; Chen et al., 2021). In the juvenile “D.” cixianensis V4833, the palatine fissure is invisible, and the adult premaxilla in V4841 is not elongated as in modern *D. sumatrensis*, where it extends close to the level of I1. Additionally, *D. sumatrensis* has a narrower rostral end of the nasal bone, a paracone on DP1 separate from the ectoloph, better-developed crochet and crista on DP2 that connect after wear, and a shorter, wider mandible (Chen et al., 2021). These characters differ from the modern *Dicerorhinus* and preclude assignment of the Jiulongkou rhino to the modern genus.

A juvenile skull (M1 fully erupted) identified as *Lartetotherium* cf. *L. sansaniense* from La Retama, Spain (Cerdeño, 1996a), shows the greatest similarity to the Jiulongkou rhino. Minor differences include a slightly longer nasal and relatively weaker crochet on DP4 in *L.* cf. *L. sansaniense*. The nasal notch in both *L.* cf. *L. sansaniense* from La Retama and “D.” cixianensis lies before the level of DP1, whereas in adult *L. sansaniense* it is positioned above DP1 to P3 (Heissig, 2012). Based on our observations, the position of the posterior end of the nasal notch remains relatively stable during ontogeny in rhinos (Fig. 4 [Figure 4: see original paper]; *Dicerorhinus sumatrensis*, *Pliorhinus ringstroemi*, and *Chilotherium wimani*). The nasal notch in adult *L.* cf. *L. sansaniense* from La Retama and “D.” cixianensis would likely maintain its juvenile position anterior to the cheek teeth, as seen in *D. sumatrensis*. Heissig (2012) observed that the nasal notch tends to extend posteriorly during evolutionary progression within *L. sansaniense*. Thus, the nasal notch states seen in *L.* cf. *L. sansaniense* and *D. sumatrensis* represent the primitive condition, indicating that these species represent an early branch of Rhinocerotini.

Rusingaceros leakeyi from Africa is the earliest known Rhinocerotini (Geraads, 2010). In this species, the crochet and crista of DP2 become more developed and connect after wear, the crochet of DP3 is developed, I1 is large, and I2 is absent. The incisor alveolus shape is similar to that of “D.” cixianensis. *Gaindatherium browni* has a large I1 and small I2 (Colbert, 1934), while *Dihoplus schleiermacheri* also has a small I2; all other known Rhinocerotini lack I2 entirely. *Rusingaceros leakeyi* possesses two horns, whereas *Gaindatherium* has only one.

In summary, the Rhinocerotini from Jiulongkou differ from *Dicerorhinus* and other known fossil Rhinocerotini. Although the juvenile nature of the material has prevented a well-established diagnosis, overall similarity and close chronology suggest that the specimen is best assigned to *Lartetotherium* as *L. cixianensis*.

5. Discussion

As previously noted, the Jiulongkou rhino differs from the modern genus *Dicerorhinus* in several aspects but remains comparatively more similar to other Late Miocene to modern Rhinocerotini that are more specialized. In fact, *Lartetotherium* cf. *L. sansaniense* from La Retama (MN5a), Spain (Cerdeño, 1996a), *L. cixianensis* (MN6), and *D. sumatrensis* show similarities during juvenile stages, whereas adults appear less similar, suggesting that more specific traits are acquired during ontogeny.

Lartetotherium is regarded as an ancestor of modern Rhinocerotini (Pandolfi, 2018, 2023; Pandolfi et al., 2021), and the major evolutionary trend appears to involve the nasal becoming shorter and narrower. *Lartetotherium cixianensis* is probably closely related to the ancestral stock of modern *Dicerorhinus* and more derived than Plio-Pleistocene Rhinocerotini. Recent genomic phylogenetic inference suggests that the divergence between *D. sumatrensis* and other Asiatic rhinos (i.e., *Rhinoceros*) occurred at approximately 15 Ma (Margaryan et al., 2020; Liu et al., 2021), an age close to that of *L. cixianensis*. The anterior position of the nasal notch and simplified cheek teeth in modern *Dicerorhinus* are rather close to those of *L. cixianensis*, supporting the interpretation that this genus was highly conservative during its evolutionary history. This phenomenon likely correlates with a relatively stable environment in the tropical/subtropical regions of southern China and southeastern Asia during the late Cenozoic, which allowed many ancient lineages to survive (e.g., *Ailuropoda*, *Mydaus*, and *Prionodon*) (Pocock, 1939, 1941; Fjeldsa and Lovett, 1997; Hwang and Larivière, 2003, 2004). Stable climate and abundant food resources would have imposed little selective pressure, whereas in more temperate regions, global temperature decline (Zachos et al., 2001; Westerhold et al., 2020) and northern Eurasian aridification (Zhang et al., 2013; Liu et al., 2016; Kaya et al., 2018) significantly altered rhino habitats. Rhinocerotini in these regions (e.g., *Dihoplus*, *Pliorhinus*, *Stephanorhinus*, and *Coelodonta*) gradually evolved larger body sizes and more complex cheek teeth (Deng et al., 2011; Tong, 2012; Pandolfi et al., 2021; Giaourtsakis, 2022).

The Jiulongkou rhino closely resembles the rhino from La Retama, MN5a of Europe, suggesting a potential biogeographic connection between eastern Asia and Europe during this time. However, such Middle Miocene connections between Eurasia were not strong, as the northern part of eastern Asia (represented by the Tunggur Fauna) formed a relatively separate biorealm from Europe and south-

southeastern Asia (Jiangzuo et al., 2020). This separation likely correlates with more open environments in eastern Asia, exemplified by abundant percrocutids and *Gobicyon*—cursorial scavengers more likely to inhabit open environments (Qiu et al., 1988; Jiangzuo et al., 2019; Xiong, 2022).

Jiulongkou differs from these localities in being the only known Middle Miocene site in China to yield Rhinocerotini. In the Tunggur Formation, two rhinos are recorded—*Acerorhinus zernowi* and *Hispanotherium tungurense*—belonging to Aceratheriinae and Elasmotheriini, respectively (Cerdeño, 1996b; Wang et al., 2003). In the Dingjiaergou Fauna, four rhinos are present: *Caementodon tongxinensis*, *Hispanotherium matritense*, *Plesiaceratherium* sp., and *Alicornops laogouensis*, belonging to Elasmotheriini (first two), Aceratheriini, and Teleoceratini, respectively (Wang et al., 2016). Two rhinos are recorded from the Hujialiang Formation at Laogou locality of the Linxia Basin—*Alicornops laogouense* and *Hispanotherium matritense*—belonging to Teleoceratini and Elasmotheriini, respectively (Deng, 2003, 2004). The rhino assemblages at these localities are similar, dominated by Aceratheriinae and Elasmotheriini within Rhinocerotinae. Jiulongkou is unique in containing Rhinocerotini, which are common in Middle Miocene deposits from Europe (Filhol, 1891; Cerdeño, 1996a; Heissig, 1999, 2012; Antoine et al., 2000; Pandolfi, 2018) and southern/southeastern Asia (Colbert, 1934; Heissig, 1972; Khan et al., 2014).

The Jiulongkou fauna includes abundant *Palaeomeryx* specimens, as well as *Chalicotherium* and crocodiles (Chen and Wu, 1976; Chen and Liu, 2013; Qiu et al., 2013), supporting the presence of trees. However, the occurrence of some open-environment species (e.g., the bone-cracking hyaenid *Percrocuta* and high-crowned *Turcocerus*) suggests a mixture of open and closed paleoenvironments. In contrast, the Dingjiaergou Fauna of similar age in a more western location (Wang et al., 2016) contains diverse aceratheriines and elasmotheriines, abundant *Gobicyon* (Jiangzuo et al., 2019) and percrocutids (Xiong, 2022), but very few *Palaeomeryx* remains, implying a more open and arid environment without Rhinocerotini. Thus, Jiulongkou shows a predominantly closed environment compared to other Middle Miocene sites, likely determined by its geography—closer to the ocean and lower in altitude, making it more humid than interior Asia.

Early Rhinocerotini are generally low-crowned and thus more likely adapted to closed environments. The presence of Rhinocerotini supports the interpretation that the Jiulongkou fauna lay near the ecological boundary between the open-dominated environments of western China and the closed-dominated environments of coastal eastern and southeastern Asia.

6. Conclusion

Through restudy of the earliest Rhinocerotini in China and new comparative anatomical analyses, we suggest that Rhinocerotini from the Jiulongkou fauna should be excluded from the modern genus *Dicerorhinus* and reassigned to *Lartetotherium cixianensis*. It differs from modern *Dicerorhinus* in several cranial traits and shows closer affinities to Middle Miocene Rhinocerotini from La Retama, suggesting intracontinental dispersal during this period. Comparative analysis indicates that the nasal notch position serves as a good indicator of evolutionary level in Rhinocerotini, with an anterior position representing the primitive stage. In this regard, the anterior nasal notch of modern *Dicerorhinus*, together with its overall similarity to *Lartetotherium cixianensis* compared to other Rhinocerotini from the Late Miocene to present, suggests this genus has been highly conservative during its evolutionary history. This conservatism likely relates to the stable environment in tropical/subtropical forests of southeastern Asia, which imposed low selective pressure due to abundant food resources. Jiulongkou is the only Middle Miocene locality in China with Rhinocerotini, and its faunal composition implies a more humid, closed environment compared to central and western China during this period.

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