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Palaeoenvironment examination of the terminal Miocene hominoid locality of the Zhaotong Basin, southwestern China, based on the rhinocerotid remains

Xiaokang Lu^a, Xueping Ji^b, Sukuan Hou^c, Shiqi Wang^c, Qinqin Shi^c, Shaokun Chen^{d,c}, Boyang Sun^c, Yikun Li^c, Yu Li^c, Tengsong Yu^e and Wenqi Li^f

^aHenan University of Chinese Medicine, Zhengzhou, China; ^bYunnan Institute of Cultural Relics and Archaeology & Research Center for Southeast Asian Archeology, Kunming, China; ^cKey Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ^dChina Three Gorges Museum Chongqing, Chongqing, China; ^eInstitute of Cultural Relics, Zhaotong, China; ^fZhaotong Institute of Cultural Relics, Zhaotong, China

ABSTRACT

Anatomic modification in evolution process of mammals was closely correlated with the environmental changes, and become the powerful evidence for reconstructing the palaeoenvironment shaped their evolution. Rhinocerotid fossils are important indicators of the ecosystems inhabited by the mammalian faunas. Here, we first described remains of two rhinocerotids from the terminal Miocene Zhaotong Basin, the most recent hominoid locality in South China, including *Acerorhinus lufengensis* and Rhinocerotini gen. et sp. indet. New remains of *A. lufengensis* display a short crochet and antecrochet, expanded lingual cones, and rounded labial wall of the trigonid and talonid. These characteristics demonstrate its feeding habits of grazing brush and high grass. The limb bones of Rhinocerotini gen. et sp. indet. enable to live in an open habitat in having the following characteristics: the Mc II facet of Mc III is large, oval, flattened, and nearly vertical in direction; the femur exhibits a very large trochanter tertius and two nearly parallel asymmetrical ridges of the distal patella trochlea. The rhinocerotid fossils described herein provide a substantial evidence of the presence of mosaic environment, and the grassland should patches within or along the margin of the forest in the terminal Miocene Shuitangba locality.

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Basin; Rhinocerotidae;
terminal Miocene

Introduction

In China, the fossils were historically regarded as ‘dragon bones’ and used in traditional medicine to obtain effects such as sedation, hemostasis, and relief of diarrhea. The earliest studies on the rhinoceros fossils from China were based on such ‘dragon bones’ procured from Chinese Medicine Store (Falconer & Cautley 1847; Koken 1885; Schlosser 1903; Ringström 1924). The superfamily Rhinoceroidea is the largest and most ecologically diverse group of perissodactyls. At least thirty-three rhinocerotid genera from the Neogene Old World have been reported (Heissig 1999; Antoine 2002; Deng 2006, 2008; Deng et al. 2011; Deng & Chen 2015; Pandolfi 2015). In East Asia, sixteen genera have been recorded during this period, including most hornless aceratheres and hysodont elasmotheres and some genera within the tribe Rhinocerotini; these rhinocerotids inhabited forests, open grassland, or brush (Ringström 1924; Bohlin 1937; Deng 2006; Deng & Chen 2015).

The relationships of the evolution of Neogene mammals as a whole in Eurasia with the uplift of the Tibetan Plateau have been discussed often (An et al. 2001; Guo et al. 2002; Deng et al. 2011; Wang et al. 2013; Deng & Ding 2015). The most widely discussed factor is the formation of the monsoon. In South China, pollen

analysis and isotope data from bulk enamel samples demonstrate that the arrival of the monsoon and the expansion of the C₄ grassland in this area occurred at 4–3 Ma, namely at the Pliocene, which is 3–4 Myr later than in Siwalik (Quade & Cerling 1995; Chang et al. 2015; Ren 2015). This established South China as a refuge for some mammals during the Late Miocene, such as *Subchilotherium* and *Gaindatherium*, both of which migrated from the Siwalik (Gao & Ma 1997; Deng & Gao 2006).

In Neogene South China, rhinoceroses were less prosperous and were restricted to the period of the Late Miocene; none of these taxa belong to a typical forest type, including *Shansirhinus*, *Subchilotherium*, *Acerorhinus*, and *Gaindatherium* (Deng & Gao 2006; Deng & Qi 2009; Lu 2013). The rhinoceroses that were present in the Pliocene South China remain unknown. The Pliocene is a crucial chronostratigraphic series for understanding the origin of certain Quaternary mammals, although it has a short range (5.33–2.58 Ma; Cohen et al. 2013), and the localities and fossil records are also limited. The Pliocene Zanda Basin on the northwestern Tibetan Plateau has been proven to be a cradle of evolution for cold-loving Ice Age mammals, including *Coelodonta thibetana*, *Panthera blytheae*, and *Vulpes qiuzhudingi*, and for mountain sheep, *Protovis himalayensis* (Deng et al. 2011; Tseng et al. 2014; Wang et al. 2014, 2016). Moreover, the recently

excavated terminal Miocene Shuitangba locality in the Zhaotong Basin on the southeast Tibetan Plateau revealed the origin of the Old World brevirostrine gomphotheriid taxon *Sinomastodon*, whose oldest species is *S. praeintermedius* (Wang et al. 2015). The rhinocerotid specimens from this locality described herein include teeth and well-preserved postcranial materials. Although they do not resolve the origin of the concerned groups, the postcranial materials will certainly provide many valuable insights into their anatomy, especially regarding features that are closely correlated with adaptation to the environment.

Regional setting

The Shuitangba locality is an open-pit lignite mine situated on the northern Yunnan-Guizhou Plateau (Figure 1). A hominoid fossil was extracted from the dark clays sandwiched between the lignite layers (Ji et al. 2013). The associated mammals include many typical elements of the Late Miocene fauna, such as *Stegodon*, *Sinomastodon*, *Sinocastor*, *Miorhizomys*, *Muntiacus*, and *Tapirus* (Zhou & Zhai 1962; Dong et al. 2014; Jablonski et al. 2014; Ji et al. 2015). Analysis of paleomagnetic data suggests an age of the terminal Miocene Baodean (East Asian Land Mammal Age) of 6.5–6.0 Ma (Ji et al. 2013). Data on clay mineralogy indicate a mildly warm and humid living environment for the Miocene hominoid fauna (Zhang et al. 2016).

The Zhaotong Basin is the northernmost hominoid locality in Yunnan Province in which rhinocerotids have been reported; another two, Yuanmou Basin and Lufeng Basin, are 250 and 290 km southwest of this locality, with ages of 8.2–7.1 Ma and 6.9–6.2 Ma, respectively (Qi & Dong 2006) (Figure 1). The

Yuanmou Basin contains typical diluvial-alluvial deposits indicative of strong seasonality, with a less humid climate than the Lufeng Basin. Fossils in the latter locality were also obtained from a lignite mine that contains more silt and sand in the sedimentary unit, distinct from the depositional environment in the Zhaotong Basin (Zhang et al. 2002; Jablonski et al. 2014). The hominoid fauna of the Zhaotong Basin are dissimilar to those of the Yuanmou Basin and Lufeng Basin. The most striking aspects are the absence of equids and the presence of various aquatic birds. The rhinocerotid specimens found at the site described in this paper consist of cheek teeth and postcranial bones.

The taxonomy reported herein follows Prothero and Schoch (1989) and Heissig (1999), and the terminology and measures follow the protocol proposed by Guérin (1980) and Qiu and Wang (2007). Institutional abbreviations: IVPP C/O, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; ZT, Zhaotong Institute of Cultural Relics, Zhaotong, Yunnan, China. Other abbreviations: DAP, anteroposterior diameter; DT, transverse diameter; H, height; L, length; W, width; art., articulation; col., collar; dia. diaphysis; dis., distal; gle., glenoid; lat., lateral; max., maximum; med., medial; min., minimal; pro., proximal; tro., trochlea; tub., tuber.

Systematic palaeontology

Fossils of *Acerorhinus lufengensis*

Order PERISSODACTYLA Owen, 1848
 Family RHINOCEROTIDAE Gray, 1821
 Subfamily ACERATHERIINAE Dollo, 1885
 Tribe CHILOTHERIINI Qiu et al., 1987

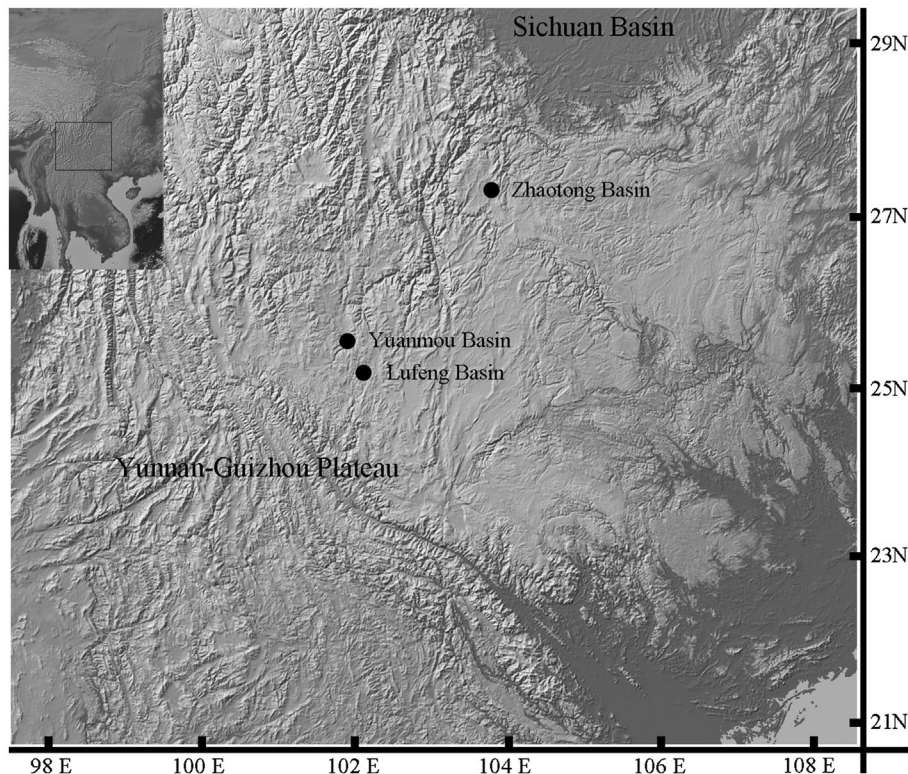


Figure 1. Location map of the Shuitangba locality in the Zhaotong Basin in northern Yunnan-Guizhou Plateau, South China.

Note: This topographic map was generated by a unprofitable software GeoMapApp (version 3.6.3) from the web <http://www.geomapapp.org> (Ryan et al. 2009).

Genus *Acerorhinus* Kretzoi, 1942
Acerorhinus lufengensis Deng et Qi, 2009
 Figure 2, Table 1

Materials

ZT-2007-01-187, left DP4; ZT-2015-01516, right P2; ZT-2015-0878, right M1; ZT-2015-0748, left p2; ZT-2007, left p4; ZT-2015-0215, left m2.

Locality

Shuitangba lignite mine, lignite bed with sand and gravels, Zhaotong Municipality, Yunnan, China; terminal Miocene, 6.5–6 Ma.

Description

The upper premolar and molar (Figure 2, Table 1) are specialised: the developed parastyle and paracone, expanded and slightly constricted protocone and hypocone, short crochet and antecrochet (its basement does not extend to the entrance of the median valley), reduced lingual and labial cingula, and enamel plications, mesostyle, metacone rib, are not present. The crista is absent under the heavy wear degree. The lower premolar p2 (Figure 2, Table 1) exhibits a reduced occlusal pattern: the trigonid lingual valley is absent; the talonid lingual valley is shallow, barely occupying the upper crown; the paralophid is slightly constricted, and the paraconid is little developed; all cingulum are absent. The lower cheek teeth p4 and m2 (Figure 2, Table 1) exhibit the same occlusal pattern: the labial wall of the trigonid and talonid are rounded; the labial groove is wide and deep and extends to the basement of the crown; the metalophid extends transversely

and slightly anteriorly; and the entolophid is nearly transverse; the lingual and labial cingula are reduced but with some weak residuals. Due to the difference in the degree of wear, the trigonid and talonid lingual valleys in p4 show a U-shaped outline in the occlusal view; the former has worn off, and the latter preserved a V-shaped outline in m2.

Comparisons

The upper cheek teeth display several diagnostic features: the parastyle and paracone rib are present, but the mesostyle and metacone rib are absent; both lingual cones are constricted, but weakly; the antecrochet and crochet are present and short; the enamel plications are absent; the lingual cingulum is absent on the upper molar. The lower cheek teeth show the rounded labial walls of the trigonid and talonid, wide and deep labial groove, short paralophid, and the lingual and labial cingula are variable. These characters distinguish it from many highly specialised rhinoceros, including *Elasmotherium*, *Aceratherium*, *Chilotherium*, *Shansirhinus*, and *Brachypotherium*, and the groups from the Late Neogene South China, including *Shansirhinus* cf. *S. ringstroemi* and *Subchilotherium intermedium*, but are consistent with the description of the genus *Acerorhinus* (Ringström 1924, 1927; Colbert 1935; Heissig 1969, 1989; Zong et al. 1996; Heissig 1999; Hünemann 1989; Deng 2005; Deng & Gao 2006; Deng & Qi 2009; Deng et al. 2013; Lu 2013).

Acerorhinus is among the most widely distributed aceratheres in Eurasia, with many less derived features. The new materials differ from *Acerorhinus* in two aspects, including the presence of the lingual cingulum of p4 and the reduced trigonid of p2. Because these two differences are based on the highly variable features

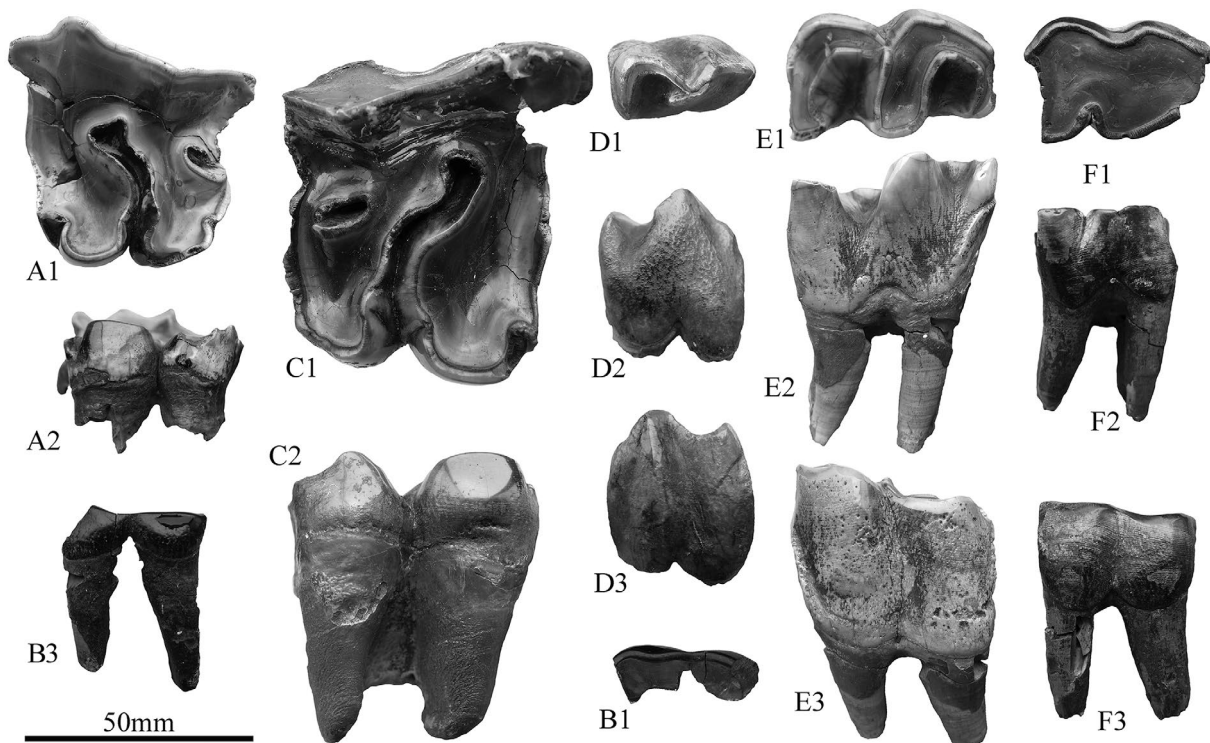


Figure 2. Cheek teeth of *Acerorhinus lufengensis* from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan.

Notes: A, ZT-2007-01-187, left DP4; B, ZT-2015-01516, right P2; C, ZT-2015-0878, right M1; D, ZT-2015-0748, left p2; E, ZT-2007, left p4; F, ZT-2015-0215, left m2. 1, occlusal view; 2, lingual view; 3, labial view.

Table 1. Measures of cheek teeth of *Acerorhinus lufengensis* from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, and from the late Miocene Lufeng Basin, Yunnan, China (length/width/height, in mm).

	New materials	Materials of Lufeng Basin		New materials	Materials of Lufeng Basin
DP4	50/50/21	–	p2	32/17/38	30.1/21.1/27
P2	32/–/11	–	p4	46/33/43	41/28.4/31.1
M1	61/67/23	57.8/68.7/24.6	m2	38/27/26	–

Note: Measures of *Acerorhinus lufengensis* from the late Miocene Lufeng Basin are from Deng and Qi (2009).

in late Neogene rhinocerotids, they are considered to represent interspecific variation (Heissig 1989; Lu 2013). Compared with two species of *Acerorhinus* from the Late Miocene hominoid localities in Yunnan, the new materials share more similarities with *A. lufengensis* than with *A. yuanmouensis* (Zong 1998; Deng & Gao 2006; Deng & Qi 2009; Lu 2013). The former has a short crochet and antecrochet and is also from the lignite pit. The latter is exceptional within the genus because the developed constrictions of the lingual cones and elongated antecrochet of the upper cheek teeth complicate the occlusal pattern of cheek teeth and therefore ensure the ability to graze hard grass or brush in the dry or seasonal environment in the Yuanmou Basin. We refer the new materials from the Late Miocene Zhaotong Basin to *A. lufengensis*.

Fossils of tribe Rhinocerotini

Subfamily RHINOCEROTINAE Gray, 1821

Tribe RHINOCEROTINI Gray, 1821

Rhinocerotini gen. et sp. indet.

Figures 3–4, Tables 2–4

Materials

ZT-2015-01696, right scapula; ZT-2007-2, proximal part of right radius; ZT-2015-0909, right Mc III; ZT-2015-0828, left Mc IV; ZT-2015-02695, left femur.

Locality

Shuitangba lignite mine, lignite bed with sand and gravels, Zhaotong Municipality, Yunnan, China; terminal Miocene, 6.5–6 Ma.

Description

All postcranial bones described herein belong to a single individual excavated from the same layer. The scapula (Figure 3, Table 2) exhibits a slender outline. The glenoid cavity is longer than its width, with a straight medial rim; just above its posteromedial rim is the coracoid process. It is a long tuberosity with an elliptical outline, showing the same distances to the tuber scapula anteriorly and the glenoid cavity posteriorly.

The radius (Figure 3) in proximal view displays an asymmetrical articular surface for the humerus: the medial portion is larger than the lateral portion. In posterior view the medial and lateral portions of the articular surface of the ulna are connected. The radius has the proximal width 112 mm (DT pro.); width and thickness of the medial portion of the humeral facet are 48 mm/76 mm (med. pro. art. DT/DAP), lateral portion 64 mm/51 mm (lat. pro. art. DT/DAP).

The metacarpal (Figure 4, Table 3) is stout in outline, and the minimum width of the shaft is located at the middle third of the shaft. The attachment for the interossei is rough and long, extending to the distal third of the shaft. In Mc III, the articulation for Mc II is large, oval, flattened, and nearly vertical in direction. The facet for Mc IV consists of two parts: the volar part is nearly vertical in direction and is not continuous with the facet for the magnum. The Mc IV has a pentagonal facet for the unciform, with a longer volar-lateral border. The facet for Mc III also consists of two parts: the volar part is not connected with the facet for the unciform. The articulation for Mc V is a curved face, bending from the proximal- to the lateral-side face, and forming an obtuse angle.

The head of the femur (Figure 3, Table 4) is oval in outline, with a V-shaped incision at the posteromedial surface. The trochanter minor is on the upper third of the shaft. The large trochanter tertius is around the middle third of the shaft; the process

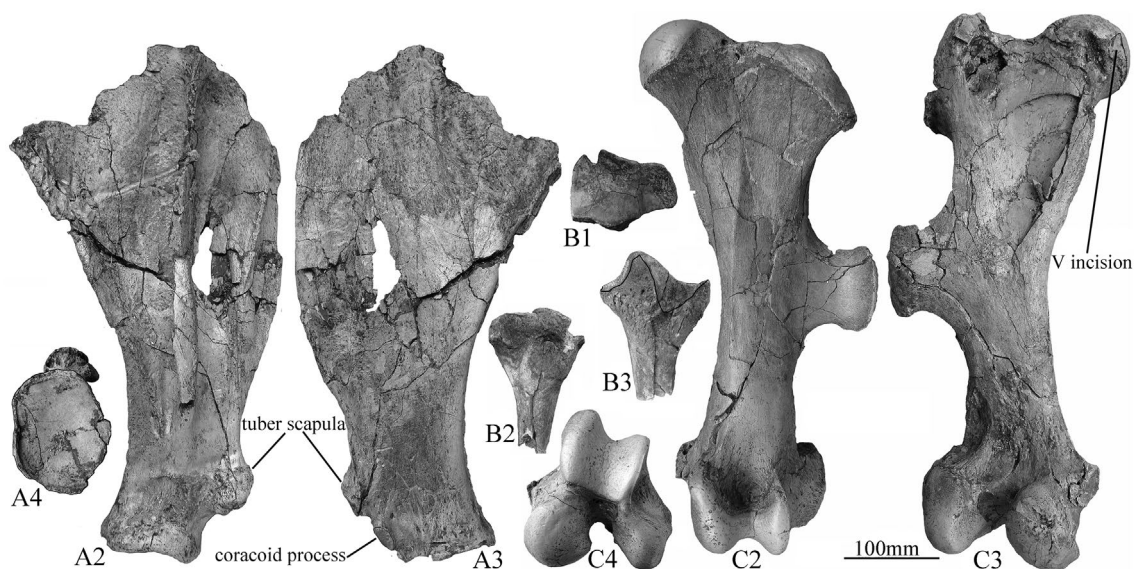


Figure 3. Limb bones of Rhinocerotini gen. et sp. indet. from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan.

Notes: A, ZT-2015-01696, right scapula; B, ZT-2007-2, right radius; C, ZT-2015-02695, left femur. 1, proximal view; 2, dorsal view; 3, ventral view; 4, distal view.

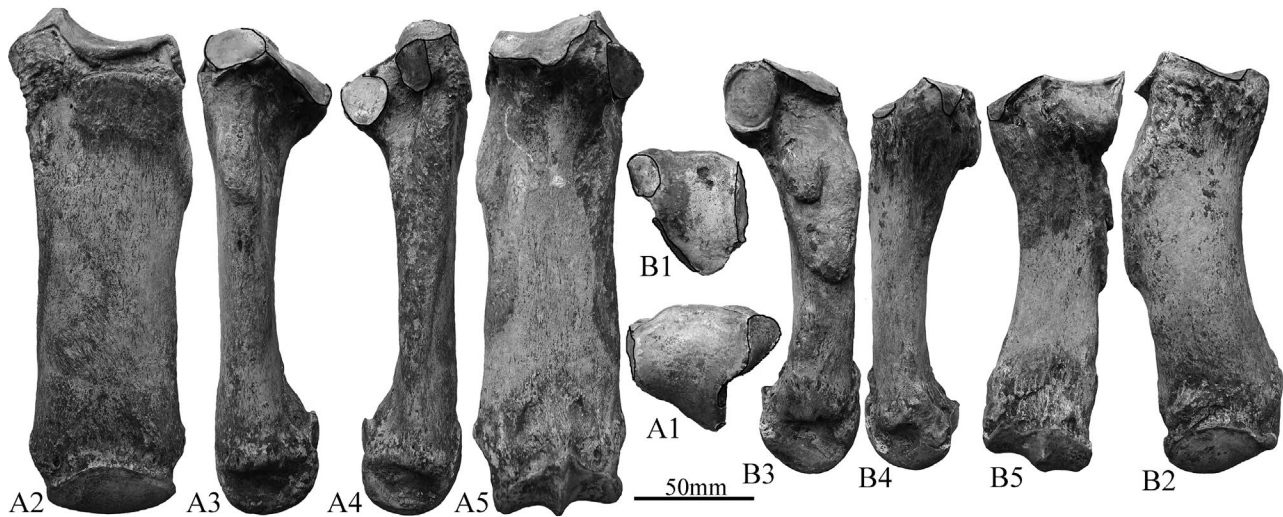


Figure 4. Metacarpals of Rhinocerotini gen. et sp. indet. from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan, China. Notes: A, ZT-2015-0909, right Mc III; B, ZT-2015-0828, left Mc IV. 1, proximal view; 2, dorsal view; 3, medial view; 4, lateral view; 5, volar view.

Table 2. Measures of scapula of Rhinocerotini gen. et sp. indet. from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan, China, and comparisons with other rhinocerotids (in mm).

Measure	New material					
	<i>C. simum</i>	<i>R. unicornis</i>	<i>C. antiquitatis</i>	<i>S. etruscus</i>	<i>C. wimani</i>	
L max.	>526	523	559	457	–	442
DAP max.	>280	241	252	–	–	185
DAP col.	113	131	141	113	91	89
DAP tub.	155	154	163	142	98	–
DT art.	>100	101	96	88	59	58
DAP art.	125	101	96	–	76	71

Note: Measures of *Ceratotherium simum* and *Rhinoceros unicornis* from Guérin (1980); *Coelodonta antiquitatis* from Borsuk-Bialynicka (1973); *Stephanorhinus etruscus* from Mazza (1988); *Chilotherium wimani* from Deng (2002).

is very large and curled dorsally; the upper and lower edges are symmetrical and equal in size. The medial ridge of the trochlea is much wider and more prominent and extends slightly higher than the lateral ridge; the two ridges are nearly parallel with each other below; the groove between them is wide.

Comparisons

To date, there are two species of *Acerorhinus* for which limb bones have been reported: *A. tsaidamensis* and *A. zernowi*

(Bohlin 1937; Cerdeño 1996). Because the materials referred to *A. zernowi* from the Tung-gur Formation of Inner Mongolia, China are doubtful, the comparisons described herein are based on materials of the former species from the Qaidam Basin in China. The new materials differ from those of *A. tsaidamensis* in showing a much higher placement of the tuber scapula, a very large third trochanter, and a large, flattened, and nearly vertical articulation of Mc II and Mc III (Bohlin 1937). Moreover, the new materials are sufficiently large to separate it from the genus *Acerorhinus*.

The new postcranial bones differ from the elasmotheres in having two crucial features: the trochanter tertius of femur is huge; there is a single articular facet between Mc II and Mc III (Antoine 2002). Similar to *C. antiquitatis*, the scapula studied here is slender in outline: the length–width ratio is 1.8; the ratio of the maximum to the minimum width is at least 2.4 (Borsuk-Bialynicka 1973). The glenoid cavity of the new scapula is unique, with a nearly straight medial rim. An identical shape was observed in the material from Sansan Basin referred to *Hoploaceratherium tetradactylum* and the extant *Rhinoceros unicornis* (Heissig 2012). In the radius of rhinocerotids, the medial articular surface for the humerus is much larger than the lateral surface. For the new radius, the proportion of anteroposterior

Table 3. Measures of metacarpals of Rhinocerotini gen. et sp. indet. from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan, China, and comparisons with other rhinocerotids (in mm).

Measure	New materials		<i>C. simum</i>		<i>R. unicornis</i>		<i>C. antiquitatis</i>		<i>D. schleiermacheri</i>		<i>S. etruscus</i>		<i>A. incisivum</i>		<i>C. wimani</i>	
	McIII	McIV	McIII	McIV	McIII	McIV	McIII	McIV	McIII	McIV	McIII	McIV	McIII	McIV	McIII	McIV
L	215	174	197.5	163	219	178	161	130	204	–	200	176	144	117	120	93
DT pro.	72	56	76	65	74	62	60	44	69	–	53	40	51	35	45	28
DAP pro.	61	55	59	48	65	54	–	–	52	–	45	41	39	36	39	32
DT dia.	58	42	60	43	66	43	–	–	60	–	45	36	42	27	34	27
DT max. dis.	71	53	80	61	82	61	57	43	69	–	54	42	54	36	42	28
DT art. dis.	55	47	65	55	69	53	–	–	56	–	–	36	46	35	36	25
DAP art. dis.	50	47	52	47	54	45	–	–	49	–	–	–	39	37	33	31

Note: Measures of the same forms mentioned above are from the same authors, and *Dihoplus schleiermacheri* from Guérin (1980), *Aceratherium incisivum* from Hünemann (1989).

Table 4. Measures of femur of Rhinocerotini gen. et sp. indet. from the terminal Miocene of the Shuitangba locality in the Zhaotong Basin, Yunnan, China, and comparisons with other rhinocerotids (in mm).

Measures	New femur	<i>C. simum</i>	<i>R. unicornis</i>	<i>C. antiquitatis</i>	<i>D. shleiermacheri</i>	<i>S. etruscus</i>	<i>A. incisivum</i>	<i>C. wimani</i>	<i>A. tsaidamensis</i>
L	566	550	602	520	523	450	411	395	395
DT head	113	118	112	100	100	–	67	85	–
DAP head	105	116	107	100	103	74	70	71	–
DT prox.	230	240	248	225	225	161	156	173	132
DT mini. dia.	85	88	86	91	76	61	59	72	–
H 3th tro.	91	109	143	–	93	70	–	86	–
DT 3th tro.	167	171	181	–	157	120	–	127	–
DT dis.	157	161	169	153	162	122	110	–	93
DAP dis.	165	200	206	–	–	150	117	–	–

Note: Measures of the same forms mentioned before are from the same authors; *Acerorhinus tsaidamensis* from Bohlin (1937).

diameter between the medial and the lateral diameter is approximately 1.5 (76 mm/51 mm), similar to that of *Rhinoceros*, *Stephanorhinus*, *Dihoplus*, and *Coelodonta* (Qi 1975; Guérin 1980; Antoine 2002; Pandolfi et al. 2016).

The trochanter tertius in the new femur is located at the middle third of the shaft and exhibits a very large process with the upper and lower borders symmetrical, similar to those of the Late Neogene and Quaternary *Stephanorhinus*, *Coelodonta*, *Ceratotherium*, and *Rhinoceros*. Interestingly, among all reported postcranial bones of rhinocerotids, only Pleistocene *Stephanorhinus* and extant *Rhinoceros* (IVPP C/O 1046) exhibit a distal trochlea with two ridges nearly parallel with each other (Mazza 1988; Mazza et al. 1993; Campanino et al. 1994; Pandolfi 2011).

Similar to other large rhinoceroses, including *Dihoplus ringstroemi*, *D. shleiermacheri*, *Ceratotherium neumayri*, *Coelodonta antiquitatis*, and *Stephanorhinus kirchbergensis*, in the Mc III described in this paper, the facet for Mc IV is volarly isolated from the magnum surface, and the length–width ratio of the shaft is approximately 3.7 (Ringström 1924; Borsuk-Bialynicka 1973; Qi 1975; Yan 1978; Guérin 1980; Mazza 1988; Antoine & Saraç 2005). The new Mc III bears a special facet for Mc II. In the materials referred to *S. kirchbergensis* from the Pleistocene Anping locality of China, the Mc II facet of Mc III is variable in shape, from a long ellipse to a shallow semi-cycle, but is still a small and curved facet (Xu 1986). Extant *R. unicornis* is a large rhinoceros, and the Mc II facet of the Mc III is large, flattened, rounded, and nearly vertical in direction (IVPP C/O 1046), similar to that of the new material.

The new limb bones from the Shuitangba locality exhibit many valuable characters, similar to the Rhinocerotini genera *Stephanorhinus*, *Rhinoceros*, and *Dihoplus*, but craniodental morphology is still necessary to discuss their taxon identity. These materials are tentatively assigned as Rhinocerotini gen. et sp. indet.

Discussion of the palaeoenvironment

The new and other known cheek teeth assigned as *Acerorhinus* exhibit no cement: in the upper cheek teeth, the occlusal surface has a concave profile, the labial side is higher than the lingual; and the medifossette is absent; the lower cheek teeth display a rounded labial wall (Deng 2000; Deng & Qi 2009). According to the suggested categories of rhinoceros cheek teeth, these features are similar to those of the brachyodont *Diceros bicornis* but different from the hypsodont *Ceratotherium simum*, whose

cheek teeth have a flat occlusal surface, persistently present oval medifossette, and a flat labial wall of the trigonid and talonid (Fortelius 1982). *Acerorhinus* is medium-sized and exhibits an occipital face that is inclined forward; the inclination is 81–87°, indicative of a high horizon of the skull (Borissiak 1914, 1915; Deng 2000). The genus probably fed on shrubs or high grass based on the morphology of the skull and cheek teeth (Zeuner 1934; Fortelius 1982; Qiu & Yan 1982).

All postcranial bones described herein belong to a single individual. The measures of the maximum length of the long bones referred to Rhinocerotini gen. et sp. indet. described above are greater than those of the extant species *C. simum*, whereas the minimum diameter of the shafts is much smaller than those of *C. simum* and *Rhinoceros unicornis*. The new postcranial bones must belong to a large rhinoceros, but one with a somewhat slender limb. Moreover, the distal trochlea of the femur described herein is unequal in size, with the medial ridge being larger than the lateral ridge. Many studies have suggested that the knee asymmetry initially evolved for convenience of locomotion is indicative of an open habitat (Kappelman 1988; Shockey 2001; Janis et al. 2012). It has been claimed that the same trend has been seen in equids and rhinoceroses. Although it is impossible to make comparisons with each rhinocerotid, it is noteworthy that in the new femur, the ratio of the medial trochlea ridge to the lateral fellow (approximately 1.14) falls within the range observed from *Stephanorhinus*, *Coelodonta*, *Ceratotherium*, *Diceros* and *Rhinoceros* (1.12–1.38) (Qi 1975; Mazza 1988; Janis et al. 2012). The new postcranial bones are similar to these genera also in having the slender scapula, developed articular surfaces between the Mc III and Mc IV, and the large trochanter tertius of the femur. Among these genera, *Ceratotherium* and *Coelodonta* are undoubtedly typical open habitat-type taxa, and *Stephanorhinus*, *Diceros* and *Rhinoceros* also prefer environments with grassland (Fortelius 1982; Thapa & Lichtenegger 2005; Gyongyi 2011; Gurung & Chalise 2015; Ojah et al. 2015). Whatever the category of the cheek teeth described herein, the limb shape of these late Neogene medium- or larger-sized rhinoceroses enabled them to move in relatively open environments, such as savanna woodlands or grasslands. All the evidence clearly demonstrate that the small niche of the rhinoceroses of the Shuitangba locality must not have been densely vegetated. However, this result is apparently inconsistent with the environment examination of this locality on the whole.

South China has long been considered to have represented a refuge for late Neogene mammals due to the delayed onset of aridification by the uplift of the Tibetan Plateau and the

occurrence of the Asian monsoon; the floodplain forest was replaced in this region by C₄ grassland at 4–3 Ma, which occurred at 10–7 Ma and 8–7 Ma in Africa and Siwalik, respectively (Dong 1987; Bonnefille 2010; Biasatti et al. 2012; Ji & Gao 2012; Ji et al. 2013; Zhang et al. 2016). The most recent clay mineralogy analysis demonstrates that there was a mildly warm and humid climate in several hominoid localities of South China during the period of the late Neogene (Zhang et al. 2016). In addition, the ape and tapir specimens and the abundant remains of large tree trunk are indicative of a forest environment (Jablonski et al. 2014).

Moreover, all of the vertebrate fossils at the Shuitangba locality, including the rhinocerotid specimens, were produced from peaty clay that intercalated between layers of lignite. Lignite mines generally result from rich plant environments. Approximately 84.4% of the total numbers of collected specimens from the terminal Miocene Shuitangba locality are postcranial bones, and large mammalian bones exhibit minimal traces of weathering and a low proportion of damage, which is typically exemplified by the limb bones described herein and the well-preserved skeleton of the oldest *Sinomastodon* (Jablonski et al. 2014; Wang et al. 2015). These facts indicate that the animals were buried quickly after death and remained relatively undisturbed or did not undergo transportation over a long distance. The bones were probably deposited in an environment near standing water, consistent with the discovery of the aquatic herb *Euryale*, aquatic pollen taxa, vertebrate fossils of aquatic birds, fish, frogs, and crocodile (Jablonski et al. 2014; Chang et al. 2015; Huang et al. 2015).

These incongruous postulations demonstrate the existence of more than one environment in the terminal Miocene Shuitangba locality. This opinion is supported by pollen evidence from the 16-meter-thick Shuitangba section: the pollen assemblage from the period when the hominoid and associated fauna lived suggests a typical evergreen broad-leaved forest with grasses in open spaces of the understory or at the woodland edge (Chang et al. 2015). In addition, the presence of terrestrial Galliformes birds also indicates the presence of spaces with shrubs, such as *Zanthoxylum* (Zhang et al. 2013; Zhu et al. 2016). The rhinocerotids described herein further demonstrate that open spaces with grass and shrubs were probably present along the margin of the forest or in patches within it.

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