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Original article

New materials of *Chalicotherium brevirostris* (Perissodactyla, Chalicotheriidae) from the Tunggur Formation, Inner Mongolia☆

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ABSTRACT

Chalicotherium brevirostris was named by Colbert based on a skull lacking mandibles from the late Middle Miocene Tunggur Formation, Tunggur, Inner Mongolia, China. Here we describe new mandibular materials collected from the same area. In contrast to previous expectations, the new mandibular materials show a long snout, long diastema, a three lower incisors and a canine. *C. brevirostris* shows some sexual dimorphism and intraspecific variation in morphologic characters. The new materials differ from previously described *C.* cf. *brevirostris* from Cixian County (Hebei Province) and the Tsaidam Basin, which may represent a different, new species close to *C. brevirostris*. The diagnosis of *C. brevirostris* is revised.

1. Abbreviations

IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
V Vertebrate paleontology collection, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
AMNH American Museum of Natural History, New York, USA
HLM Hessischen Landesmuseum, Darmstadt, Germany
MHNT Muséum d'Histoire Naturelle, Toulouse, France
GSP Geological Survey of Pakistan, Quetta, Pakistan

2. Introduction

Tunggur, the region where the Tunggur Formation is actually or potentially exposed (Qiu et al., 1988; Fig. 1), is well known in the vertebrate paleontology community for producing rich mammalian fossils. The American Museum Central Asiatic Expeditions first discovered and excavated the Tunggur area in 1930. Fossils housed in the AMNH were subsequently described and placed within 28 species (Wang et al., 2003). Fossils found by the Sino-Soviet Paleontological Expedition in 1959 have remained mostly undescribed until now, except for a beaver and a carnivore (Li, 1963; Zhai, 1964). In 1986–1987, an IVPP team made substantial progress in understanding the Tunggur geology and paleontology (Qiu et al., 1988). The most important result of this expedition so far is a monograph on Tunggur small mammals (Qiu, 1996).

Because of its richness in fossils and simplicity of stratigraphy and tectonics, Tunggur was soon recognized as one of the most important Neogene Locality in East Asia, and the Tunggur fauna became the representative for the Chinese Middle Miocene mammalian age, named Tunggurian. So far a total of 76 mammalian species have been recorded (Wang et al., 2003; Deng et al., 2007). Thanks to the screen-washing technique, small mammals were extensively studied (Qiu, 1996), while large mammals still lack revision.

Along with *Platybelodon* Borissiak, 1928; *Zygolophodon* Vacek, 1877; *Anchitherium* von Meyer, 1834; *Acerorhinus* Kretzoi, 1942; *Listriodon* von Meyer, 1846; *Kubanochoerus* Gabunia, 1955; *Palaeotragus* Gaudry, 1861; *Pseudarctos* Schlosser, 1899; *Amphicyon* Lartet, 1836; *Tungurictis* Colbert, 1939 and *Alloptox* Dawson, 1961, the Chalicotherioidea is one of the representative elements in the Tunggur fauna. This unusual perissodactyl group is characterized by the presence of clawed phalanges. It is known from Eocene to Pleistocene and widely distributed in Eurasia, North America and Africa (Lucas and Schoch, 1989; Coombs, 1989, 1998).

However, chalicotheres are never common as fossils. The Chalicotheriidae are split into two subfamilies: the Chalicotheriinae and the Schizotheriinae. The classification of Chalicotheriinae has long been disputed. According to Butler (1965), the Chalicotheriinae comprise *Chalicotherium* Kaup, 1833 and *Nestoritherium* Kaup, 1859. Coombs (1989) indicated that a generic distinction was probably inappropriate for *Nestoritherium*. de Bonis et al. (1995) resurrected

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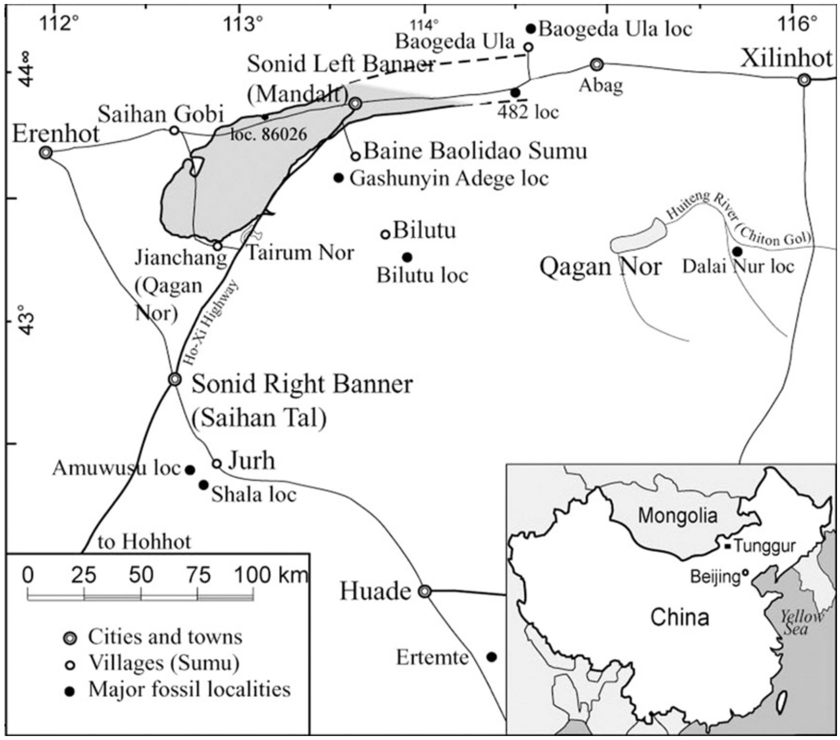

Fig. 1. Location map of the Tunggur Tableland. Loc. 86026: 2 km northwest to the tripod of Huerguolajin. Adapted from Wang et al., 2003.

the genus name *Macrotherium* Lartet, 1837, and ascribed *Chalicotherium rusingense* from the Early Miocene of Rusinga, Kenya, to a new genus: *Butleria* de Bonis et al., 1995. Geraads et al. (2001) suggested that the generic name *Macrotherium* is a junior synonym of *Chalicotherium* and should be abolished. They used the name *Anisodon* Lartet, 1851, for material formerly referred to *M. grande* and named a new genus: *Kalimantsia* Geraads et al., 2001. Using the data matrix derived from de Bonis et al. (1995), Anquetin et al. (2007) added additional characters to perform a new cladistic analysis, dividing Miocene Chalicotheriinae into *Anisodon*, *Chalicotherium*, *Butleria* and *Kalimantsia*, and proposing a subdivision between an *Anisodon* clade and a *Chalicotherium* clade.

Colbert (1934) described a partially preserved skull and some postcranial specimens as *Macrotherium brevirostris*, and *Macrotherium* sp. for some large phalanges from the Tunggur fauna. However no mandibles were included. Some postcranial specimens of *M. brevirostris* were later recognized as Schizotheriinae (Butler, 1965; Coombs, 1974, 1989, 2009). Since then, new materials of *M.* cf. *brevirostris* were discovered from Cixian, Hebei Province (Hu, 1959) and Tsaidam, Qinghai (Wang and Wang, 2001). In this paper, we describe in detail new materials found from the Tunggur Formation during 1986–1987, and try to revise all the Middle Miocene Chalicotheriinae from China.

Dental terminology follows Coombs (1978b) and Zapfe (1979).

3. Systematic paleontology

Order PERISSODACTYLA Owen, 1848
Superfamily CHALICOTHERIOIDEA Gill, 1872
Family CHALICOTHERIIDAE Gill, 1872
Subfamily CHALICOTHERIINAE Gill, 1872
Genus **Chalicotherium** Kaup, 1833
Chalicotherium brevirostris (Colbert, 1934)
Figs. 1–4; Tables 1 and 2

1934. *Macrotherium brevirostris* nov. sp. Colbert, p. 377, 379, figs. 11, 12.

Holotype: AMNH No. 26518, a skull, complete on the left side except for the tips of the premaxillaries and the postero-dorsal region of the cranium. The right side has been to a great extent weathered away.

New materials: a right mandible with p2-m3 (V 16308), a left mandible with p2-m3 (V 16309.1), a left p4 (V 16309.2) and a right m1 (V 16309.3).

Locality and horizon: 2 km northwest to the tripod of Huerguolajin, Inner Mongolia (IVPP loc. 86026); Tunggur Formation, late Middle Miocene.

Diagnosis (revised from Colbert, 1934): chalicothere of medium to large size; maxilla high; zygomatic arch long, glenoid articulation extends forward onto the posterior part of the zygomatic arch; paroccipital process long and postglenoid process heavy; pterygoids and internal nares large; angulus mandibulae expanding ventrally; masseteric fossa shallow; mental foramen located at anterior part of diastema; mandibular foramen located at the same level as tooth row; dental formula 0?/3 - 0?/1 - 3/3 - 3/3; well developed paraconule on upper molars; size of lower incisors based on alveoli increases from the mesial one to the distal one; metastylid moderately strong, slightly separated from metaconid; labial cingula developed, but weak on lower molars; posterior cingulum of m3 well developed.

Description:

V 16308 (Fig. 2(1–3); Tables 1 and 2): the right mandible is well preserved with an almost complete corpus and part of the ramus, and all lower postcanine teeth. However, only the alveoli of the lower incisors and canine are preserved. The corpus is deep and slenderly built. Table 1 gives height measurements on the labial side. The labial side is flat, and the lingual side below the tooth row is slightly convex. The ventral border is straight, expanding ventrally at the angulus mandibulae, and turning upwards at p2 with an angle ~20°. There is a retromolar space. The diastema

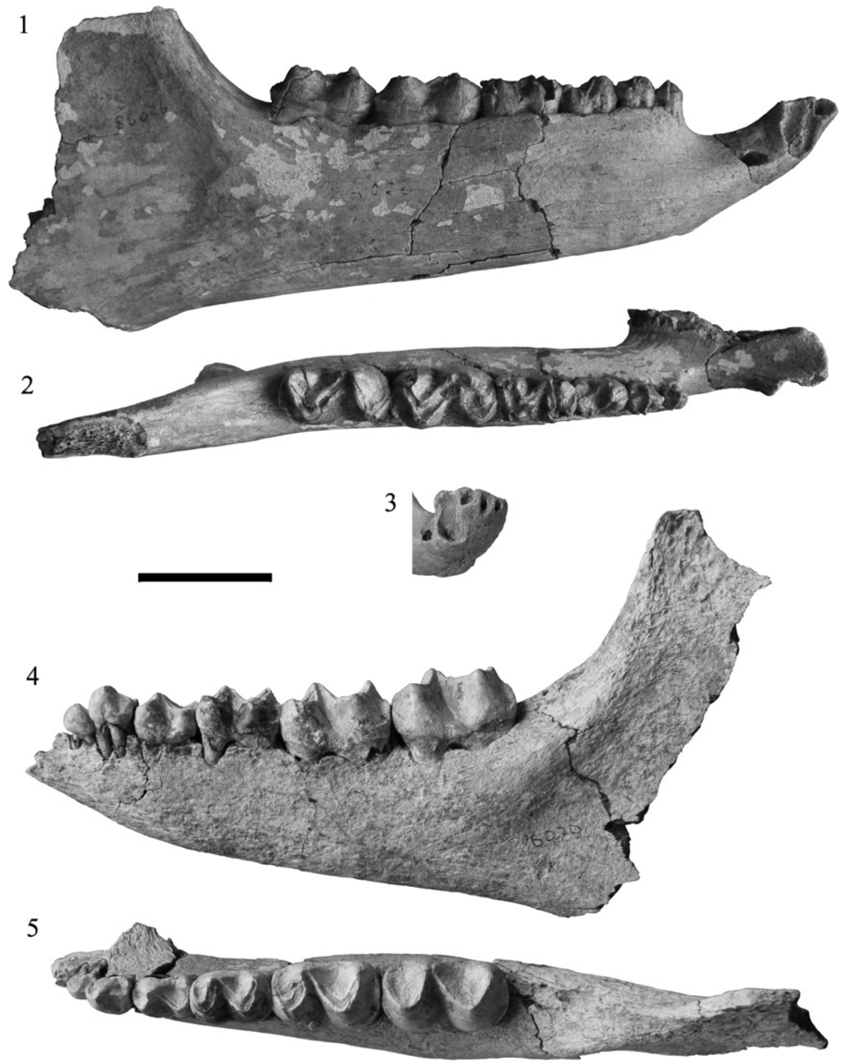

Fig. 2. Mandibles of *Chalicotherium brevirostris* from Tunggur, Inner Mongolia, China. **1–3**: V 16308: right mandible: 1: labial view; 2: occlusal view; 3: anterolabial view. **4, 5**: V 16309.1: left mandible: 4: labial view; 5: occlusal view; scale bar: 5 cm.

between the canine and p2 is 33.3 mm long and the dorsal brim about 10 mm lower than alveolus line. The mental foramen is large and oval-shaped with a maximum diameter of 9.1 mm, and is located below the diastema, closer to the canine. The masseteric fossa is very shallow. The mandibular foramen is oval-shaped (maximum diameter 13 mm), and opens lingually at the same level as the tooth row. There is an obvious depressed pterygoid fossa. The mandibular symphysis is stout, wide, and the maximum length is 73.7 mm, extending posteriorly to the level of middle part of p3. In dorsal view, there is a posteriorly tilted concave surface on the symphysis. The maximum thickness of the symphysis is 26.5 mm, gradually thinning anteriorly.

From the preserved alveoli, we can tell that there were three incisors and one canine on each side. Hence, the lower dental formula is 3-1-3-3. The incisor alveoli increase in size from i1 to i3. The canine appears to have been stout. The diameters of the alveoli measure 4.1 mm (i1), 6.2 mm (i2), 7.2 mm (i3), and 8.9 mm (c), respectively. The premolars are short and narrow compared to the molars. Hence the lower premolar row is much shorter than the lower molar row (ratio of p/m lengths: 40.21%). Molars gradually increase in size from m1 to m3, though m3 is a little narrower than m2. Trigonids of the molars are shorter than the talonids. The measurements of cheek teeth are given in Table 2.

Only half of the **p2** preserves enamel. Fortunately, we can still tell the tooth morphology by the remains. It is remarkably smaller than the other lower cheek teeth, with only one sharp main cusp, which extends backward to a weak lophid. There is a weak posterolingual cingulum. Two roots are present. The **p3** has also lost part of the enamel. Its tooth morphology is similar to that of p2, though it is larger and has a much broader talonid. The **p4** is submolariform, and has lost part of its enamel. The protoconid and metaconid are high, while the paraconid is low. The paralophid slopes lingually, and the protolophid is horizontal, thus forming a weak trigonid basin. The metastylid, hypoconid and entoconid are low and form a lower talonid basin. All cingula are weak. The **m1** is partially broken. The paraconid is weak, the metaconid is the highest cusp though broken, and the metastylid is weak. The paralophid and protolophid are nearly perpendicular to the tooth row, and thus the trigonid appears U-shaped. The entoconid is large, as high as the metaconid. The talonid is V-shaped with a blunt angle at the hypoconid. The labial and posterolabial cingula are well developed. The **m2** has a low paraconid. Its metaconid is the highest cusp. The metastylid, at nearly the same height as the entoconid, is slightly lower than the metaconid. The metastylid is fused with the metaconid, with a shallow groove forming between them as they wear. The paralophid and protolophid are curved and nearly perpendicular to the tooth row, and thus the trigonid is U-shaped. The metalophid and hypolophid are straight, and the talonid is V-shaped with a sharp angle at the hypoconid. The metaconid is widely expanded to enclose the trigonid basin

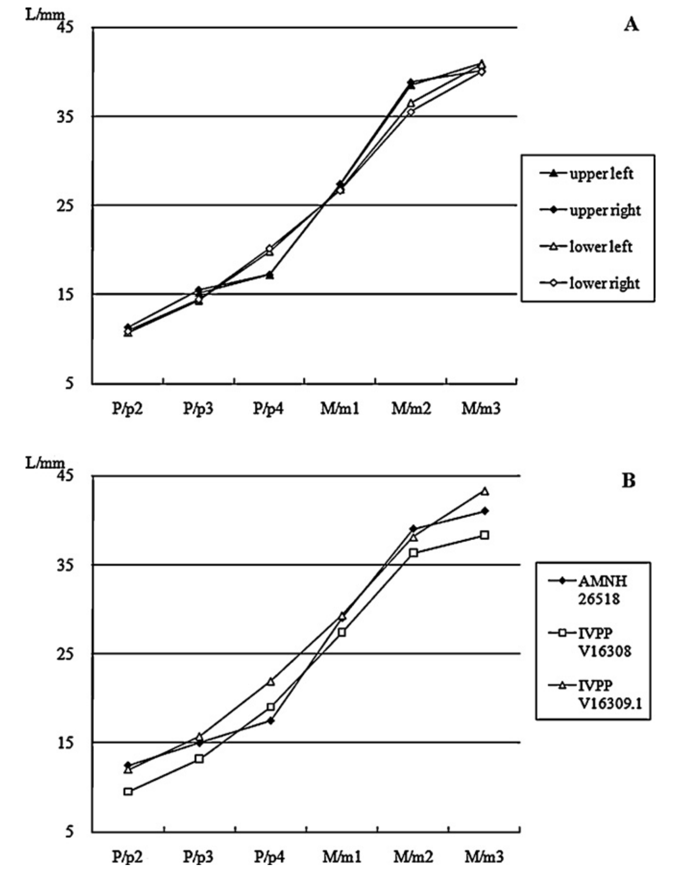

Fig. 3. Comparisons of tooth length curves at postcanine teeth. A. One individual of *Anisodon macedonicum* (DKO 234). B. Three individuals of *Chalicotherium brevirostris* (AMNH 26518, IVPP V 16308 and V 16309.1).

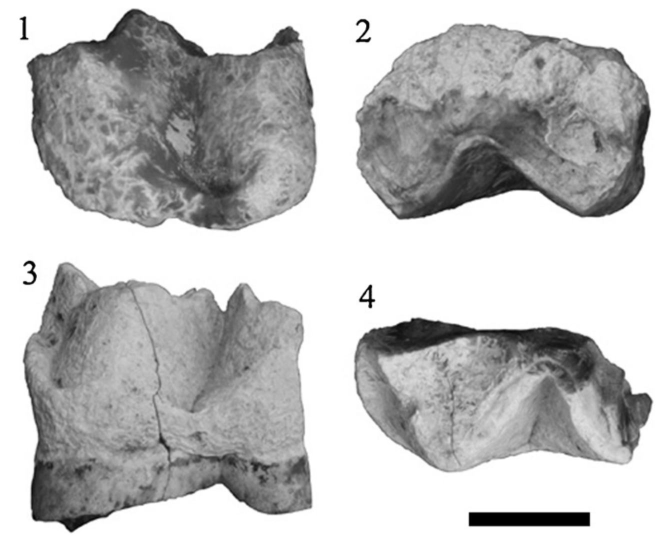

Fig. 4. Additional teeth of *Chalicotherium brevirostris* from Tunggur, Inner Mongolia, China. **1, 2**: V 16309.2: left p4: 1: labial view; 2: occlusal view: **3, 4**: V 16309.3: right m1: 3: labial view; 4: occlusal view; scale bar: 1 cm.

together with the curved paralophid. Labial cingula are well developed; the anterolabial cingulum is weak, and the posterolabial cingulum tilts up posteriorly and broadens to form a banded posterior cingulum. Lingual cingula are weak, just visible at the opening of the talonid basin, and the paralophid slopes down and curves lingually to form a weak anterolingual cingulum. The metaconid and entoconid of **m3** are sharp and cone-shaped; the metaconid is the highest cusp, and the paraconid is the lowest cusp. The metastylid is slightly separated from the metaconid and lower than the metaconid, nearly the same height as the protoconid, hypoconid and entoconid. The paralophid and protolophid are slightly curved and nearly perpendicular to the tooth row, making the trigonid U-shaped. The metalophid and hypolophid are straight, and the talonid is V-shaped with a sharp angle at the hypoconid. The labial cingulum is well developed, and the posterior cingulum is band-shaped and slopes labially. Lingual cingula are weak, just visible at the opening of the talonid basin, and the paralophid slopes down and curves lingually to form a weak anterolingual cingulum.

V 16309.1 (Fig. 2(4, 5); Tables 1 and 2): the left jaw preserves the corpus and part of the ramus, with all postcanine teeth. It appears to be a young adult on the basis of the barely worn m3. The morphology is similar to that of V 16308, with some detail differences. The corpus is strongly built, and increases in height posteriorly, especially rapidly posterior to m3 (Table 1). The ventral border curves upward at p3. The mental foramen is not preserved. However, there is a big broken foramen for the mandibular nerve with some pinholes anterior to the root of p2. This foramen goes posteriorly, suggesting that the mental foramen should be well anterior to this position. The mandibular foramen is partly broken, and the maximum diameter is almost vertical and estimated as 23 mm long. The mandibular symphysis is not well preserved. From what remains, it should be stout and wide, extending to p4. The ratio of the premolar row to the molar row is 42.17%. The measurements of cheek teeth are given in Table 2. The **p2** is small and low, and embedded in the crown of p3. The main cusp extends anteriorly, lingually and posteriorly as lophids to form a weak "trigonid basin" and "talonid basin". The main cusp of **p3**, the protoconid, has a sharp lophid extending posteriorly to form a "talonid basin" along with a low cone-shaped cuspid, the entoconid. The protoconid also has a weak lophid curving anterolingually to form a weak "trigonid basin". The **p4** is submolariform. The metastylid is hardly separable from the metaconid. The paralophid slopes and curves anterolingually, forming a weak cingulum, and the trigonid is U-shaped. There are weak labial cingula. There is a weak cingulum at the opening of talonid basin. The **m1** is well preserved. The metaconid and entoconid

Table 1
Corpus measurements (in mm) of IVPP V 16308 and V 16309.1.

	IVPP V 16308			IVPP V 16309.1		
	Height	Thickness	Thickness-height ratio (%)	Height	Thickness	Thickness-height ratio (%)
Anterior edge of p2	48.7	–	–	26.4	–	–
Between p2 and p3	48.9	–	–	28.0	–	–
Between p3 and p4	50.5	26.0	51.5	37.9	–	–
Between p4 and m1	50.9	26.6	52.3	40.6	27.3	67.2
Between m1 and m2	52.7	29.7	56.4	43.9	28.5	64.9
Between m2 and m3	56.3	29.1	51.7	49.4	32.1	65.0
Posterior edge of m3	67.5	27.1	40.1	64.5	31.5	48.8

Table 2
Lower cheek teeth measurements (in mm) of IVPP V 16308 and V 16309.1.

	L	W	W/L (%)	L (trigonid)	L (talonid)
IVPP V 16308					
p2	9.5	7.80	82.11	–	–
p3	13.2	11.5	87.11	–	–
p4	19.0	14.8	77.89	9.4	9.9
m1	27.4	17.4	63.50	11.1	16.2
m2	36.3	21.8	60.06	14.0	22.0
m3	38.3	20.4	53.26	14.2	24.1
p2-p4	41.5	–	–	–	–
m1-m3	103.2	–	–	–	–
p2-m3	144.6	–	–	–	–
IVPP V 16309.1					
p2	12.0	9.6	80.00	–	–
p3	15.7	12.9	82.17	–	–
p4	21.9	15.6	71.23	7.7	12.9
m1	29.3	18.2	62.12	12.2	17.3
m2	38.1	22.5	59.06	13.8	24.1
m3	43.3	25.8	59.58	18.9	24.1
p2-p4	47.1	–	–	–	–
m1-m3	111.7	–	–	–	–
p2-m3	158.5	–	–	–	–
IVPP V 16309.2					
Left p4	23.3	15.5	66.52	10.4	12.6

L: length; W: width.

are high and sharp, and the metastylid separates slightly with the metaconid. The labial cingulum is well developed, the anterolabial cingulum is weak, and the posterolabial cingulum tilts up posteriorly and broadens to form the banded posterior cingulum. The lingual cingulum is only developed at the opening of the talonid basin. The **m2** is the same as that in V 16308, except less worn. There is a convex nubble with more foramina below the protolophid almost on the labial base of crown. This roughened area may be the result of microorganism activity. The **m3** has the same structure as that in V 16308, but is nearly unworn.

There are some differences in tooth sizes between V 16308 and V 16309.1, though the tooth length curves are nearly parallel except for the longer m3 on V 16309.1 (Fig. 3). The ramus of V 16308 is slightly thinner, the teeth are smaller and the tooth row is shorter. Through the study by Coombs (1975), size variation may occur in all chalicotheriids as a result of sexual dimorphism. Hence, V 16308 may be a female individual. The corpus of V 16309.1 is very low, but its m3 has just erupted and is unworn, which suggests that it is a subadult individual and the jaw growth is still incomplete. Coombs (1978b, 1979) suggested that the intraspecific variation of dental morphology in *Moropus elatus* and *Tylocephalonyx skinneri* might be widespread among chalicotheres. We suggest that the differences among cheek teeth are caused by many factors, such as growth stages, sexual dimorphism, variety and richness of food, differences of chewing pattern, degree of wear, and so on, which cause intraspecific individual variations. Therefore, these minor differences between V 16308 and V 16309.1 are intraspecific, not interspecific variations.

V 16309.2 (Fig. 4(1, 2): Table 2), this preserved left p4 is almost the same as p4 of V 16309.1, though it is much larger heavily worn and the labial cingulum is much developed.

V 16309.3 (Fig. 4(3, 4): this a right broken m1 preserves part of the crown. In structure and talonid size, it is similar to the m1 of V 16309.1, except that it is less worn.

4. Comparisons

4.1. Comparison with Schizotheriinae

The lower jaws of Chalicotheriinae are distinguishable from those of Schizotheriinae by more robust mandibles, height of the mandibular corpus increasing posteriorly, and molars low-crowned and relatively short (Coombs, 1989; de Bonis et al., 1995; Anquetin et al., 2007).

In Table 1, we can see the thickness-depth ratio of V 16308 and V 16309.1 corpora. In comparison, "*Chalicotherium*" *salinum* (GSP 6006) displays a somewhat lower value of 51% at the level of the m1 (Chavasseau et al., 2010), while a mandible of *Schizotherium* cf. *S. avitum* (AMNH 103336) shows a much lower ratio of 39.5% between m1 and m2 (estimated from Coombs, 1978a: fig. 4). *Phyllotillon huangheensis* (V 9959) is even more slender (35.1% between m1 and m2; Qiu et al., 1998). Therefore the corpora of V 16308 and V 16309.1 are comparatively robust.

They display the increase in depth posteriorly (Table 1), which is consistent with lower jaws of the Chalicotheriinae.

According to Chavasseau et al. (2010), the characteristic molar elongation of Schizotheriinae seems more accentuated on m2 and m3 than on m1. For this reason, we only compare the m2 and m3 in this paper. With width-length indices of 60.06 and 59.06, the m2 of V 16308 and V 16309.1 are proportionally less elongated than those of Schizotheriinae; such as *Metaschizotherium bavaricum*, *M. fraasi*, and *Ancylotherium pentelicum* (respectively 50.9–55.1, 51.3–51.7, and 57.3; Coombs, 2009), *Phyllotillon naricus* (49.6-54.6; Forster-Cooper, 1920; Coombs, 2009), *P. huangheensis* and *Moropus elatus* (respectively 53 and 50; Qiu et al., 1998), *Schizotherium priscum* (54.1–57.6; Coombs, 1978a; Qiu et al., 1998), and *S. ordosium* (54.7–55.4; Teilhard de Chardin, 1926; Qiu et al., 1998). Among Chalicotheriinae, they are between 51.6 and 64 (Falconer, 1868; Hu, 1959; Butler, 1965; Schaefer and Zapfe, 1971; Pickford, 1982; Xue and Coombs, 1985; de Bonis et al., 1995; Qiu, 2002). These data show that this index cannot unambiguously distinguish the two subfamilies, but Chalicotheriinae has a relatively greater width-length index and the materials described in this paper fall within the upper part of this range.

Except *S. priscum* from Basel (61.6; Qiu et al., 1998), the m3 width-length indices of Schizotheriinae are calculated between 47 and 55.9 (Forster-Cooper, 1920; Hu, 1959; Coombs, 1978a; Qiu et al., 1998; Coombs, 2009), while they range between 46.7 and 58 in Chalicotheriinae (Falconer, 1868; Hu, 1959; Butler, 1965; Schaefer and Zapfe, 1971; Pickford, 1982; Xue and Coombs, 1985; Zapfe, 1989; de Bonis et al., 1995; Qiu, 2002). With m3 width-length index of 53.26 and 59.58, V 16308 and V 16309.1 should belong to Chalicotheriinae, which has relatively greater width-length index.

Finally, the specimens from Tunggur show distinct characters of Chalicotheriinae, such as relatively robust mandible, height of the mandibular corpus increasing posteriorly, and cheek teeth relatively low-crowned and short.

4.2. Comparison with other genera of Chalicotheriinae (including Hesperotherium Qiu, 2002)

The monospecific genus *Kalimantsia* is only represented by a skull from the Late Miocene of Europe (Geraads et al., 2001) and cannot be compared.

Butleria is known by a single species, *B. rusingensis* (Butler, 1965), from the early Miocene of Kenya. The new Tunggur lower jaws are medium to large-sized, larger than *Butleria*. The mandibular foramen is higher than that of *Butleria*, whose mandibular foramen lower border is 22 mm below the level of the alveolar border. The symphysis extends to p3-p4, in contrast to the level of p2 on *Butleria*. The lower premolar row is relatively shorter than that of *Butleria* (p/m ratio 53%). The size of incisor alveoli increases from i1 to i3, while i2 of *Butleria* is the biggest. On lower molars, the metastylid is weaker than in *Butleria*; the trigonid is U-shaped while it is V-shaped on *Butleria*.

Hesperotherium is known by a single species, *H. sinense* Qiu, 2002, from the late Pliocene to middle (?) Pleistocene of China. The lower premolar rows of the new Tunggur lower jaw specimens are longer than *Hesperotherium* (p/m lengths ratio 35%), whose premolar row is even shorter than m3. They have three incisors and one canine, while *Hesperotherium* has lost all incisors and the canine. The p4 is submolariform whereas it is not in *Hesperotherium*. On lower molars, the talonid is more elongated than the trigonid whereas in *Hesperotherium* the trigonid on m3 is the same length as the talonid.

Anisodon is known by four species: *A. grande*, *A. macedonicus*, *A. wuduensis*, and *A. sivalense* (Anquetin et al., 2007). The new Tunggur lower jaw specimens show long snout and have retromolar space, which are distinguishable from *Anisodon*. On lower molars, the metastylid is stronger than in *Anisodon*; the trigonid is U-shaped while it is V-shaped on *Anisodon*.

4.3. Comparison with other species of Chalicotherium

According to Anquetin et al. (2007), *Chalicotherium* includes two species: *C. goldfussi* and *C. brevirostris*. Kaup (1833) described and illustrated a right M3 (HLM Din. 3167) as the holotype of *C. goldfussi* and mentioned an undescribed right m3 as the paratype, so no comparison is possible with the lower parts described in this paper.

Anquetin et al. (2007) described new materials (MHNT VAL-3 and VAL-4) of *C. goldfussi* from the Valentine Quarry (MN8) of Saint-Gaudens (Haute-Garonne, France). They are different from those of *C. brevirostris* in having no ventral expansion of the angulus mandibulae, a long diastema between the canine and p2 (nearly the same length as m3), the mental foramen just posterior to the symphyseal constriction, strong and distinct metastylids and no lingual cingulum on lower molars (Table 3).

4.4. Comparison with other Asian chalicotheriines

Hu (1959) described a nearly complete adult lower jaw (V 2406.1) collected from southeast of Jiulongkou village (Jiulongkou Formation), Cixian County, Hebei Province, and identified as *M.* cf. *brevirostris*. Wang and Wang (2001) referred it to *Chalicotherium* cf. *brevirostris*. The mandibular symphysis extends posteriorly to the p4 level, the corpus increases in height posteriorly, and cheek teeth structure (brachyodont, premolars apparently smaller than the molars, trigonid of molars smaller than talonid, trigonid U-shaped and talonid V-shaped) resemble the Tunggur specimens V 16308 and V 16309.1. However, the corpus of V 2406.1 is very robust, the height is 53.5–85 mm below p2 to m3, which is much higher than in V 16308 and V 16309.1; the lower cheek teeth are slightly wider, except that m2 and m3 are much longer; the metastylid on molars is weak; the p3 is submolariform with the protoconid and metaconid connected by a weak protolophid; the p4 is molariform; the labial cingula are much more developed, and the lingual cingulum at the opening of the m2 talonid is more distinct; p4 has a well developed posterolabial cingulum and lingual cingulum at the opening of the talonid; and the premolar row is much shorter (p/m ratio is 38.4%; Table 3). A right P3 (V 4832) identified as *Macrotherium* sp. from the Jiulongkou fauna is wider than P3 of AMNH 26518, and the metaloph is located near the middle of the crown and forms a more closed central valley (Chen and Wu, 1976). Other additional fossils (V 4832) include a right DP2-4 and an occipital fragment of an immature skull, which show a larger chalicothere than *C. brevirostris* and might be referred to the same species as V 2406.1. Chen and Wu (1976) compared fossils from the Jiulongkou fauna with others and suggested that the Jiulongkou fauna should be earlier than the Tunggur fauna and comparable to the Shanwang fauna. Chalicotheres from the Jiulongkou Formation may be a new species close to *C. brevirostris*. The material so far discovered is not adequate for naming a new species.

Wang and Wang (2001) described a right fragmentary jaw (V 12531) with nearly complete m2-m3 as *C.* cf. *brevirostris*. It was found in the Tuosu fauna in the upper part of the Shang Youshashan Formation, Tsaidam Basin (Fang et al., 2007). The specimen is a young individual with the m3 still not fully erupted. The corpus (height 55.5 mm at m2/m3) is lower than V 2406.1 from the Jiulongkou fauna, and falls in the range of V 16308 and V 16309.1, but could still have grown higher. The molars are much longer than those of *C. brevirostris*, metastylids are almost fused with the metaconids and there is no sign of a cingulum surrounding the trigonid. According to Wang et al. (2003), the Tunggur fauna is approximately 11.8–13 Ma, and the Tuosu fauna is dated to 9.5–11.4 Ma (Fang et al., 2007). So the large chalicothere from Tsaidam may also be a new species.

"*Anisodon*" *salinum* was discovered in the middle Miocene Chinji Formation and early Late Miocene Nagri Formation of the Siwaliks of Pakistan (Forster-Cooper, 1922; Colbert, 1935; Pickford, 1982). The holotype is a left M3, and the most complete specimen is GSP 6006, which contains a left m1-m3, and right p2, m1 and m3. The specimen is a young individual with the m3 still not fully erupted. The symphysis extends to the level of p2, which has a single root, and the molars display longer trigonids and reduced metastylids (Chavasseau et al., 2010). These characters are different from the new specimens from Tunggur. Material referred to "*Anisodon*" *salinum* was also discovered in the Late Miocene (Deng and Qi, 2009) of Lufeng, Yunnan (Qi, 1979). Ducrocq et al. (1994) also identified *C. brevirostris* from the Middle Miocene of

Table 3
Comparisons of the mandibular and lower dentition features of some representatives of the genus *Chalicotherium*.

	C. brevirostris	IVPP V 2406.1 and V 12531	*C. goldfussi*
Corpus height at p2 to m3 (adult)	48.7–67.5 mm	53.5–85 mm	?
Diastema between the canine and p2	Long to 33.3 mm	Estimated short	Very long estimated to 56 mm (Anquetin et al., 2007: fig. 5)
Mental foramen	At anterior part of diastema	?	Posterior to the symphyseal constriction
Posterior extent of the mandibular symphysis	p3-p4	p4	?
Angulus mandibulae	Expanded ventrally	Expanded ventrally	No ventral expansion
Ratio of premolar row to molar row	40.21–42.17%	38.40%	?
Lower incisors	Three	None?	Three
Metastylids on lower molars	Moderately strong	Weak	Strong and distinct
Lingual cingulum on lower molars	Visible at the opening of talonid	Distinct at the opening of talonid	None

Huai Siew in Thailand. Unfortunately, these materials have never been described or figured and cannot be compared.

"*Chalicotherium*" *yuanmouensis* (Ma, 1997) was discovered from the Late Miocene of Yuanmou, Yunnan (Gao and Ma, 1997). The materials include a right mandible fragment with m2 and m3, and some single teeth. The molars are not much longer than the premolars, the p4 is molariform, and the cingulum on molars is weak, all of which are differences from the materials from Tunggur.

5. Discussion

The holotype (AMNH 26518) of *C. brevirostris* (Colbert, 1934) was collected from 25 miles northeast of Gur Tung Khara Usu, Inner Mongolia. No lower jaw has been found there. The materials described in this paper were collected from IVPP loc. 86026 (2 km northwest to the tripod of Huerguolajin), which Wang et al. (2003) considered to be the IVPP Aletexire Locality and probably the CAE (American Museum Central Asiatic Expeditions) locality "20 miles northeast of Gur Tung Khara Usu". So it is just 5 miles away from where AMNH 26518 was collected. There is no other determinate species of *Chalicotherium* reported from this area. The ratio of the upper premolar row to the molar row of AMNH 26518 is 41.3%, which is intermediate between V 16308 (40.2%) and V 16309.1 (42.1%). Hence, the lower jaws V 16308 and V 16309.1 most probably belong to *C. brevirostris*.

We have chosen a complete skull with associated mandibles of *Anisodon macedonicum* (DKO 234) from Greece (de Bonis et al., 1995) as a reference to examine whether the lower teeth from our study match the upper teeth on the type of *C. brevirostris*. On Fig. 3, the M2 of *A. macedonicum* is obviously longer than m2 and P4 is obviously shorter than p4. Although there are some individual differences, *C. brevirostris* has almost the same tendency and the upper and lower tooth lengths match well (Fig. 3). This comparison helps to validate the correspondence of lower to upper tooth lengths, which remains subject to verification by complete specimens.

The snout length of *C. brevirostris* has been discussed for a long time. The snout is approximately corresponding to the part anterior to the nasal notch. Although the anterior part of the chalicothere snout is often not preserved, we can compare upper tooth row patterns to infer the snout length. Parallel upper tooth rows in *Chalicotherium* suggest that there might be a large space for a snout anterior to the upper premolars. In contrast upper tooth rows converging strongly anteriorly in *Anisodon* suggest that the anterior part of the maxilla and premaxilla converges rapidly and there is thus not much space for the snout. In chalicotheres, the nasal notch is incised approximately above the P4 position. Experimentally, we regarded the length anterior to M1 in skulls and the length anterior to m1 in mandibles as the indication of snout length. Without access to original specimens, we calculated from the figures (including those of *C. brevirostris* for data collection coherence) the relative snout lengths in Chalicotheriinae (Table 4). It is clear that *Butleria* and *Chalicotherium* have longer snouts whereas other members of the Chalicotheriinae have shorter snouts. This result contradicts Colbert's original naming of *C. brevirostris* (Colbert, 1934), but is in agreement with conclusions by Anquetin et al. (2007).

Table 4
Comparisons of relative snout lengths in Chalicotheriinae (the ratio of the length anterior to M1/m1 to the upper/lower molar row in skull/mandible).

	Skull	Mandible
Anisodon grande (Anquetin et al., 2007: fig. 4)	0.9	0.89
Anisodon macedonicum (de Bonis et al., 1995: fig. 1)	0.85	0.8
Anisodon sivalense (Falconer, 1868: fig. 1, 3, 6)	0.96	0.84
Anisodon wuduensis (Xue and Coombs, 1985: fig. 2)	0.65	0.63
Chalicotherium goldfussi (Anquetin et al., 2007: fig. 5)	–	> 1.00
Chalicotherium?goldfussi (Anquetin et al., 2007: fig. 6)	1.01	–
Chalicotherium brevirostris (Colbert, 1934: fig. 11; part 2 in this paper: Fig. 2)	1.09	0.95
Butleria rusingense (Butler, 1965: fig. 7, 8)	1.28	1.2
Kalimantsia bulgarica (Geraads et al., 2001: fig. 2)	0.71	–
Hesperotherium sinense (Qiu, 2002: fig. 2)	–	0.69

6. Conclusions

New mandibular materials of *C. brevirostris* from Tunggur complement previously known characters for this species. Contrary to Colbert (1934), followed by Xue and Coombs (1985), *C. brevirostris* has a relatively long snout and a long diastema for a Chalicotheriinae, and retains three lower incisors and a canine. Sexual dimorphism and intraspecific individual variation in this species are reflected in the size of teeth and the degree of robustness of the corpus.

C. brevirostris lived in northern China during the late Middle Miocene (MN7-8). It is different from *C. goldfussi* in the angulus mandibulae expanding ventrally, the shorter diastema between the canine and p2, the mental foramen opening at the anterior part of the diastema, the metastylid moderately strong and just a little separate from the metaconid on the molars, and the visible lingual cingulum at the opening of the talonid. The mandible of *C. brevirostris* is different from those previously referred to *C.* cf. *brevirostris* from Hebei province and the Tsaidam Basin in its lower corpus, shorter molars, nonmolariform p3, submolariform p4 and longer premolar row. These materials may represent a new species close to *C. brevirostris*, but are not adequate for naming a new species.

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