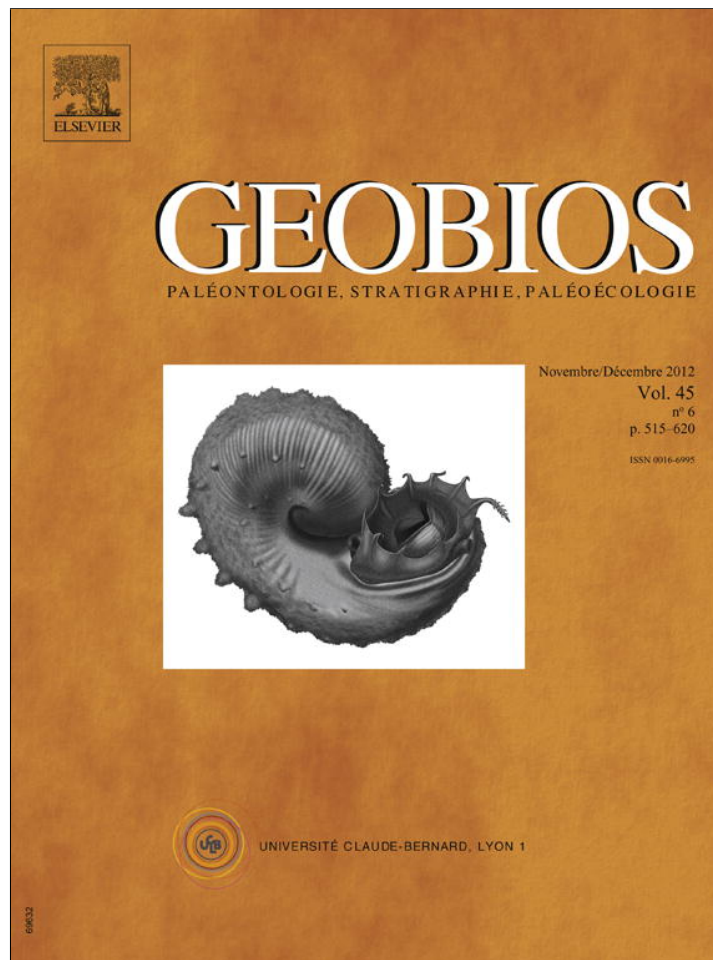


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Original article

## A juvenile skull of *Ancylotherium* (Mammalia, Perissodactyla, Chalicotheriidae) from the Pliocene of China<sup>☆</sup>

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### ABSTRACT

Though rarely found, chalicotheres have long been considered as indicators of wooded environment because of their unique anatomical structure and inferred ecological habits. A juvenile skull of a chalicothere with its articulated mandible was unearthed from the Duikang locality, Guanghe County, Gansu Province, China. This specimen can be identified as *Ancylotherium* sp. based on its short symphysis, shallow mandible, high crown and large size of upper molars, obvious crochets on upper milk teeth, complex structure of DP2 and dp2, and developed metastylids on the lower milk teeth. This rare skull differs from all other known species of the genus *Ancylotherium*. Nonetheless, existence of *Ancylotherium* in China is confirmed without doubt; at least five species in China (from Gansu, Sichuan, Shanxi and Shaanxi provinces respectively) can be attributed to this genus. *Ancylotherium* and its contemporaneous faunal components at the Duikang locality, together indicate a subarid steppe environment with small patches of forest in the Linxia Basin during the Early Pliocene.

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### 1. Introduction

Chalicotheres are a group of extinct and unusual perissodactyls with clawed terminal phalanges. They are known from lower Eocene (Tong and Wang, 2006) to Pleistocene (Qiu, 2002) deposits of the Old World and North America. Their upper teeth are bunoselenodont, and the lower teeth are bunolophodont. Chalicotheriidae of the late Cenozoic are recognized within two major lineages: Schizotheriinae and Chalicotheriinae. The former has high-crowned and elongated upper molars, and has been found in Asia (Oligocene to Early Pleistocene), Europe (Oligocene to Late Miocene), Africa (Middle Miocene to Early Pleistocene), and North America (Miocene); the latter has low-crowned and quadrate upper molars, and has been found from Asia (Late Oligocene to Early Pleistocene), Europe (Middle to Late Miocene), and Africa (Early Miocene).

Fossils of Chalicotheriidae are generally rare, and only a few badly preserved specimens have previously been discovered in China. Through continuous fieldwork in the past decade, a number of well-preserved fossil chalicotheres have been unearthed in the Linxia Basin of Gansu Province. The Linxia

Basin is situated in the transitional zone between the Tibetan Plateau and the Loess Plateau. During the uplift of the Tibetan Plateau, a late Cenozoic continuous sedimentary sequence was developed in the Linxia Basin, from which a great number of mammal fossils were unearthed (Deng et al., 2004). Among the fossil assemblages, the *Dzungariotherium* fauna (Late Oligocene), the *Platybelodon* fauna (Middle Miocene), the *Hipparion* fauna (Late Miocene and Early Pliocene), and the *Equus* fauna (Early Pleistocene) are the richest in taxonomic diversity and specimen quantity. Chalicothere fossils have been found from all four assemblages (Fig. 1), but only a few specimens have been reported to date. Qiu et al. (2004b) described some teeth of *Schizotherium ordosium* from the Jiaozigou Formation (Late Oligocene), and Qiu et al. (2004a) identified a juvenile mandible of Early Pleistocene age as *Hesperotherium* sp. Chen et al. (2012) named a new species, *Nestoritherium linxiaense*, from the lower Liushu Formation (Late Miocene). Deng et al. (2011) mentioned a skull of *Ancylotherium* and a juvenile *Hesperotherium* skull with mandible from the Duikang locality, but the latter identification was incorrect (due to the unprepared state of this specimen at that time); it is now also described as *Ancylotherium* in the present paper. The two skulls from the Duikang locality contribute significantly, not only to the knowledge of the osteology and taxonomy of this animal, but also to paleoenvironment studies of the Pliocene in the Linxia Basin.

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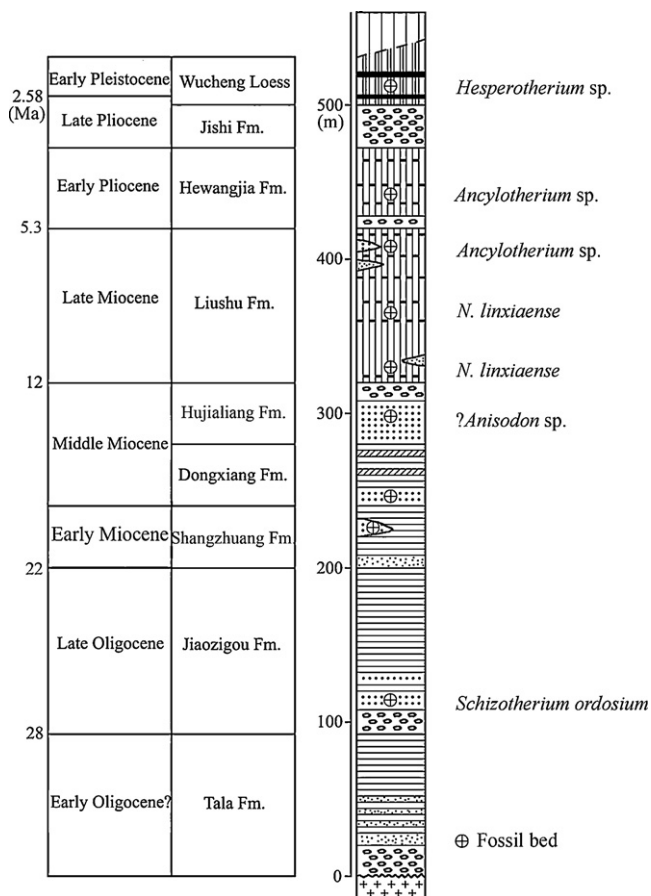


Fig. 1. Stratigraphic column and occurrences of chalicothere fossils in the Linxia Basin, China.

The Duikang locality is located 6.5 km southwest of Guanghe County, Gansu Province. Fig. 2 shows the location of Duikang and other Chinese *Ancylotherium* localities. The section at Duikang, which has been described in details by Deng et al. (2011), includes

two formations: the Liushu Formation (Late Miocene) and the Hewangjia Formation (Early Pliocene). Both formations are red clay deposits, but the principal part of the former is light yellow-brown carbonate-cemented siltstones and the latter is yellowish-brown calcareous mudstones. The fossiliferous lens containing *Ancylotherium* was excavated from the bottom of the Hewangjia Formation, about 0.8 m above the Mio-Pliocene boundary. Fossils found from the Duikang locality include *Hystrix gansuensis*, *Alilepus* sp., *Sinictis dolichognathus*, *Parataxidea sinensis*, *Hyaenictitherium wongii*, *Adcrocuta eximia*, *Chasmaporthetes kani*, *Felis* sp., *Hipparion hippidioidus*, *H. platyodus*, *H. licenti*, *H. (Proboscidiiparion) pater*, *Shansirhinus ringstroemi*, *Cervavitus novorossiae*, *Palaeotragus microdon*, *Samotherium* sp., *Sinotragus* sp., *Gazella blacki* and *Ancylotherium* sp. *H. (Proboscidiiparion) pater* and *Chasmaporthetes kani* are biostratigraphical markers for the Pliocene. Furthermore, paleomagnetic results dated the basal red clay of the Hewangjia Formation in the Linxia Basin to 5.3 Ma (Fang et al., 2003; Deng et al., 2011). Considering the position of the fossiliferous lens in the Hewangjia Formation, this fauna, within chron C3n.4n, can be dated to the Early Pliocene (MN14), with an absolute age of about 5.0 Ma (Deng et al., 2011).

The studied fossils are all stored in the Hezheng Paleozoological Museum, Gansu Province (prefixed HMV). **Abbreviations:** L, length; W, width; aW, width of trigonid; pW, width of talonid; MN, European Neogene Mammal Zone. The anatomical terminology used in this paper follows Coombs (1978).

2. Systematic paleontology

Order PERISSODACTYLA Owen, 1848  
 Family CHALICOTHERIIDAE Gill, 1872  
 Subfamily SCHIZOTHERIINAE Holland and Peterson, 1914  
 Genus **Ancylotherium** Gaudry, 1862  
*Ancylotherium* sp.  
 Figs. 3–5; Tables 1 and 2

**Referred material:** HMV 1874: A juvenile skull with its articulated mandibular rami; snout and occipital region lost.

**Horizon and locality:** Early Pliocene (early Gaozhuangian of the Chinese Neogene Mammal Unit, or MN14 in Europe) from Duikang locality in Guanghe County, Gansu Province, China.

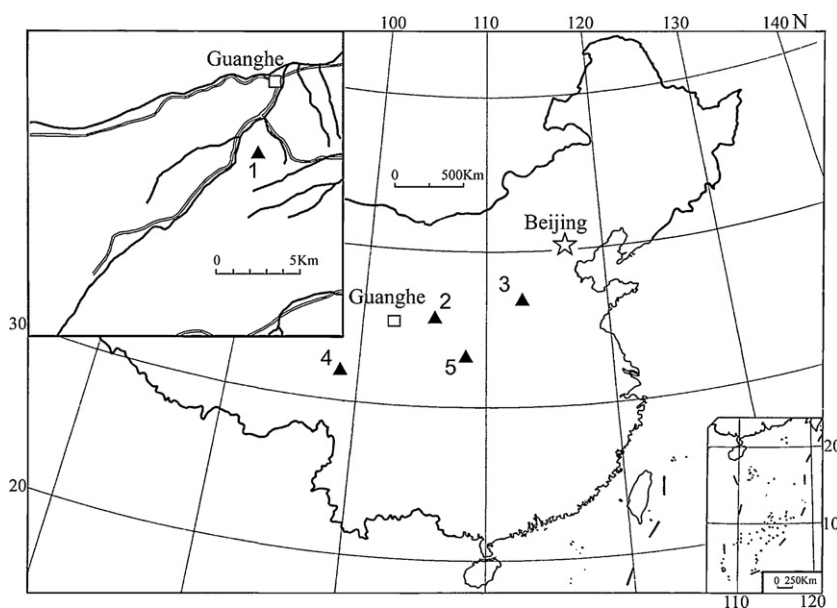


Fig. 2. Map of China with the location of Duikang and other *Ancylotherium*-bearing Chinese localities. 1. Duikang, Gansu Province. 2. Pingliang, Gansu Province. 3. Anle, Shanxi Province. 4. Wangbuding, Sichuan Province. 5. Zhen'an, Shaanxi Province.

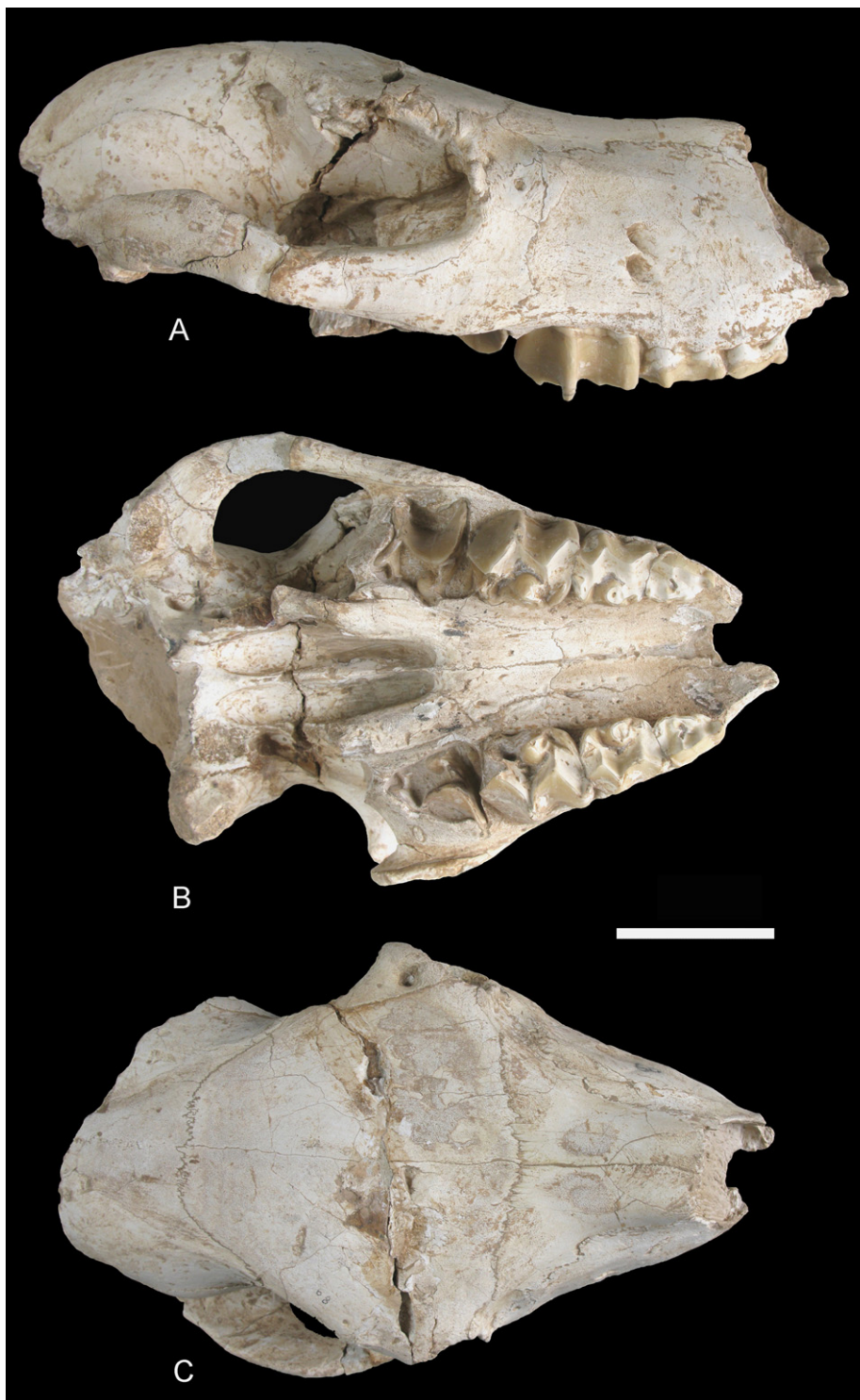


Fig. 3. *Ancylotherium* sp., skull of HMV 1874 from Duikang (Gansu Province, China). A. Lateral view. B. Ventral view. C. Dorsal view. Scale bar: 6 cm.

#### Description:

**Skull.** This skull belongs to a juvenile individual with DP2–DP4 and erupting M1. Its premaxilla, left zygomatic arch and occipital region are missing. The sutures are clear and all the bones preserved can be identified.

**Dorsal view:** The nasals are flat and triangular with their tips lost. The nasal base is very wide and rapidly becomes narrower from the base to the tip. The nasal-frontal suture is slightly convex anteriorly. The frontal is flat. The anterior part of the frontal is broader and the posterior is narrower, with the broadest part at the

postorbital processes. The postorbital processes are relatively well developed with a rounded supraorbital foramen. The braincase is slightly inflated. The parietal crests are very weak and do not meet posteriorly to form a single sagittal crest. The posterior part of the zygomatic arch expands outward as a semi-circle.

**Lateral view:** The bottom of the nasal notch should be situated above the level of the anterior edge of DP3. Only a small part of the nasal base can be observed, and its margin is located behind DP4. The nasal-lacrimal suture is smooth. The maxilla is long with a trapezoid shape. The posterior margin of the maxilla is a straight





Fig. 4. *Ancylotherium* sp., mandible of HMV 1874 from Duikang (Gansu Province, China). A. Lateral view. B. Occlusal view. Scale bar: 6 cm.



Fig. 5. *Ancylotherium* sp., upper and lower cheek teeth of HMV 1874 from Duikang (Gansu Province, China). A. Right upper cheek teeth. B. Right lower milk teeth. Scale bar: 2 cm.

line perpendicular to the horizontal plane and located at the level of the metacone of DP4. The rounded infraorbital foramina, two on the right side and one on the left side of the maxillary face, are located at the level of the DP3/DP4 boundary. The lacrimal bone is an irregular quadrangle with a weak lacrimal tubercle. The orbit is

elliptical, with its upper margin slightly thickened. The postorbital process on the frontal is very strong, but on the zygomatic bone is very weak. The zygomatic arch is short, strong and very low. The orientation of the jugal-squamosal suture is oblique to the horizontal plane. The upper margin of the temporal bone is curved.

**Table 1**  
Measurements of skull and mandible of *Ancylotherium* sp. (HMV 1874), in mm.

Measurements	
Distance between anterior margin of palatine bone and choanae	49.5
Maximum width of choanae	31.7
Distance between infraorbital foramen and orbit	51.0
Distance between DP2 and orbit	114.9
Maximum width of nasal base	107.7
Length of nasal-lacrimal suture	19.9
Width between lacrimal tubercles	149.6
Width between postorbital processes	~180.0
Minimum width of braincase	108.0
Length of zygomatic arch	~150.5
Distance between infraorbital foramen and upper teeth row	17.4
Height of orbit	~39.0
Thickness of zygomatic arch	13.6
Height of zygomatic arch	18.0
Distance between dp2 and mental foramen	33.6
Distance between dp2 and posterior border of symphysis	16.7
Height of horizontal ramus in front of dp2	37.7
Thickness of horizontal ramus in front of dp2	17.5
Height of horizontal ramus in front of m1	48.1
Thickness of horizontal ramus in front of m1	31.6

**Ventral view:** The anterior part of the maxilla is broken but it can still be seen that the maxilla becomes narrower in front of DP2. Both upper tooth rows converge anteriorly. The length of the upper milk tooth row is 90.9~93.5 mm. The groove between the ventral border of the zygomatic arch and the upper tooth row is obvious, but shallow. The palatal surface is smooth and concave medially. The anterior margin of the palatine bone is located at the level of the protocone of DP4, and the posterior margin is U-shaped. The choanae are long oval and their anterior borders are located at the level of the protocone of M1. The connection of the basisphenoid and vomer cannot be found. The median keel of the basisphenoid forms a narrow ridge, which divides the choanae into two ellipses. Though the tips of the pterygoid bones are broken, the preserved parts show that they are thick. The glenoid fossa is flat. The cross section of the postglenoid process is elliptical and its longitudinal axis is oblique to the sagittal plane of the skull.

**Mandible.** Only the anterior parts of the horizontal rami with dp2–dp4 are preserved. The symphysis is short and slender, ending before dp2. There is no tooth preserved before dp2; the anterior tip of the preserved mandible is very narrow. Only one well-developed mental foramen can be found under the tip, which may mean that the lower incisors and canines are very weak or absent. The rami are shallow and thin. The depth of the rami gradually increases posteriorly. In dorsal view, there is a shallow depression in the medial symphysis. The length of the lower milk tooth row is 85.7~86.9 mm.

**Upper teeth:** DP2 has an anterostyle making this tooth triangular in occlusal view. The anterostyle is also triangular, with lingual and labial constriction grooves. The labial wall of DP2 is flat. The crown surfaces of DP3 and DP4 are molariform, with W/L ratios of 84.3~85.9% and 92.9~93.3%, respectively. The paracone is labial to the metacone. The parastyle and mesostyle are well developed, but the metastyle is very weak. The protocone is conical with its lingual wall vertical. The cross section of the hypocone is triangular. The protoconule is very weak and low. The protoloph originates from the paracone and connects to the anterior base of

the protocone. The ectoloph is W-shaped and surpasses the midline of the crown surface. For all the upper milk teeth, the crochets are well developed on the metalophs and the cingula are relatively developed around the teeth.

The erupting M1 is larger than DP4 and its outline is almost quadrate. The paracone is well developed and remarkably higher than the metacone. The parastyle and mesostyle are sharply developed. The ectoloph is W-shaped and its anterior lobe is much longer than the posterior one. The conical protocone is situated slightly posterior to the paracone and protoconule. The obvious protoconule is very low and close to the protocone. The protoloph is long and connects the protocone and paracone with the protoconule in between. The hypocone is lower than the protocone. The metaloph is short. The central valley is spacious, but the postfossette is very shallow. The anterior cingulum is relatively strong. Other features are not observed because the tooth has not completely erupted. L × W: ~38 mm × ~38 mm.

**Lower teeth:** The lower milk cheek teeth are all heavily worn. These teeth are all composed of separated trigonid and talonid. The trigonid is narrower than the talonid on each tooth. Only the talonid of dp4 is V-shaped, whereas all the other trigonids and talonids are U-shaped. The metastylid is substantial on dp3 and dp4. The development of all the lophs is on a similar level. The cingulum of each tooth is well developed. The m1 is erupting but broken.

### 3. Comparisons and discussion

#### 3.1. Comparisons and identification

##### 3.1.1. Systematic position of HMV 1874 in *Chalicotheriidae*

Deng et al. (2011: fig. 4e) mentioned a collected skull (HMV 1875) with P2, DP3–4, slightly worn M1 and erupting M2 of *Ancylotherium* sp. from Duikang. Some forged parts, the parietal bone, the right occipital bone and one (or two) tooth, are found on this prepared skull. On this skull, DP3 is nearly squarish and heavily worn; DP4 is rectangular and moderately worn. DP4 of HMV 1875 has similar morphology to that of HMV 1874, but lacks a crochet. M1 is also similar with that of HMV 1874 but it has a marked crochet, which is unclear on HMV 1874. Considering that HMV 1874 and HMV 1875 are from the same assemblage, these two skulls are likely to belong to the same species and the small amount of morphological diversity can be ascribed to ontogenetic and intraspecific variation.

To date, several Chinese chalicothere-bearing Late Miocene localities have been reported, including Tianzhu in Gansu Province, Yuanmou in Yunnan Province, and Huoxian (= Hohsien) in Shanxi Province (Tung et al., 1975; Zheng, 1982; Gao and Ma, 1997), which were once thought to be Pliocene, but subsequently correlated to the Late Miocene (Qiu and Qiu, 1990; Deng, 2006). Another potential Pliocene locality is Wangbuding in Dege County, Sichuan Province (Zong et al., 1996; Qiu et al., 2002; Chen, 2003), but the age of this locality is still doubtful. The Duikang mammal fossil assemblage has been demonstrated to be Early Pliocene in age on the basis of stratigraphic, paleontologic and paleomagnetic results (Deng et al., 2011). To date, Pliocene chalicotheres have been found elsewhere only in Africa (Butler, 1965; Coombs, 2010) until the

**Table 2**  
Measurements of teeth of *Ancylotherium* sp. (HMV 1874), in mm.

	dp2			dp3			dp4			DP2		DP3		DP4	
	L	aW	pW	L	aW	pW	L	aW	pW	L	W	L	W	L	W
Left	16.9	7.6	9.1	30.0	12.3	13.5	35.6	16.9	17.8	25.0	19.8	28.8	24.3	35.7	33.3
Right	16.8	7.4	9.2	30.1	11.6	13.9	35.5	16.9	17.7	24.8	19.9	28.3	24.3	36.4	33.8

discovery of the Duikang materials, which means these two skulls are the first evidence of Pliocene chalicotheres in Eurasia.

Chalicothere fossils are very rare, thus the occurrence of a juvenile skull of *Ancylotherium* with erupting M1 is significant. However, at the same time it is difficult to make a confident identification based only on the cranial characters of this age stage. Nonetheless, the mandible and teeth are clearly inferable to the Schizotheriinae based on the short symphysis, the shallow mandible and the large size and occlusal structure of the cheek teeth. This specimen can be further referred to *Ancylotherium* based on the following characters:

- there is a crochet on DP3 and DP4;
- the DP2 and dp2 are large and relatively complex;
- the lower incisors are very weak or absent.

Taken together, these characters differ from those identifying other genera of this subfamily, including *Schizotherium*, *Borissiakia*, *Moropus*, *Tylocephalonyx*, *Metaschizotherium* and *Phyllotillon*.

### 3.1.2. Comparison with European and Western Asia *Ancylotherium*

Three species of *Ancylotherium* are currently known, and three additional species have been referred to this genus. *A. pentelicum* is a Late Miocene species from Southern Europe and Western Asia. As the type species, it represents the best and most complete material of this genus, including several skulls and large number of postcranial bones (Schaub, 1943; Garevski, 1974; Garevski and Zapfe, 1983; Sen, 1994; Geraads et al., 2001, 2007; Roussiakis and Theodorou, 2001; Saraç et al., 2002). The best preserved juvenile skull is from Bulgaria (Geraads et al., 2001), which has intact deciduous teeth and erupting M2. Geraads et al. (2006) reported the upper milk molars from Samos. Coombs (1973) described two isolated upper milk teeth and a juvenile mandible with dp2–dp4, also from Samos. The skull of HMV 1874 is similar to the Bulgarian specimen, especially the contour, but a little smaller in size. They share the following characters: wide nasal base, well-developed postorbital process, and separated weak parietal crests. Despite these similarities, HMV 1874 and *A. pentelicum* still have some different characters on the deciduous teeth. DP2 of HMV 1874 has lingual and labial constriction grooves, which are not visible on *A. pentelicum*. DP2 in both cases has a well-developed cingulum, but it is stronger in *A. pentelicum*. Each upper milk molar of HMV 1874 has one or two crochets, but the crochet is weaker on DP3 and DP4 of *A. pentelicum*. Most upper milk molars of *A. pentelicum* are more elongated than those of HMV 1874. Saraç and Sen (2005) described a broken juvenile skull from Turkey and identified it as *A. pentelicum*, but further observation shows that this skull belongs to a species of Chalicotheriinae. Geraads et al. (2011) also referred this Turkish skull to Chalicotheriinae.

### 3.1.3. Comparison with African *Ancylotherium*

*Ancylotherium cheboitense* and “*Chemositia tugenensis*” are two species from the Late Miocene of the Tugen Hills (Kenya), established on the basis of two different foot bones (Pickford, 1979; Guérin and Pickford, 2005). *Ancylotherium hennigi* is a Late Pliocene to Early Pleistocene chalicothere also from Africa. Materials of this species are always fragmentary, and cannot be directly compared with HMV 1874. These three species occur geographically quite far from China; they are not likely to be the same species than HMV 1874.

### 3.1.4. Comparison with Chinese *Ancylotherium*

Two species, “*Huanghootherium*” *anlungense* and “*Gansuodon*” *pingliangense*, from the Late Miocene of China, have been referred to *Ancylotherium* (Coombs, 1989; McKenna and Bell, 1997; Geraads et al., 2006). *A. anlungense* was described based on a fragmentary

skull with right M2–3 (Tung et al., 1975). This species has a flat frontal bone but other characters cannot be compared with HMV 1874 directly. There is no crochet on upper molars of this species, which is different from the upper milk premolars of HMV 1874 and may be different from its upper molars as well. *A. pingliangense* was described based on two fragmentary jaws probably from Pingliang, Gansu Province (Wu and Chen, 1976). The size of its M1 is  $48 \times 47.4$  mm, which is much larger than that of HMV 1874; also the protocone of M1 is stronger than that of HMV 1874.

The chalicotheres from Wangbuding, Sichuan Province, were once identified as Hyracidae (Zong et al., 1996). One skull from this locality is a true hyrax, but other specimens (2 left mandibles and 1 upper jaw) represent one species of Schizotheriinae. There is no description of the milk teeth of this species. Based on photos in Zong et al. (1996: plate X, 2–4, p. 254), it can be noted that this species is smaller than HMV 1874 and has less developed trigonid. The age of the Wangbuding fauna is still unclear: both Pliocene *Metailurus* and Pleistocene *Ursus* and *Sivapanthera* were found in this fauna.

In the Pleistocene, an upper jaw with P4–M2 of *Ancylotherium* sp. was reported from Zhen'an, Shaanxi Province (Li and Deng, 2003). It is still unclear whether this specimen belongs to *Ancylotherium* because of its small size (the dimension of its M1 is  $29.4 \times 25.8$  mm).

The Duikang skulls can be positively identified as *Ancylotherium*, but are different from other known species in this genus. However, HMV 1874 is very immature, making it unreliable to establish a new species at the present.

### 3.2. Comments on Chinese *Ancylotherium*

At this point, five possible species can be included into *Ancylotherium* from China: *A. anlungense* from Anle, Shanxi Province; *A. pingliangense* from Pingliang, Gansu Province; *Ancylotherium* sp. 1 from Wangbuding, Sichuan Province; *Ancylotherium* sp. 2 from Zhen'an, Shaanxi Province; and the Duikang fossil described herein.

Geraads et al. (2006) thought that *A. anlungense* and *A. pingliangense* are synonyms with *A. pentelicum*. But the teeth of these two species are morphologically different from each other and from *A. pentelicum*. *A. anlungense* has a very high crown height, and its hypocone on M2 is almost isolated. *A. pingliangense* has a very well developed cingulum, and its M2 has a similar size to M3. There is no crochet on any teeth of these two species, whereas crochets are usually found on European and African *Ancylotherium*. Some other paleontologists also have classified *A. anlungense* and *A. pingliangense* within *Ancylotherium* (Coombs, 1989; McKenna and Bell, 1997). The discovery of HMV 1874 confirms that *Ancylotherium* existed in China, and it seems feasible to include *A. anlungense* and *A. pingliangense* in *Ancylotherium* as different valid species.

Zong et al. (1996) mistakenly identified the chalicothere fossils from Wangbuding as *Postschizotherium*, a large hyrax. The lack of detailed description makes this material difficult to identify. Fortunately, the unclear photographs show some Schizotheriinae characters: the mandible is thin and shallow; the symphysis ends before p2; the metastylid is well developed on dp3 and dp4. Considering the age of the Wangbuding fauna (late Pliocene or early Pleistocene), chalicothere fossils from this locality should be identified as *Ancylotherium*.

The upper jaw from Zhen'an has been identified as *Ancylotherium* based on its crown height and occlusal structure (Li and Deng, 2003), but this specimen is very small in size, even smaller than some species of Chalicotheriinae. The taxonomic position of this maxilla is, therefore, still controversial.

Otherwise, there are still some questionable postcranials in China. Colbert (1934) figured one metatarsal and two phalanges



from Nei Mongol and identified them as *Macrotherium*. Bohlin (1936) described an astragalus from the Shansi Province as *Chalicotherioidea* gen. and sp. indet. Coombs (1978) identified all these materials as probable *Ancylotherium*. But more recent study has referred to the metatarsal of Colbert (1934) as belonging to an uncertain genus of Schizotheriinae (Fahlke and Coombs, 2009). It is difficult to confirm the identity of these specimens until more material becomes available.

### 3.3. Paleoenvironment of Duikang

Despite the absence of analogues, chalicotheres are always considered as browsers via morphological comparison, microwear, mesowear and isotope studies (Coombs, 1983; Schulz et al., 2007; Schulz and Fahlke, 2009; Tütken and Vennemann, 2009; Semperebon et al., 2010). Their browsing habits make chalicothere fossils indicators of wooded environments. Chalicotheriinae apparently lived in more heavily forested habitat than Schizotheriinae (Coombs, 1989). Considering the faunal components in the Duikang locality, *Hipparion*, *Sinotragus* and *Gazella* fossils indicate an opened grassland environment, while two species of Giraffidae, *Palaeotragus* and *Samotherium*, as well as *Ancylotherium*, are browsers. Taken as a whole, the components of the Duikang mammal assemblage indicate a subarid steppe environment with mixed small patches of forest in the Linxia Basin during the Early Pliocene (Deng et al., 2011).

## 4. Conclusions

The Duikang chalicothere is the first confirmed discovery of a Pliocene chalicothere in China and in Eurasia. The skull with its articulated mandible (HMV 1874) is identified as *Ancylotherium* based on the short symphysis of the mandible and the large size and occlusal structure of the cheek teeth, which are different from any other known species of this genus. The Duikang chalicothere confirms the existence of *Ancylotherium* in China. Four other species of this genus are likely from the Gansu, Sichuan, Shanxi and Shaanxi Provinces in China. *Huanghootherium* and *Gansuodon* are synonymous with *Ancylotherium*. *Ancylotherium*, as well as *Palaeotragus* and *Samotherium*, indicates a wooded environment. Based on these and other components of the Duikang mammal assemblage, a subarid steppe environment with mixed small patches of forest was present in the Linxia Basin during the Early Pliocene.

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