Original article

A new elasmothere (Perissodactyla, Rhinocerotidae) from the late Miocene of the Linxia Basin in Gansu, China[☆]

Un nouvel élasmothère (Perissodactyla, Rhinocerotidae) du Miocène supérieur du Bassin de Linxia (Gansu, Chine)

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Abstract

Ningxiatherium euryrhinus sp. nov. is a relatively large elasmothere rhino from the Linxia Basin in northwestern China found in the early Bahean, which corresponds to the early Vallesian (MN 9), *ca.* 11.1 Ma. It is much larger than the extant *Ceratotherium simum* and has a single horn. *Ningxiatherium* is similar to the late Miocene *Parelasmotherium* from Gansu and Shanxi, but differs in having partially ossified nasal septum, terminal nasal horn boss, shallower nasal notch above the P3/P4 boundary, and much shorter premolars. *N. euryrhinus* sp. nov. differs from *N. longirhinus* from the late Miocene of Zhongning, Ningxia in northwestern China by its larger size, relatively wider nasals, shallower nasal notch, and sub-quadrangular occlusal surface of M3. In the Linxia Basin, the other early late Miocene (Bahean or Vallesian) elasmotheres are known from complete skulls or isolated teeth. They include two genera and three species: *Parelasmotherium linxiaense*, *P. simplum*, and *Iranotherium morgani*. They lack a nasal septum, but *Ningxiatherium* has one. The age of *N. euryrhinus* is early late Miocene based on direct association with biochronologic indicator taxa, such as *Dinocrocuta gigantea*, *Hipparion dongxiangense*, and *Chilotherium primigenius*. *N. euryrhinus* is more primitive than *N. longirhinus* sp. nov. in having a sub-quadrangular M3, a shallower nasal notch, and the presence of DP1 in adults.
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Résumé

Ningxiatherium euryrhinus sp. nov. est un assez grand rhinocéros élasmothère du Bassin de Linxia, dans le Nord-Ouest de la Chine, trouvé dans le Baheanien inférieur, qui correspond au Vallésien inférieur (MN 9), *ca.* 11.1 Ma. Il est beaucoup plus grand que le *Ceratotherium simum* actuel et possède une seule corne. *Ningxiatherium* ressemble au *Parelasmotherium* du Miocène supérieur de Gansu et Shanxi, mais en diffère par un septum nasal partiellement ossifié, une bosse nasale cornée terminale, une incisure nasale moins profonde au-dessus des P3/P4 et des prémolaires beaucoup plus courtes. *N. euryrhinus* sp. nov. diffère de *N. longirhinus* du Miocène supérieur de Zhongning, Ningxia dans le Nord-Ouest de la Chine, par une taille plus grande, des nasaux relativement plus larges, une incisure nasale moins profonde et une surface occlusale sub-quadrangulaire de la M3. Dans le Bassin de Linxia, les autres élasmothères du début du Miocène supérieur (Baheanien ou Vallésien) sont connus par des crânes complets ou par des dents isolées. Ils comprennent deux genres et trois espèces : *P. linxiaense*, *P. simplum* et *Iranotherium morgani*. Contrairement à *Ningxiatherium*, ils n'ont pas de septum nasal. D'après son association directe avec des indicateurs biochronologiques, tels que *Dinocrocuta gigantea*, *Hipparion dongxiangense* et *Chilotherium primigenius*, *N. euryrhinus* sp. nov. date du Miocène supérieur. *N. euryrhinus* est plus primitif que *N. longirhinus* par sa M3 sub-quadrangulaire, son incisure nasale moins profonde et par la présence de DP1 chez les adultes.
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Abbreviations

HMV   Vertebrate paleontology collection, Hezheng Paleo-zoological Museum, Gansu, China

IVPP V   Vertebrate paleontology collection, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

M   Vertebrate paleontology collection, Museum of Evolution, Uppsala, Sweden

1. Introduction

The late Miocene locality of Guonigou, located in the Linxia Basin (Gansu, China), has yielded a rich and diverse land mammal fauna (Fig. 1). Biochronology indicates that the site is correlated to MN 9 (Deng et al., 2004), which dates to approximately 11.1 Ma (Deng, 2006a). Among the faunal remains, are remarkably preserved rhinocerotids belonging to the tribe Elasmotheriini Dollo, 1885. The material from the Linxia Basin is distinguished by its abundance and the exceptional preservation of skulls, mandibles, and postcranial remains. A complete elasmothere skull is described here as a new species, and it improves our overall knowledge of the tribe Elasmotheriini.

Killgus (1923) established *Parelasmotherium schansiense*, a giant elasmothere of the late Miocene, based on isolated teeth collected from Shanxi, China. Another late Miocene representative of elasmotheres in northwestern China is *Sinotherium lagrelii*. It was originally described from rather limited material, including a fragmentary skull and some isolated cheek teeth from the Baode Fauna housed at the Museum of Evolution in Uppsala, Sweden (Ringström, 1924). It is relatively large and hypsodont compared to the middle Miocene elasmotheres. Qiu and Xie (1998), and Deng (2001, 2007) described two species of *Parelasmotherium* – *P. simplum* and *P. linxiaense* – from the late Miocene of the Linxia Basin, in Gansu. No specimens of *S. lagrelii* have been recovered from Gansu.
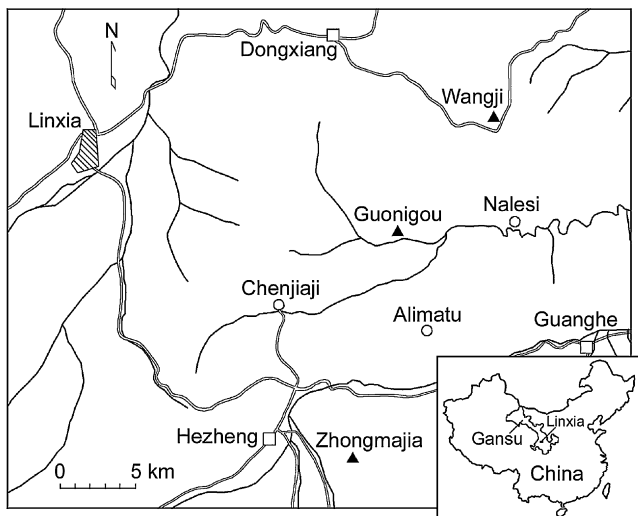

Fig. 1. Location map.
Carte de localisation.

Chen (1977) studied a complete elasmothere skull from the late Miocene sandstones in Zhongning, Ningxia. She recognized that it represented a new elasmothere genus and species, *Ningxiatherium longirhinus* because it had a larger size, longer nasals, an ossified nasal septum, narrower zygomatic arches, deeper nasal notch above P4/M1 boundary, and wider cheek teeth compared with the late Miocene nasal-horned elasmothere, *Iranotherium morgani*, which has been recorded recently from the late Miocene of the Linxia Basin (Deng, 2005). Antoine (2002) considered *Ningxiatherium* to be a synonym of *Parelasmotherium*, but Deng (2007) confirmed the systematic position of *Parelasmotherium* as an independent genus from *Ningxiatherium*. While many phylogenetically significant cranial characters can be observed in the late Miocene specimen of *Ningxiatherium* from Linxia, Gansu, they are absent in the specimen of *N. longirhinus* from Zhongning, Ningxia. For these reasons, I have elected to formally designate the Linxia skull as a new species instead of including it in *N. longirhinus*.

The other mammalian fossils from Guonigou include the hyenid *Dinocrocuta gigantea*, felid *Machairodus* sp., gomphothere *Tetralophodon* sp., equid *Hipparion dongxiangense*, elasmotheres *P. linxiaense*, and bovid *Shaanxispira* sp. (Deng, 2001). In the Linxia Basin, the rhinocerotids *P. simplum* from Wangji (Qiu and Xie, 1998) and *Chilotherium primigenius* from Zhongmajia (Deng, 2006b) are collected from the same horizon than Guonigou.

Terminology and taxonomy follow Heissig (1972, 1999), Guérin (1980) and Antoine (2002). The measurements are according to Guérin (1980) and given in millimeter. Boundaries for Neogene Chinese Land Mammal Ages and their subdivisions follow the recent revision by Deng (2006c); biochronology of the Linxia vertebrate fossil localities follows Deng et al. (2004).

2. Systematic paleontology

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
Subfamily RHINOCEROTINAE Gill, 1872
Tribe ELASMOTHERIINI Dollo, 1885
Genus *Ningxiatherium* Chen, 1977
Ningxiatherium euryrhinus sp. nov.
Figs. 2–5; Tables 1 and 2

Etymology: Eury-, Latin, wide; rhinus, Greek, nose or snout. The species name indicates that this rhino has very wide nasals.

Holotype: HMV 1449, a completely adult skull with both cheek tooth rows (left: P3–M3; right: DP1, P2, P4–M3), pressed dorsal-ventrally. Some distorted features due to the dorsal-ventral crushing are indicated.

Diagnosis: Large-sized elasmothere. M3 located in front of orbit. Nasals very wide, with a ventrally inclined anterior part and a thick ossified septum; terminal nasal horn boss rough and large, frontal horn absent; nasal notch situated above P3/P4 boundary; premaxilla narrow and long, fused each other, without incisors; anterior and lower rims of orbit raised; skull roof shallowly concave, with a high occipital elevation and
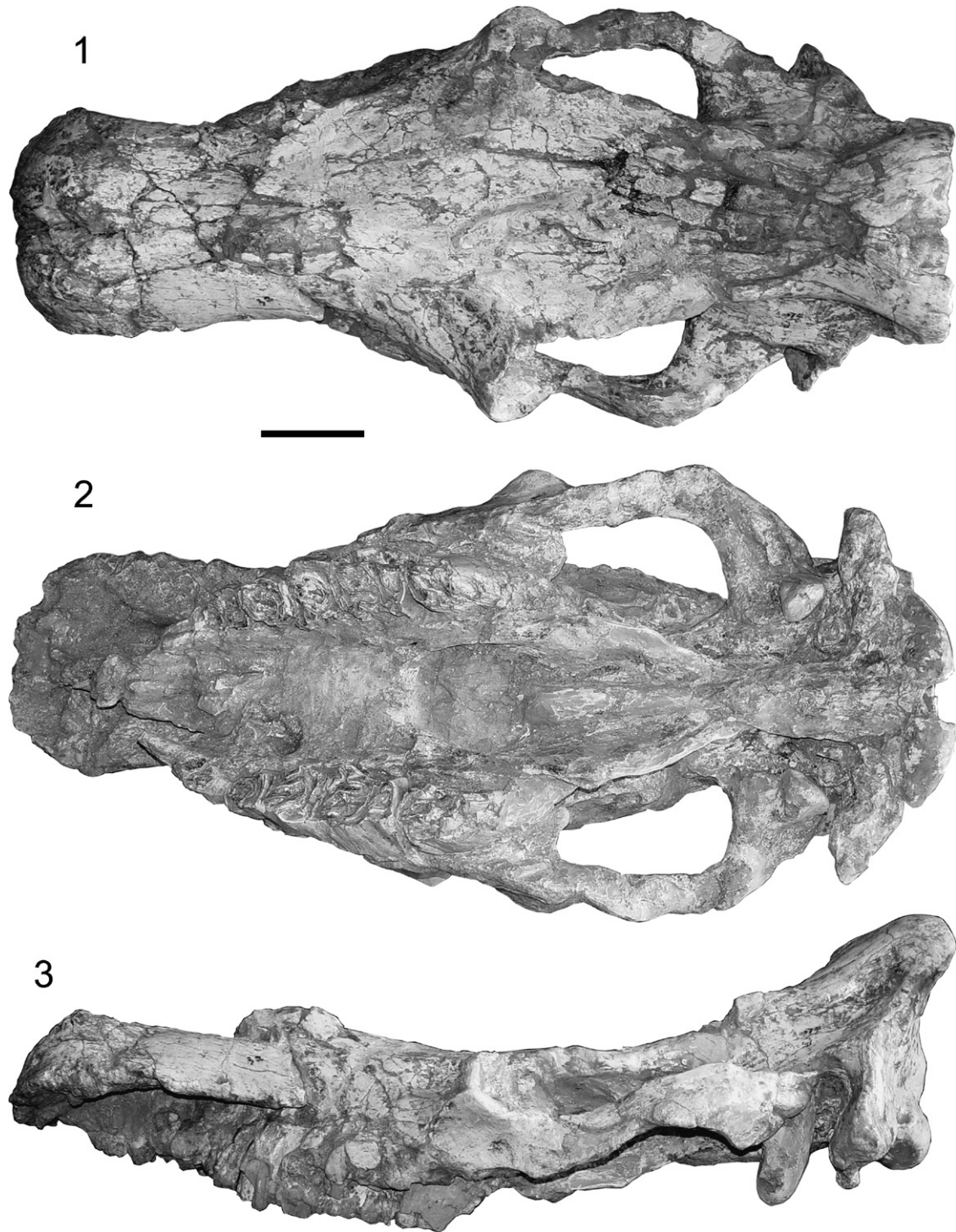
Fig. 2. Skull of *N. euryrhinus* sp. nov. from Guonigou, Linxia (Gansu, China), HMV 1449, scale bar = 10 cm. **1**. Dorsal view. **2**. Occlusal view. **3**. Lateral view. *Crâne de* N. euryrhinus *sp. nov. de Guonigou, Linxia (Gansu, Chine), HMV 1449, barre d'échelle = 10 cm. (**1**) Vue supérieure. (**2**) Vue occlusale. (**3**) Vue latérale.*

broadly separated parietal crests; occipital surface vertical. Extremely hypsodont; enamel wrinkled; premolars short; posterior valley closed; parastyle weak or absent. These character states are considered derived within rhinocerotids.

Locality and horizon: Guonigou in Nalesi Township, Dongxiang County, Gansu Province, China; early late Miocene (Chinese Bahean or European Vallesian with an age of about 11.1 Ma, corresponding to MN 9).

3. Description

3.1. Skull

The skull is dolichocephalic, with a maximal cranial width/length ratio smaller than 0.46, and it has a basal length of 875 mm (Table 1), much larger than the extant *Ceratotherium simum*, which has a maximum length of 748 mm (Guerin, 1980:
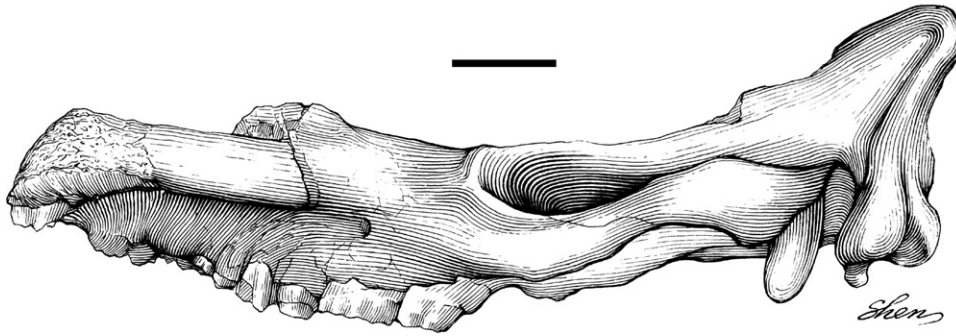
Fig. 3. Skull of *N. euryrhinus* sp. nov. from Guonigou, Linxia (Gansu, China) in lateral view, HMV 1449, scale bar = 10 cm.
Crâne de N. euryrhinus *sp. nov. de Guonigou, Linxia (Gansu, China), profil, HMV 1449, barre d'échelle = 10 cm.*
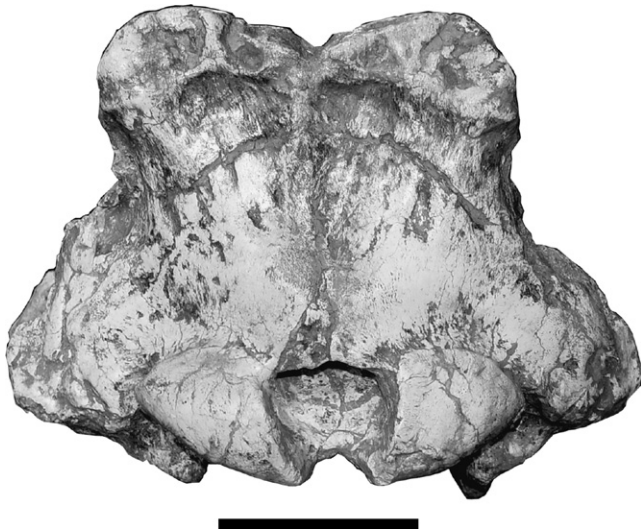

Fig. 4. Occipital surface of *N. euryrhinus* sp. nov. from Guonigou, Linxia (Gansu, China), HMV 1449, scale bar = 10 cm.
Face occipitale de N. euryrhinus *sp. nov. de Guonigou, Linxia (Gansu, Chine), HMV 1449, barre d'échelle = 10 cm.*

the nasals are completely pressed in this specimen. The anterior nasal area is inclined strongly downward. The cross section of the nasals is flat, and the ventral surface has some protuberances by the central septum. The terminal nasal horn boss is huge and rough, and it is divided by a wide and deep V-shaped central groove into two high domes with a sharp apex. The horn boss occupies the anterior two fifth of the dorsal surface of the nasals, and the posterior three fifth is smooth.

The infraorbital foramen is rounded in shape and large in size with a diameter of 22.5 mm, and it is situated above the middle of M2 with a distance of 50 mm to the bottom of the nasal notch (Fig. 3). The nasal notch is situated above the P3/P4 boundary. The ossified nasal septum is thick, with a thickness of 24 mm at the anterior region. The anterior end of the septum is expanded laterally, representing two lateral branches, between which is a vertical central depression. Each side of the septum has a spherical tubercle at the connection with the nasal. It is 44 mm wide between the two tubercles, and 40 mm long to the middle of the anterior margin of the nasals. The anterior margin of the septum is inclined posteriorly, with a spherical tubercle at middle and two spherical tubercles at its lower part that connect with the premaxilla. It is 56 mm wide between the latter two tubercles. The premaxilla is 142 mm in front of DP1, and it is 18 mm thick and 45 mm wide at middle.

There is a large depression in front of the orbit. The anterior and lower rims of the orbit are strongly raised laterally, without supraorbital and lacrimal tuberosities and postorbital processes. The position of the orbit is high, with its upper rim close to the skull roof (Figs. 2(3) and 3). The posterior part of the zygomatic

Table 2). The tooth row is strongly shifted anteriorly, so that the posterior margin of M3 is at the same level with the anterior border of the orbit (Fig. 2(3)). The fused nasals are very broad and long, with well-developed lateral processes (Fig. 2(1)). The nasal tip is broad and rounded, with a rough and serrate margin, and a width of 246 mm. The nasal lateral area declines sharply with a height of 65 mm from the turning point to the margin, but
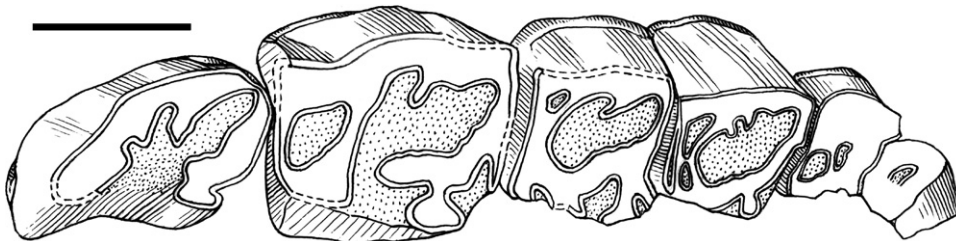

Fig. 5. Right upper teeth of *N. euryrhinus* sp. nov. from Guonigou, Linxia (Gansu, China), HMV 1449, occlusal view, scale bar = 5 cm. Complemented and consummated according to the reversed left upper teeth.
Dentition supérieure droite de N. euryrhinus *sp. nov. de Guonigou, Linxia (Gansu, China), HMV 1449, vue occlusale, barre d'échelle = 5 cm. Reconstitution à l'aide des dents supérieures gauches inversées.*

Table 1

Measurements and comparisons (in millimeters) of skull of *N. euryrhinus* sp. nov. (HMV 1449) from Guonigou, Linxia (Gansu, China).

Mesures et comparaisons (en millimètres) du crâne de N. euryrhinus *sp. nov. (HMV 1449) de Guonigou, Linxia (Gansu, Chine).*

Measures	*N. euryrhinus* HMV 1449	*N. longirhinus* V 5163	*P. linxiaense* HMV 1411[a]	*I. morgani* HMV 0979, 1098
1 Distance of occipital condyle–premaxillary tip	875	864	925	712–775
2 Distance of occipital condyle–nasal tip	985	904	1015	700–745
3 Distance of nasal tip–occipital crest	1010	935	973	710–750
4 Distance of nasal tip–bottom of nasal notch	318	267.7	369	145–176
5 Minimal width of braincase	190	146	166	123–140
6 Distance of occipital crest–postorbital process	390	349.5	365	310–348
7 Distance of occipital crest – supraorbital tuberosity	425	381	420	355–380
8 Distance of occipital crest–lacrimal tubercle	475	456	~450	390–453
9 Distance of nasal notch - orbit	268	259.4	217	216–204.5
13 Distance of occipital condyle - M3	450	445	438	330–395
14 Distance of nasal tip–orbit	570	521	565	350–375
15 Width of occipital crest	224	205	183	190–212.4
16 Width between mastoid processes	379	268	306	251–309
17 Minimal width between parietal crests	121	108.4	113.6	80–91
18 Width between postorbital processes	270	222	228	211–244
19 Width between supraorbital tuberosities	282	~248	231.5	253–260
20 Width between lacrimal tubercles	400	~284	~207	282–295
21 Maximal width between zygomatic arches	460	360	–	340–420
22 Width of nasal base	235	134.5	158.4	117–140
23 Height of occipital surface	154.5	212	193.5	137–138
25 Cranial height in front of P2	137[a]	281	232.7	173–193
26 Cranial height in front of M1	154[a]	279	237.3	180–251
27 Cranial height in front of M3	144[a]	260	240	196–259
28 Palatal width in front of P2	139	49.6	96.8	67–68
29 Palatal width in front of M1	140	79	104	68–93
30 Palatal width in front of M3	160	90	125	77–131
31 Width of foramen magnum	71	71.7	88	44–57
32 Width between occipital condyles	215	181.4	186	133–183

[a] This skull is pressed dorsal-ventrally, so some measurements for its widths and heights are not accurate.

Table 2

Measurements and comparisons (in millimeters: length × width × height) of upper teeth of *N. euryrhinus* sp. nov. (HMV 1449) from Guonigou, Linxia (Gansu, China).

Mesures et comparaisons (en millimètres : longueur × largeur × hauteur) des dents supérieures de N. euryrhinus *sp. nov. (HMV 1449) de Guonigou, Linxia (Gansu, Chine).*

Upper teeth	*N. euryrhinus* HMV 1449	*N. longirhinus* V 5163	*P. lingxiaense* HMV 1411	*I. morgani* HMV 1098	*S. lagrelii* Ringström, 1924
DP1	16 × 28 × –		26.2 × 30.5 × 34.6	29 × 28 × 28	
P2	22.5 × 30.5 × –		36.6 × 43 × 40.2	23 × 37.5 × 30	42 × ~46 × 47
P3	29.5 × 46 × 20.5		45.1 × 53.8 × 54	32 × 54 × 29	52 × 58 × ~80
P4	46 × 48.3 × 62	43.3 × 67 × –	48.8 × 65 × 95	41 × 65.5 × 32	50 × 77 × 83
M1	46.5 × 72 × 33	43 × 70 × –	62.7 × 72 × 57	43.5 × 76 × 28.5	92 × 75 × 106
M2	82 × 70 × 81	62 × 81.4 × –	89.3 × 70.4 × 100	63.5 × 84 × 30	~70 × 71 × 185
M3	69 × 64 × >72	78.2 × 68.3 × –	88.8 × 61 × 96.5	79 × 66 × 43	106 × 60 × 90

arch is not expanded laterally, and its position is at the middle of the skull, with a straight upper margin. The posterior margin of the zygomatic arch is inclined antero-inferiorly, with two sharp processes at the levels of the anterior and posterior borders of the orbit. The zygomatic arch is 57 mm wide at middle, and it is slightly narrowing posteriorly.

The skull roof is broadly and shallowly concave, with the largest width at the anterior border of the orbit, and a high elevation of the occipital. The braincase is broad and low, with steep lateral walls. There is no horn boss on the frontal. The parietal crests are weak and broadly separated, and between them it is flat (Fig. 2(1)).

The occipital surface is vertical and bell-shaped, with a constriction at the middle, and the occipital crest is at the same level as the condyles. The nuchal tuberosity is weak and broad, the central crest is weak and present on the upper part of the occipital surface, the lateral crest is very weak, and the exterior crest is weak and more posterior than the mastoid process. In dorsal view, the occipital crest is straight and serrated, with a deep central groove. In posterior view, the horizontal part of the occipital crest is broadly and shallowly concave, with a deep and rounded central groove, and the lateral part is strongly divergent inferiorly. The upper part of the lateral occipital crest is inclined anteriorly, while the lower part, which corresponds

to the lateral margin of the posttympanic process, is vertical. The foramen magnum is circular, and its upper border is slightly lower than the upper border of the condyle. The condyles are large and roundly triangular in shape. The nuchal ligament depression is large and shallow, with an unclear boundary. On each side above the depression, there is a long and triangular prominence with two small pits and one crest (Fig. 4).

The notch between the condyles is broad, with a width of 33 mm. The pterygoid bones are low and inclined posteriorly, and the valley between them is very broad, with a width of 138 mm. The vomer is thick, with a thickness of 26 mm at the middle, and its margin is rounded, with a distance of 62 mm to the palate (Fig. 2(2)). The anterior border of the temporal fossa is grooved in the middle, with a distance of 48.5 mm to the posterior margin of M3. The temporal condyle is straight, and slightly convex in lateral view, behind which the surface is smooth and concave. The postglenoid process is a robust cone with three edges and an anterior height of 77 mm, and it is slightly oblique antero-interiorly. The anterior surface of the postglenoid process is wide and concave, the posterior surface is a rounded edge, and the base is 46 mm thick anteroposteriorly and 46 mm wide extero-interiorly. The posttympanic process is completely fused with the paraoccipital process and broadly separated from the postglenoid process. It is strongly expanded laterally, thick inferiorly and narrows superiorly, with a thickness of 54 mm at the basal middle and a thickness of 13.5 mm at the lateral middle. It is inclined anteriorly, and its lower border is at the level of the upper part of the postglenoid process. The paraoccipital process is comparatively weak. It is narrow extero-interiorly, with a wide and rounded medial margin and a narrow and oblique lateral margin; its anterior surface is wide and slightly concave, and posterior surface is convex medially and concave laterally. The paraoccipital process is vertical, 40 mm high medially, 26 mm thick and 58 mm wide at the base. The temporal crest is straight and inclined anteriorly. The jugular foramen is large and circular, situated at the middle between the paraoccipital process and the condyle and near the basioccipital bone. The basioccipital bone has an angle of 120° with the basisphenoid, and the posterior part of the former is broad and slightly convex, much lower than the occipital condyle. The basilar tuberosity is rough and slightly projected. The palate is very broad, and its posterior border is broadly U-shaped at the level of the hypocone of M2, with a posterior width of 113 mm. The maxillary tuberosity is absent. In the ventral view, the zygomatic arch is thick, with the thickness of 35 mm at the middle and 63 mm at the back; its margin has a lateral edge and some edges that go from anterior-laterally to postero-medially; its anterior part is rough, while its posterior part is smooth and slightly concave. There is a wide and deep V-shaped groove between the zygomatic arch and the maxillary bone.

3.2. Upper cheek teeth

The premolar row is very short, with a DP1-P4 length of 99.5 mm, while the molar row is relatively long, with a M1–M3 length of 193 mm (Fig. 5). The cheek tooth rows are straight and parallel to each other. The enamel is shallowly wrinkled, mainly on the interior wall of the median valley. The labial cingulum is thick and high, with the anterior and posterior ends extended toward the occlusal surface, while the lingual cingulum is absent. The crochet is absent. There is no cement covering on the cheek teeth, but the cement filling is thick in the median and posterior valleys. The crowns of P4, M2 and M3 are extremely high, while other teeth have a low crown after wear (Table 2), which means that P4 and M2 come into action long after M1 has been worn. The upper incisors are absent.

DP1 has been worn to the base, and it is small and simple, strongly oblique postero-lingually. P2–P4 have a well-developed bridge; their metalophs are very narrow, straight on P2, short and oblique anteriorly on P3 and curved posteriorly on P4. They have no anterior and posterior cingula; their posterior valleys are closed, circular on P2 and P3, and separated into two small rings on P4 (larger labially). They have no parastyle, medifossette, and paracone and metacone ribs. Their protocones have a wide and rounded lingual margin. P2 and P3 have no crista, while P4 has a strong and bifurcated crista, a low cristella and a robust postcrista. P3 and P4 have no protocone constriction, and their bridge is broad to form a lingual wall. The labial wall of P4 has a groove in the middle, in front of and behind which it is slightly convex. The lingual wall is straight, with a narrow and deep middle groove toward the base. The hypocone of P4 has a posterior constriction, and the protoloph is strongly oblique posteriorly.

On the molars, the labial wall is slightly convex, and the parastyle is weak or absent; the protocone is strongly constricted as an oval, with a flat lingual margin; the hypocone is constricted, with a deeply concave lingual margin; the crista is posteriorly oblique; the metaloph is long. On M1, the antecrochet is wide, long, lingually oblique, and connected with the hypocone; the crista is moderately long and triangular in shape, with a sharp tip. The anterior groove is very wide; the posterior valley is closed, small or disappeared. The paracone rib is absent; the metastyle is short; the lingual valley is large, with a narrow entrance; the anterior wall of the median valley is weakly wrinkled; the protoloph is transverse. On M2, the antecrochet is wide, long, lingually oblique, and extends to the two-third width of the median valley; the crista is moderately long and robust, with a rounded tip; the anterior groove is wide and deep; the posterior valley is closed and large; the paracone rib is absent; the metastyle is long; the metacone fold is marked; the protoloph is posteriorly oblique, and the metaloph is lingually narrow. On M3, the ectoloph and the metaloph can be distinguished, so that the occlusal surface is nearly quadrangular. The protoloph is posteriorly oblique; the protocone is narrow and long, with a weak lingual groove; the antecrochet is very short and posteriorly oriented; the crista is transverse, robust and very long, extending over the half width of the median valley and ending with a sharp tip. The anterior groove is narrow and deep, and the anterior cingulum is absent; the crochet is widely triangular, with a lingually oriented tip, and is parallel to the crista; the parastyle fold is marked, and the posterior groove is filled and covered by cement; the posterior

cingulum is a large and narrow pillar at the base, with a height of 15 mm.

4. Comparison and discussion

The first published record of the taxon herein named *N. euryrhinus* was in the faunal list of the Guonigou fauna (Deng, 2001). He listed one of the Guonigou elasmotheres as *Ningxiatherium* sp., and described another one as a new species, *P. linxiaense*. Antoine (2002) referred *N. longirhinus* from Zhongning, Ningxia to *P. schansiense* (Killgus, 1923), but his revision for the elasmothere was probably due to two factors, extensive wear or loss of the cheek teeth of *N. longirhinus*, and the lack of *Parelasmotherium* skulls, so that he was unable to correctly compare the dental and cranial morphology of the two elasmotheres. Deng (2007) demonstrated that *Ningxiatherium* is a valid and independent genus, different from *Parelasmotherium*.

Among the large terrestrial mammals that inhabited China during the Neogene, elasmotheres are probably the least studied, particularly those of the late Miocene. To date, only three small regions in China have produced late Miocene samples of elasmotheres that include a few skulls, one mandible, and some teeth: Baode in northwestern Shanxi (Killgus, 1923; Ringström, 1924; Chow, 1958), Linxia in southeastern Gansu (Qiu and Xie, 1998; Deng, 2001, 2005, 2007), and Zhongning in central Ningxia (Chen, 1977). All are of importance in understanding the elasmotherine biogeography and phylogeny during the late Neogene.

Elasmotheres apparently became relatively rare in China after the Baodean Land Mammal Age (late Miocene), in contrast to their much greater abundance and diversity in the middle Miocene faunas (Zhai, 1978; Yan, 1979; Guan, 1988, 1993; Cerdeño, 1996; Antoine, 2003; Deng, 2003; Deng and Wang, 2004). They are absent or exceedingly scarce in all large, well-sampled Pliocene faunas. Elasmotheres appeared again in the early Pleistocene, almost simultaneously in Hebei (Nihewan Fauna, Yangyuan County; Teilhard de Chardin and Piveteau, 1930; Deng and Zheng, 2005) and Shaanxi (Xunyi Site, Xunyi County; Guan, 1998). Unlike older records, the taxa involved in both regions can be confidently referred to the Pleistocene genus *Elasmotherium*.

Elasmotherium has a huge frontal horn and strongly wrinkled tooth enamel. In contrast, the Guonigou skull described herein has no trace of a horn boss on its frontals, and its teeth have slightly wrinkled enamel. Skull HMV 1449 has a similar nasal horn to *Parelasmotherium*, *Iranotherium*, and *Hispanotherium*, all of which were placed in to the group Iranotheriina (formerly Iranotheriinae) by Kretzoi (1943). *Sinotherium* also is a large-sized elasmothere, but it is not known whether it has nasal or frontal horns.

The cranial and dental characters of the elasmothere skull of HMV 1449 are easily recognizable as typical of Elasmotheriini (Heissig, 1989, 1999). Chen (1977) established a new genus and species *N. longirhinus* based on a complete skull with upper cheek tooth rows from P4 to M3 of an old individual from Zhongning, Ningxia in China. *N. euryrhinus* is easily
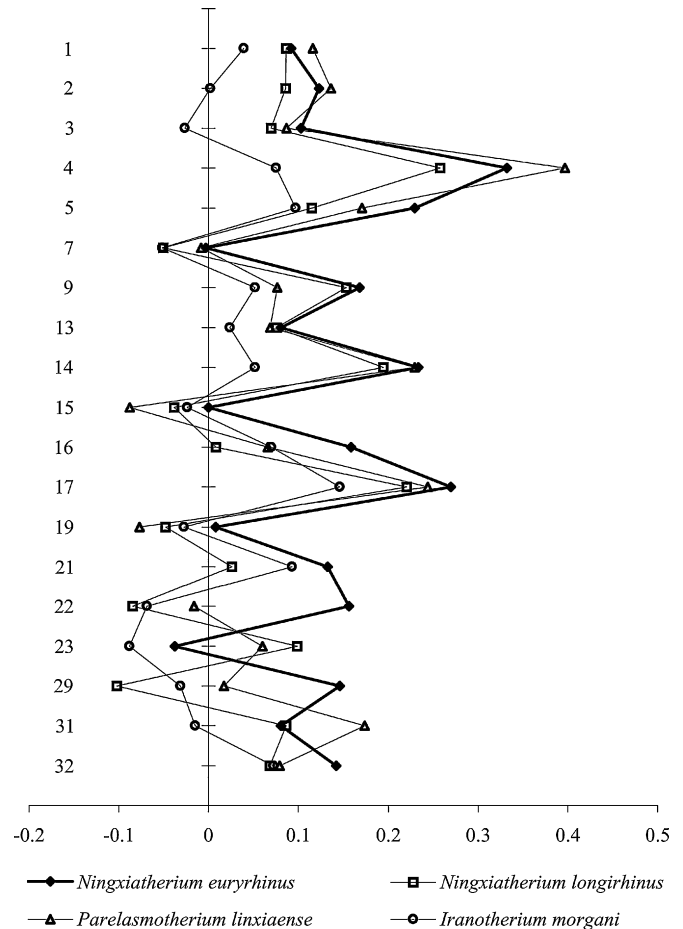

Fig. 6. Log-ratio diagram for skull measurements of *N. euryrhinus* sp. nov. and other three elasmothere species using *C. simum* (in average, Guérin, 1980: Table 2) as a standard for comparison. Numbers on the left of the Y-axis are measurement numbers in Table 1.
Diagramme de Simpson des mesures crâniennes de N. euryrhinus *sp. nov. et de trois autres espèces d'Élasmothères, avec* C. simum *(moyenne, Guérin, 1980 : Tableau 2) comme référence. Les numéros à gauche de l'axe des Y correspondent à ceux des mesurés du Tableau 1.*

distinguished from *N. longirhinus* by its larger size, much wider nasals (Fig. 6), well-developed nasal lateral apophysis, shallower nasal notch that is above the P3/P4 boundary, bell-shaped or trapezoid occipital surface, larger occipital condyles, more posteriorly oblique protoloph of P4, stronger crista of molars, open median valley of M2, and sub-quadrangular occlusal surface of M3. *N. euryrhinus* has DP1 in the adult individual, while DP1 is not found in *N. longirhinus*. The presence of DP1 can be variable, so we need more specimens to determine this difference. Because a sub-quadrangular M3, a shallower nasal notch, and the presence of DP1 in adults are plesiomorphic characters in the rhinocerotid evolution (Prothero et al., 1986; Cerdeño, 1995; Antoine, 2002), *N. euryrhinus* is more primitive than *N. longirhinus*. On the other hand, that condition of M3 can appear as a reversal in the evolutionary process, as in *Coelodonta*. The new material proves that P4 and M2 of *Ningxiatherium* come into action long after M1 has been worn like those of *Parelasmotherium*, which was not known from the only skull of *N. longirhinus* which has

cheek teeth worn to their roots (Chen, 1977). The cheek teeth of HMV 1449 give us more information about the dental structures of the genus *Ningxiatherium* (Fig. 5 and Table 2).

P. linxiaense is known primarily from isolated teeth and a skull also from Guonigou in the Linxia Basin (Deng, 2001, 2007). Similarities with *N. euryrhinus* include relatively large size (Fig. 6), dolichocephalic skull, long and wide nasals, long premaxillary bones, anteriorly declined nasal tip, highly positioned orbits behind M3, laterally projected lower orbital margins, shallowly concave skull roof, wide and low braincase, absence of frontal horn, very broadly separate parietal crests, trapezoid-shaped occipital surface, separated postglenoid and posttympanic processes, wide notch between occipital condyles, much later eruption of P4 and M2 than M1, narrow metalophs of premolars, strong molar cristae, and strongly oblique M3 protolophs. On the other hand, *N. euryrhinus* differs from *P. linxiaense*, which coexisted in the same locality and bed, by having a partially ossified nasal septum (Figs. 2(3) and 3); a sharply declining lateral nasal area; a terminal (not middle) nasal horn boss; a deep central nasal groove; a shallower nasal notch above the P3/P4 boundary; fused premaxillary tips; a strongly projecting anterior orbit margin; the absence of postorbital process; the absence of a facial crest; a relatively high elevation of the occipital; the maximum width of the skull roof found at the level of the anterior margin (not the supraorbital tuberosity); a concave occipital crest in occipital view (not straight); a vertical occipital surface (not inclined posteriorly); a weak nuchal tuberosity; a weak lateral occipital crests; a thick and rounded lower margin of vomer; a weak basal tuberosity; comparatively weaker postglenoid processes; the absence of the sagittal crest on the basal tuberosity; a very shorter premolar row, the absence of crista on P2 and P3, the absence of antecrochet on P4, the absence of the paracone rib and the parastyle of the upper cheek teeth; a thick and high labial cingulum; an unconstricted protocone of P4, a sub-quadrangular occlusal surface and a strongly constricted protocone of M3.

Hispanotherium tungurense from the Tunggur site in Inner Mongolia (Cerdeño, 1996) and *N. euryrhinus* differ in that skull of *N. euryrhinus* is much larger; the anterior orbital margin of *N. euryrhinus* is more posteriorly positioned, behind the cheek tooth row; the nasal notch of *N. euryrhinus* is deeper, at the level of the P3/P4 boundary; and the nasal horn is more anteriorly positioned, at the nasal terminal. Also, the occipital crest of *H. tungurense* is directed posteriorly, passing the level of the condyle, a state not observed in the skull of *N. euryrhinus* (Fig. 2(3)). The distance between nasal notch and orbit in *H. tungurense* is relatively shorter than that in *N. euryrhinus* (Table 1). The ratio of the premolar row relative to the molar row in *H. tungurense* is markedly larger than that in *N. euryrhinus*.

The typical late Miocene elasmothere of Eurasia, *I. morgani* was discussed by Deng (2005). Both *I. morgani* and *N. euryrhinus* have anteriorly shifted cheek teeth, posteriorly positioned and laterally projected orbits, low and wide braincases and broadly separated parietal crests. Other similarities are dolichocephalic skulls, wide nasals with an inclined tip, trapezoid-shaped occipital surfaces, weak nuchal tuberosities, thick vomers, and the absence of the crochet on molars. In *I. morgani*, however, the orbit, infraorbital foramen, and nasal notch are more anteriorly positioned; the nasal horn is situated in the middle; the nasal septum is absent; the posterior part of the zygomatic arch is high, the occipital surface is inclined anteriorly, the occipital lateral crest is strong, the nuchal ligament pit is deep, the premolar row is relatively long, the labial cingulum is absent, the parastyle is strong, the protocone is strongly constricted on premolars, and the occlusal surface of M3 is triangular. *I. morgani* is smaller in size than *N. euryrhinus*.

Detailed cranial comparisons between *N. euryrhinus* and *Sinotherium lagrelii* from Baode, Shanxi are impossible, because *S. lagrelii* has only a fragmental skull with a cheek tooth row (M 3884). The cranium is mainly composed of partial maxillary and frontal bones (Ringström, 1924). The orbits of *N. euryrhinus* and *S. lagrelii* are very laterally raised, and posteriorly shifted behind M3. But *N. euryrhinus* differs in its short premolar row, and having very long premaxillae. In *S. lagrelii*, the premaxilla is very retracted, the posterior border of the nasal notch is deeper, maybe above M1, the maxillary face is short and high, the facial crest is very high, with an anterior end above the posterior border of M1, and the upper cheek teeth are differentiated into crown and prism parts, with particularly complex enamel crenulation. These features are not found in *N. euryrhinus*. Other comparisons between them are limited by the fragmentary nature of known specimens of the Baode species.

Cerdeño (1995) considered the ossification of the nasal septum to be a synapomorphy. Both *Coelodonta* and *Elasmotherium* have the most derived state with a totally ossified septum, and both *Stephanorhinus* and *Ningxiatherium* have a partially ossified nasal septum. The cladistic analysis of Cerdeño (1995) showed that *Coelodonta* has the closest relationship to *Stephanorhinus*, and a monophyletic clade includes the two genera as a sister group of the *Elasmotherium–Ningxiatherium* group. But, I think that this phylogenetic relationship is unreasonable, and Cerdeño (1995: 5) has also indicated that the character of the totally ossified septum evolved independently in *Coelodonta* and *Elasmotherium*.

Deng (2007) suggested that *Ningxiatherium* and *Parelasmotherium* are sister groups. In order to test the phylogenetic relationship of *N. euryrhinus* among elasmotheres and some basal rhinocerotids, the characters are scored on Antoine (2002: Appendix 2). The character list of Antoine (2002) is not changed, but some species are revised, and three species, *P. linxiaense*, *N. longirhinus*, and *N. euryrhinus* are added to his matrix. The matrix contains 282 characters and 260 parsimony informative characters, and all characters are unordered. PAUP 4.0b (Swofford, 2000) is employed. The current matrix consists of 32 taxa coded at the species level with four outgroups (*Tapirus terrestris*, *Ronzotherium filholi*, *Hyrachyus eximius*, and *Trigonias osborni*) and 28 ingroup taxa (Appendix A). A heuristic search using 1000 random replicates and tree-bisection-reconnection (TBR) is performed. All branches with minimum length of zero are collapsed. The analysis results in
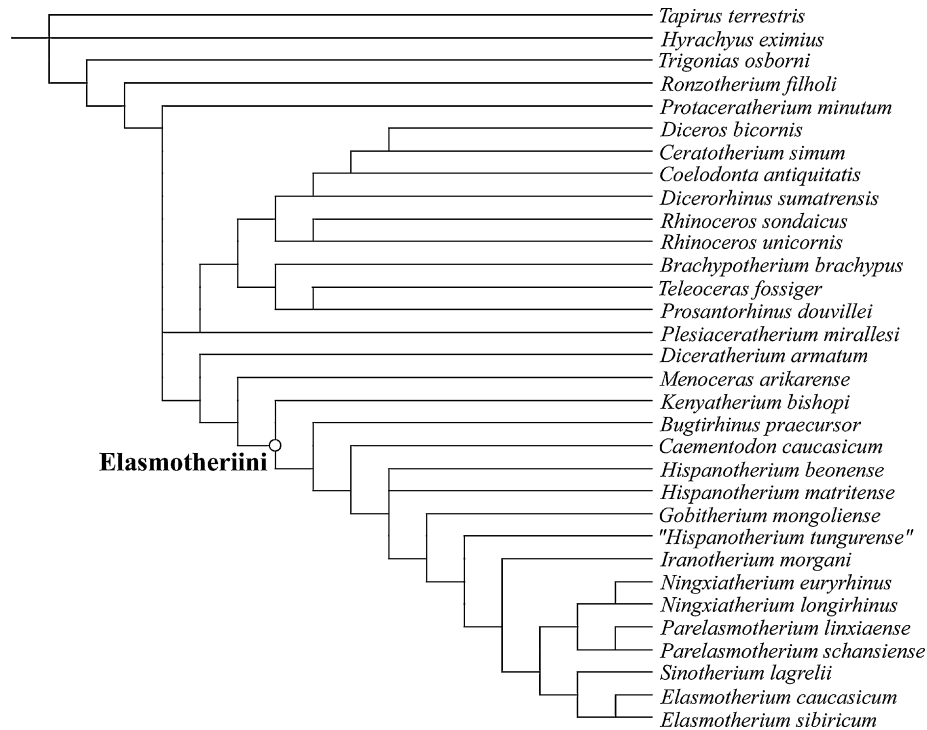
Fig. 7. Cladogram of elasmothere relationship.
Cladogramme des relations des Elasmothères.

1120 best trees, and 21 most parsimonious are retained. The tree length is 1120, and its CI is 0.3402. The current cladistic analysis supports the viewpoint of Antoine (2002). Moreover, the *Ningxiatherium–Parelasmotherium* clade is the sister group of the *Sinotherium–Elasmotherium* clade, and all of them comprise the most derived clade in the elasmotheres excluding *Stephanorhinus* and *Coelodonta* (Fig. 7).

5. Conclusions

The particularly complete skull from Guonigou described here does not completely match that of any known elasmotheres. Although this skull conforms to the generic characters of *Ningxiatherium*, it also differs from the sole known species of this genus, *N. longirhinus*, in other characters, such as larger size, much broader nasals, a well-developed nasal lateral apophysis, a shallower nasal notch above the P3/P4 boundary, a bell-shaped or trapezoidal occipital surface, larger occipital condyles, the presence of DP1 in adults, a more posteriorly oblique protoloph of P4, a stronger molar crista, an open median valley of M2, and a sub-quadrangular occlusal surface of M3. This skull is pressed dorsal-ventrally, but some distorted features due to the dorsal-ventral crushing are excluded. As a result, this skull from Guonigou is described here as a new species, *N. euryrhinus* sp. nov.

The relatively large, single-horned elasmothere, *N. euryrhinus*, lived in the Linxia Basin of northwestern China during the late Miocene, which corresponds to the early Bahean of the Chinese land mammal ages or the early Vallesian (MN 9). This new elasmothere from Guonigou shares some

cranial and dental features with *P. linxiaense* from the same locality in the Linxia Basin. But *P. linxiaense* differs from the new species in the absence of a nasal septum and a labial cingulum, the presence of a middle nasal horn, a deeper nasal notch above P4/M1 boundary, a posteriorly inclined occipital surface, relatively long premolars, and a strong parastyle.

The classification of the tribe Elasmotheriini has changed repeatedly during the last two decades. The prevalent view of the history of elasmotheres involves an evolutionary trend from lacking an ossified nasal septum towards having one, which was totally ossified, with a wide variety of intermediate, partially ossified states. The new skull from Guonigou provides more cranial and dental characters of the genus *Ningxiatherium* to support the *Ningxiatherium-Parelasmotherium* clade as the sister group of the *Sinotherium-Elasmotherium* clade.

Appendix A. Supplementary data

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