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SKULL OF *PAELASMOTHERIUM* (PERISSODACTYLA, RHINOCEROTIDAE) FROM THE UPPER MIOCENE IN THE LINXIA BASIN (GANSU, CHINA)

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ABSTRACT—A relatively complete skull of *Paelasmotherium*, a giant elasmotherine rhinocerotid with a huge nasal horn, is described from an early late Miocene locality of the Linxia Basin in Gansu, China. Comparing the new cranial material of *Paelasmotherium*, we confirm that *Ningxiatherium* belongs to a valid and independent genus. New knowledge concerning the cranial and dental morphology of *Paelasmotherium* allows insight into the phylogenetic position of this genus among elasmotheres. A sister-group relationship between *Paelasmotherium* and *Ningxiatherium* is proposed on the basis of cranial and dental evidence. Shared derived characters that support this relationship include: anterior rims of orbit far behind the level of M3; raised lower rim of orbit; long, wide, fused nasal bones that angle ventrally; a retracted nasal notch at the level of the P4/M1 boundary; broadly separated parietal crests; tooth rows restricted to the anterior half of skull; extremely expanded hypocones of molars; very narrow metalophs; and a lingually elongated protoloph of M3. *Paelasmotherium* was obviously a grazer, as shown by the high crown, strong wear, massive cement, and wrinkled enamel on its teeth. The coexistence of *Paelasmotherium* and *Ningxiatherium* in the Linxia Basin indicates that the ecological differentiation occurred during the early late Miocene. The two genera occupied different ecological niches with distinct diets, grazing grasses for *Paelasmotherium* and browsing leaves for *Ningxiatherium*.

INTRODUCTION

Killgus (1923) established *Paelasmotherium*, a giant elasmotherine rhinoceros of the late Miocene, based on the type species *Paelasmotherium schansiense*, collected from Shanxi, China. Ringström (1924) considered this species synonymous with, or a subspecies of, *Sinothierium lagrelii* collected from Baode, Shanxi. Qiu and Xie (1998) pointed out that *Paelasmotherium* is smaller in size, with upper cheek teeth undifferentiated into crown and prism parts (see Ringström, 1924:133, figs. 82, 83), and almost no enamel crenulation. These characters are markedly different from those of *Sinothierium*. As a result, they suggested restoring the genus *Paelasmotherium*. They also referred *Sinothierium simplum*, established by Chow (1958), to the genus *Paelasmotherium*, and added some specimens from Wangji, Dongxiang (Gansu, China) to *P. simplum*. Deng (2001) described another new species of this genus, *Paelasmotherium linxiaense* based on some new tooth specimens found from the late Miocene deposits at Guonigou in Nalesi Township, Dongxiang County. Unlike *P. schansiense* and *P. simplum*, *P. linxiaense* has weak enamel plications, marked crista, and an expanded hypocone. Additional character differences between *Paelasmotherium* and *Sinothierium* were recognized with the discovery of lower cheek teeth of *P. linxiaense* (Deng, 2001). Although Antoine (2002) considered *Ningxiatherium* to be *Paelasmotherium*, and united *Paelasmotherium schansiense*, *P. simplum*, *P. linxiaense*, and *Ningxiatherium longirhinus* as *P. schansiense*, a recently uncovered skull of *P. linxiaense* from Guonigou affirms the differences in the cranial characters of *Paelasmotherium* and *Ningxiatherium*. These differences support the systematic position of *Paelasmotherium* as a genus independent from *Ningxiatherium*.

Abbreviations—AMNH, American Museum of Natural History, New York; HMV, specimen prefix of the Hezheng Paleozoological Museum, Gansu, China. IVPP V, specimen prefix of

the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China. Terminology and taxonomy follow Heissig (1972, 1999), Guérin (1980), and Antoine (2002). The measurements are according to Guérin (1980) and given in mm.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Owen, 1845
Subfamily RHINOCEROTINAE Gill, 1872
Tribe ELASMOTHERIINI Dollo, 1885
Genus *PAELASMOTHERIUM* Killgus, 1923
PAELASMOTHERIUM LINXIAENSE Deng, 2001
(Fig. 1–3, Tables 1–2)

Holotype—IVPP V 12650. 1–5, right M2, left and right M3, right m1 and left m2, apparently belonging to one individual.

Revised Diagnosis—Large-sized elasmothere. Skull long. M3 located in front of orbit. Nasal horn boss rough and large, frontal horn absent; nasals angle ventrally; nasal notch deep; premaxillary narrow and long, without incisors; lower rim of orbit raised; skull roof concave, with broadly separated parietal crests; nuchal tuberosity strong. Cheek teeth hypsodont; enamel wrinkled; crista well developed; hypocone expanded.

Described Specimen—HMV 1411, a skull with broken zygomatic arches. Because of crushing, this skull is abnormally narrow, and the lowering of the nasal notch in front and vertical position of the occipital surface may be due to distortion.

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).

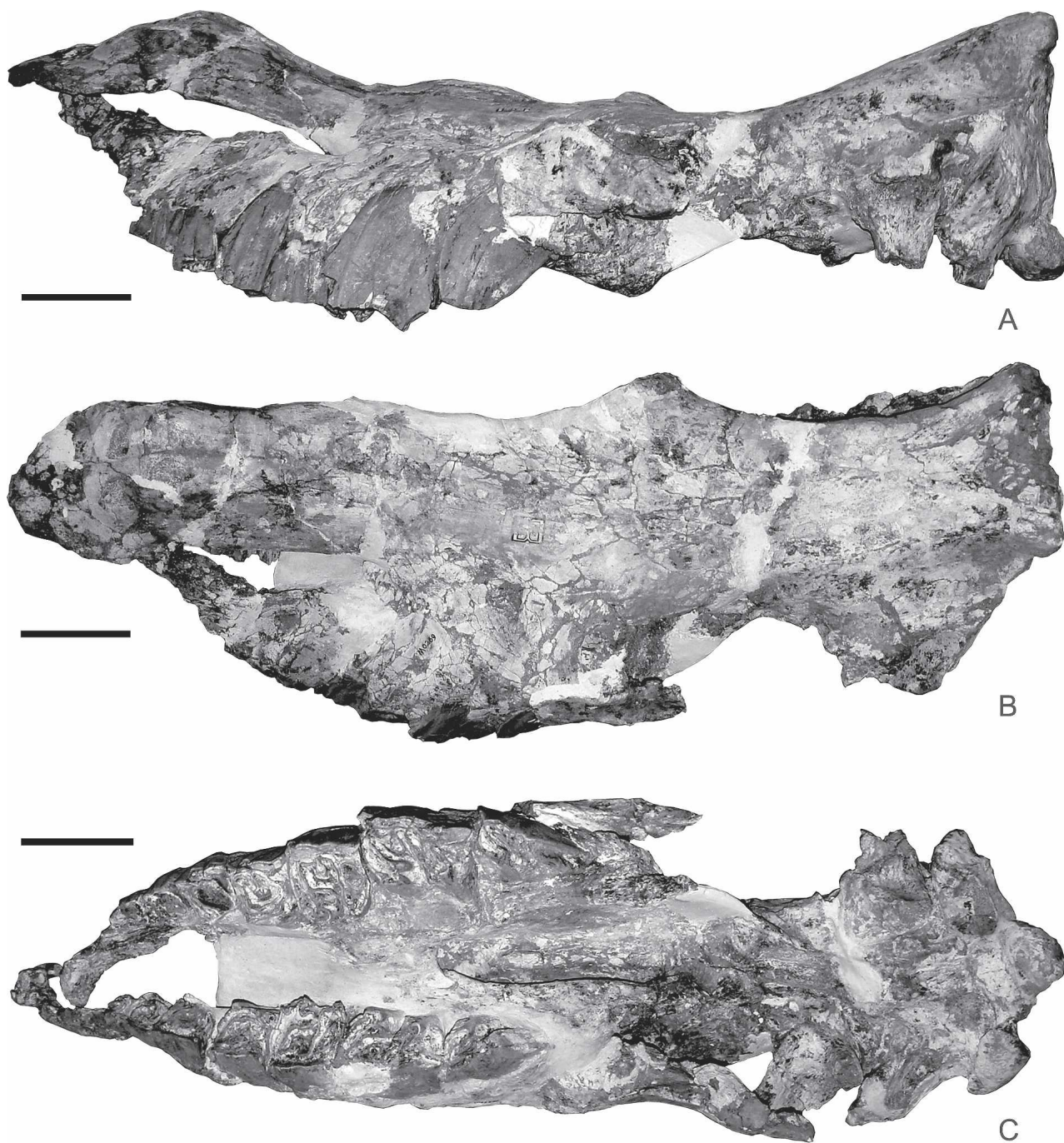


FIGURE 1. Skull of *Parelasmotherium linxiaense* from the upper Miocene at Guonigou, Dongxiang in the Linxia Basin (Gansu, China), HMV 1411. **A**, lateral view; **B**, dorsal view; **C**, occlusal view. Scale bars equal 10 cm.

DESCRIPTION

Skull—The skull is long. The tooth row is strongly shifted anteriorly so that the posterior border of M3 is in front of the anterior rim of orbit. The nasals are fused and very long, their transverse profile is semicircular. The anterior part of nasals is laterally expanded and anteriorly narrowed, with a somewhat rough and truncated tip; the middle and posterior parts are wide, with parallel lateral borders. In lateral view, the nasals are pointedly bent at the uplifted middle point. The ventral surface of nasals is concave, undulate in front with some prominences, but smooth behind. The median horn boss on nasals is a rough and

large dome with a weak central groove and a diameter of about 80 mm, and the other part of the nasal roof is very smooth.

The nasal notch is deeply U-shaped, without a septum, and its posterior border is at the level of the P4/M1 boundary. The premaxillary is relatively thin, narrow and long, with a length of 88 mm in front of the tooth row and a prominence on the junction to the maxillary. Premaxillary tips are sharp and curved medially, but there is a wide space between them. The maxillary surface is broad, with vertical prominences corresponding to tooth roots on its lower part and a large depression in front of the orbit, and the lower border of the maxillary zygomatic process is 43 mm from the alveolar margin. The nasal and the lacrimal

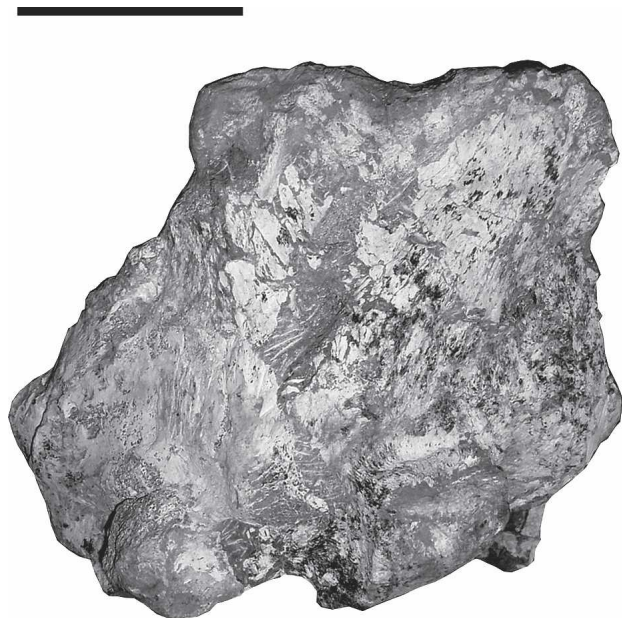


FIGURE 2. Occipital surface of *Paelasmotherium linxiaense* from the upper Miocene at Guonigou, Dongxiang in the Linxia Basin (Gansu, China), HMV 1411. Scale bar equals 10 cm.

bones are completely fused with each other. The orbit is close to the skull roof, and its lower rim is raised. The supraorbital tuberosity is weak, the lacrimal tubercle is absent, and the postorbital process is well developed. The anterior end of the zygomatic arch is narrow and slightly uplifted, at the level of the posterior margin of M3. The facial crest is well developed, with an angle of 100° and a vertical ascending branch.

The skull roof is broadly concave, with a high occipital elevation, and the maximum width between supraorbital tuberosities. The frontal bone is flat, without any horn boss. The braincase is wide and low. The parietal crests are relatively weak and broadly separated, with a smooth surface and the minimal width of 113.6 mm between them. The occipital surface is trapeziform, with a very large nuchal tuberosity and without exterior and median crests; the lateral crests are strong and rounded, and the triangular part between them is relatively elevated. The mastoid process is inclined anteriorly, laterally and inferiorly. The occipital crest is straight in dorsal view and slightly concave in occipital view. The lateral margin of the occipital crest is divergent inferiorly and declines anteriorly, with an angle of 40° to the central crest. The foramen magnum is narrow, long, and dumbbell-shaped, and its upper border is obviously lower than that of the occipital condyle. The nuchal ligament depression is shallow and inversely triangular, with an inversely triangular prominence at the center.

The occipital condyles are strong and wide, with a marked central crest, and the notch between them is broad, with a width of 34 mm. The pterygoid bones have a posteriorly sloping posterior margin, and the valley between them is wide and deep. The vomer is narrow, long, rounded, and far from the palate surface. The anterior border of the temporal fossa is at the level behind M3, with a distance of 43 mm between them. The postglenoid process is robust and curved anteriorly, with a rhombic cross section short at the front and long at the back.

The basal tuberosity is well developed and divergent laterally, and its sagittal crest is very high. The posterior part of the basal-occipital bone is markedly lower than the occipital condyles and the notch between them. The posttympanic and paroccipital processes are fused at their bases, and the former has a distance of

7.5 mm from the postglenoid process. The temporal crest is projected laterally and slopes anteriorly. The posttympanic process is declined anteriorly, expanded laterally, and thick, with a width of 34.5 mm. The paroccipital process is strong, with a narrow and triangular cross section, straight medially and sharp laterally.

The posterior border of the palate is widely U-shaped at the level of the midline of M2. The posterior nares are relatively wide. The maxillary tuberosity is absent. On the ventral view, the zygomatic arch is thick, with a lateral edge and a width of 45.4 mm at the middle. Its anterior end is slightly projected. There is a narrow and deep groove between the zygomatic arch and the maxillary.

Upper Teeth—Upper incisors are absent. Cheek teeth are very hypsodont, and M2 is 100 mm high in HMV 1411, indicating that *Paelasmotherium linxiaense* may have evolved ever-growing, rootless cheek teeth (Heissig, 1989:411). The upper premolar row is 158.4 mm long. The molar row is 184 mm long at the occlusal surface and 233.4 mm at the base. Both upper cheek tooth rows are convergent anteriorly. Cheek tooth enamel is wrinkled, with especially rich plications on premolars; cement fills in fossettes, but it does not cover labial walls. Upper cheek teeth are not differentiated into crown and prism parts.

Among upper premolars, P2–4 have no lingual or labial cingula except the weak labial cingulum of P3. The bridge (see Heissig, 1972:fig. 2) of P2–4 is well developed, without lingual valley; labial wall is generally flat, with a marked metacone rib; lingual margin is flat and slightly declined posteriorly; protocone is rounded; parastyle is expanded and short, with a pointed end; and metacone rib is wide and low.

In the adult specimen, DP1 is well developed and double-rooted, with antero-lingual cingulum that is well developed lingually and posteriorly, and fused with the anteriorly extended part of hypocone so that it looks like a bridge. The hypocone of DP1 is connected with metacone, with a narrow metaloph.

P2 has a large medifossette. Its metaloph is oblique posteriorly; paracone rib is marked; crista is large, with a truncated end; cristella is weak, while postcrista is strong; and protocone is not constricted.

P3 has no medifossette. Its protocone is not constricted, and has a weak anterior valley; metaloph is slightly oblique posteriorly; antecrochet is absent; crista is strong and bifurcated; and postcrista is narrow and long. A narrow and long enamel lake is situated in the connection of the protoloph and ectoloph. The posterior valley is closed to form a transversely narrow and long posterior fossette.

P4 has a well-developed medifossette with rich plications on the lingual and labial walls, two small plications lingually and three large plications labially. Its protocone is small and projected, with deep anterior and posterior grooves; hypocone has an obvious posterior valley; and metaloph is slightly curved posteriorly. On the right P4, the crista and postcrista are well developed and connected with the antecrochet to form two medifossettes, and a narrow and long plication on the posterior wall of the metaloph is near the bridge. On the left P4, the medifossette is large, with rich plications on the fused crista and crochet, three labially and two lingually, and a small plication on the posterior wall of the metaloph is near the bridge.

On upper molars, anterior and labial cingula are absent; labial wall of ectoloph is markedly undulate; parastyle is wide, short on M1, but strongly projected on M2–3. Protocones of M1–2 are strongly constricted, with a deep anterior groove, and a flat lingual margin. The metalophs of M2–3 have a narrow neck to connect the ectoloph. The hypocones of M1–2 are strongly expanded, with a marked anterior groove on M1.

M1 has a very strong, wide and long antecrochet whose end is slightly curved lingually and has a small plication near the hypocone. Its protocone has a wide pointed U-shaped anterior valley; crochet is very weak or absent; crista is strong; posterior

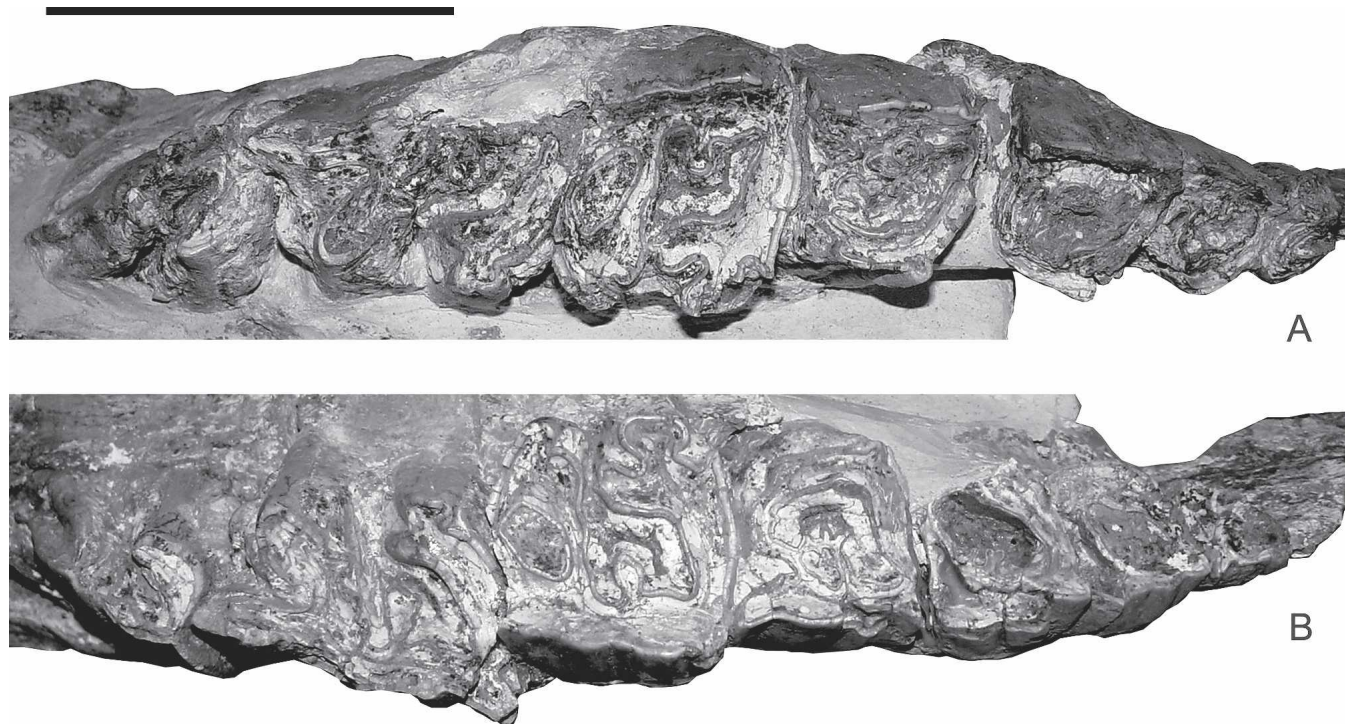


FIGURE 3. Teeth of *Parelasmotherium linxiaense* from the upper Miocene at Guonigou, Dongxiang in the Linxia Basin (Gansu, China), HMV 1411, occlusal view. **A**, right upper tooth row; **B**, left upper tooth row. Scale bar equals 10 cm.

fossette is large and rounded; paracone rib is weak; metastyle is moderate long; and metaloph is narrow and long.

M2 is markedly fan-shaped in labial view. Its protocone has a marked basal lingual groove; antecrochet is well developed, with

a somewhat pointed end that is slightly curved lingually; crochet is marked and extended anteriorly; crista is very strong, with an expanded end; paracone rib is weak; cristella is wide, low, and rounded; metastyle is very long; metaloph is wide and long, with

TABLE 1. Measurements and comparisons (mm) of skull of *Parelasmotherium linxiaense* (HMV 1411) from the upper Miocene at Guonigou, Dongxiang in the Linxia Basin (Gansu, China).

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

*This skull is pressed laterally, so some measurements for its widths are not accurate.

TABLE 2. Measurements and comparisons (length × width × height, mm) of upper teeth of *Parelasmotherium linxiaense* (HMV 1411) from the upper Miocene at Guonigou, Dongxiang in the Linxia Basin (Gansu, China).

Upper teeth	<i>P. linxiaense</i>		<i>P. simplum</i> Qiu and Xie, 1998	<i>I. morgani</i> HMV 1098	<i>S. lagrelii</i> Ringström, 1924	<i>N. longirhinus</i> V 5163
	HMV 1411	V 12650				
DP1	26.2 × 30.5 × 34.6			29 × 28 × 28		
P2	36.6 × 43 × 40.2			23 × 37.5 × 30	42 × ~46 × 47	
P3	45.1 × 53.8 × 54			32 × 54 × 29	52 × 58 × ~80	
P4	48.8 × 65 × 95			41 × 65.5 × 32	50 × 77 × 83	43.3 × 67 × –
M1	62.7 × 72 × 57		69 × 67 × 65	43.5 × 76 × 28.5	92 × 75 × 106	43 × 70 × –
M2	89.3 × 70.4 × 100	100 × 80 × 132	80 × 74.8 × 118	63.5 × 84 × 30	~70 × 71 × 185	62 × 81.4 × –
M3	88.8 × 61 × 96.5	90 × 77.5 × 109	74 × 50 × 128	79 × 66 × 43	106 × 60 × 90	78.2 × 68.3 × –

an obviously wrinkled anterior wall; and posterior cingulum is reduced.

M3 has a triangular occlusal surface. Its protocone is not constricted, and has a smooth lingual margin; antecrochet and crista are absent; crochet is narrow, long, and extended lingually; protoloph is strongly oblique posteriorly, with a very narrow connection with ectometaloph that has a wide and deep posterior groove; posterior cingulum is an isolated basal pillar, and the lingual cingulum is absent; parastyle is narrow, sharp, and projecting forward, with a wide and shallow paracone fold.

On the basis of three isolated teeth, which possibly belong to the same individual, Qiu and Xie (1998:20) suggested that M2 may have been higher than M1 in the same individual of *Parelasmotherium*. This was considered a common feature in high-crowned rhinocerotids, indicating that M2 erupts much later than M1. In the complete tooth row of the HMV 1411 skull, the measured height of M1 is 57 mm and the height of M2 is 100 mm, thus affirming the viewpoint of Qiu and Xie (1998).

COMPARISON WITH THE HOLOTYPE

The dental characters described for this skull (HMV 1411) are easily recognizable as typical of Elasmotheriini, and the teeth are highly similar to those of the holotype of *Parelasmotherium linxiaense*. There were altogether six teeth of *P. linxiaense* described by Deng (2001), including five teeth of the holotype: one M2, two M3, one m1, and one m2, as well as another unworn m3. M2 and M3 of the holotype can be compared with the corresponding teeth of the HMV 1411 skull. Both molars of the holotype and HMV 1411 are not differentiated into crown and prism parts. They have no anterior, labial and lingual cingula, but have a reduced posterior cingulum lower than the moderately worn surface. Their parastyles are strongly extended.

Both M2 teeth are narrow in occlusal view, with a longer labial length than lingual one, and an increased width toward to the base. Their protocones are strongly constricted, with deeply V-shaped anterior and posterior grooves, and a flat lingual margin with a marked basal lingual groove. They have a wide, short antecrochet with a somewhat pointed end, a weak paracone fold, a well-developed crista, a relatively long metastyle, a low and rounded cristella, a wide and open median valley, and a narrow and deep posterior valley. The protoloph and metaloph are strongly oblique posteriorly. Metalophs connect with the ectoloph by a narrow neck so that the hypocone looks very large. Hypocones are not constricted, with a round lingual margin.

Both M3 teeth have a triangular occlusal surface, a wide and shallow paracone fold, a narrow and long crochet, a wide and deep middle valley, a wide and deep posterior groove on the ectometaloph, and well-developed anterior and posterior cingula. Their protolophs are strongly oblique posteriorly, with a very narrow connection with ectoloph and without antecrochet.

There are some differences between the molars of HMV 1411 and the holotype, but they are mainly due to different degrees of wear. For example, M2 of HMV 1411 has a more or less undu-

lating labial wall, but the holotype is flat. M2 of HMV 1411 has a crochet extended anteriorly, but the holotype has no an obvious crochet. The holotype has a postcrista, but M2 of HMV 1411 has no an obvious postcrista. The metaloph on M2 of HMV 1411 has a wrinkled anterior wall, but the holotype has a smooth one. The protocone on M3 of HMV 1411 is not constricted, but that of the holotype has weak anterior and posterior grooves.

As the skull of HMV 1411 and the holotype of *Parelasmotherium linxiaense* were collected from the same locality and have highly similar size and morphology, we believe they represent the same species.

COMPARISON WITH THE SKULLS OF OTHER ELASMOTHERES

In the tribe Elasmotheriini, *Elasmotherium* has a huge frontal horn and strongly wrinkled tooth enamel. In contrast, the Linxia skull has no trace of a horn boss on its frontals, and its teeth have slightly wrinkled enamel. Skull HMV 1411 has a similar nasal horn to *Ningxiatherium*, *Iranotherium*, and *Hispanotherium*, all of which were placed in the group *Iranotheriina* (formerly *Iranotheriinae*) by Kretzoi (1943). *Gobitherium* entirely lacks horns (Osborn, 1924:3). Though Antoine (2002:98) considered that it has a small nasal horn and belongs to the elasmotheres.

The skull of *Parelasmotherium linxiaense* resembles that of *Ningxiatherium longirhinus* from Zhongning, Ningxia (Chen, 1977), in the following characters: large size, dolichocephalic and narrow skull shape, presence of a large nasal rugosity, great free nasal length, anteriorly wide and pointedly bent nasal bones, anteriorly placed horn, long distance between the nasal notch and the orbit, orbit strongly retracted behind the M3 level, and laterally raised orbital rim. They differ in the presence of a partially ossified nasal septum in *Ningxiatherium*, which is absent in the Linxia skull. The nasal notch is above M1 in the Linxia skull, deeper than in *Ningxiatherium* (above P4). The occipital crest is straight in *Parelasmotherium*, and concave in *Ningxiatherium*. There are many differences between the dental features of the two genera. *Ningxiatherium* is moderately hypsodont, but *Parelasmotherium* is extremely hypsodont. DP1, which is present in adult *Parelasmotherium*, is absent in *Ningxiatherium*. The protocone of M3 is not constricted in *Parelasmotherium*, but strongly constricted in *Ningxiatherium*.

Iranotherium morgani has complete skulls found from Margha, Iran (Mecquenem, 1908) and Linxia, China (Deng, 2005a). The skull and teeth of *P. linxiaense* have some common characters with those of *I. morgani*, including the large size, dolichocephalic skull shape, broadly separated parietal crests, highly crowned teeth, weakly undulated ectoloph, slightly wrinkled enamel, strongly constricted protocone, and closed median valley of premolars. Despite the above similarities, *Iranotherium* and *Parelasmotherium* have many differing characters. Nasals have a deep central groove and lateral projections, with a shallow nasal notch above P2/P3 in *Iranotherium*. *Parelasmotherium* has a deep nasal notch above P4/M1, but no central groove or lateral

projection on its nasals. In *Iranotherium*, the anterior orbital rim is retracted above M3 and laterally raised, with a weak postorbital process on the frontal and a flat maxillary face before the orbit. In *Parelasmotherium*, the anterior orbital rim is more retracted behind M3 but not raised, and the lower orbital rim is raised laterally, with a strong postorbital process on the frontal and a concave face before the orbit. In *Iranotherium*, the nuchal tuberosity is weak, the nuchal ligament depression is deep, and the occipital crest is concave, where as in *Parelasmotherium*, the nuchal tuberosity is strong, the nuchal ligament depression is shallow, and the occipital crest is flat. The vomer is thick, and the basal rugosity is weak in *Iranotherium*, while the vomer is thin and the basal rugosity is strong in *Parelasmotherium*. On their cheek teeth, the two forms differ in the labially superposed DP1 above P2 in *Iranotherium*, which is normally arranged in *Parelasmotherium*, and the weak crista in *Iranotherium*, which is well developed in *Parelasmotherium*.

Among the material of *Hispanotherium*, the skull (AMNH 26531) of *H. tungurensis* from Tunggur in Inner Mongolia, China is relatively complete (Cerdeño, 1996), and it is much smaller than the Linxia skull. *P. linxiaense* has some characters similar to *H. tungurensis*, such as the broadly separated parietal crests, median nasal horn, rather convex horn boss, high crowned cheek teeth with massive cement filling, strongly constricted protocone, lingually fused protocone and metaloph of premolars and M1, and well-developed crochet and crista. The skulls differ in the rather folded ectoloph with a strong parastyle and well-developed paracone and metacone folds in *Hispanotherium*, which is relatively flat in *Parelasmotherium*, and the posteriorly directed occipital surface with an occipital crest exceeding condyle level in *Hispanotherium*, which is relatively steep in *Parelasmotherium*. The nasal notch is above P3 in *Hispanotherium*, much shallower than in *Parelasmotherium*. The anterior border of the orbit is behind M3 in *Parelasmotherium*, much more retracted than in *Hispanotherium* (above M2).

Both *Elasmotherium* and *Sinootherium* are large. Their teeth are differentiated into crown and prism parts, and have particularly complex enamel crenulation. In contrast, *Parelasmotherium* is smaller in size without differentiation into crown and prism parts in upper cheek teeth, and almost no fine enamel crenulation (Killgus, 1923; Qiu and Xie, 1998; Deng, 2001). *Sinootherium lagrelii* has a fragmental skull with cheek tooth row, which is mainly composed of partial maxillary and frontal bones (Ringström, 1924). These cranial characters of *Sinootherium* are obviously different from those of *Parelasmotherium*. In *Sinootherium*, the facial crest is very high, with an anterior end above the posterior border of M1; orbit is very laterally raised; anterior orbital border should be placed behind M3; maxillary face is short and high; infraorbital foramen is simple; premaxillary is very retracted; and posterior border of the nasal notch may be above M1.

The material of *Gobitherium mongoliense* includes only the anterior portion of a skull (AMNH 19185) with the right zygoma, complete orbit, frontals, nasals and portions of four cheek teeth, P4-M3 (Osborn, 1924). *G. mongoliense* is much smaller than *Parelasmotherium linxiaense*. For example, the distance between the nasal tip and bottom of the nasal notch is 369 mm in *P. linxiaense*, and 224 mm in *G. mongoliense*; length and width of M2 are 89.3 mm and 70.4 mm respectively in *P. linxiaense*, and 45 mm and 44 mm in *G. mongoliense*. Although both nasal bones of *G. mongoliense* and *P. linxiaense* are long and arched, their skulls are very different in shape. *G. mongoliense* has smooth nasal and frontal bones, which indicate the entire absence of horns, while *P. linxiaense* has a huge nasal horn. The nasals of *G. mongoliense* exhibit a lateral projection, not observed in *P. linxiaense*. The anterior rim of the orbit is above the middle of M1 in *G. mongoliense*, but above the posterior border of M3 in *P. linxiaense*.

PHYLOGENETIC DISCUSSION

Pavlov (1892), who presented a phylogeny for rhinoceroses, considered that *Coelodonta* was the direct ancestor of *Elasmotherium*. Ringström (1924) held elasmotheres to be a separate family, but he also brought out a very strong point against his own view. He indicated that elasmotheres had lost all anterior teeth like advanced members of Rhinocerotidae, such as the African white rhinoceros *Ceratotherium simum* (Ringström, 1924:137, 142). Matthew (1931) placed elasmotheres in the subfamily Rhinocerotinae based on hypsodont cheek teeth, specialized or lost front teeth, and only a frontal horn. Kretzoi (1943) considered Elasmotheriidae a family, and divided it into the subfamilies Elasmotheriinae, with a huge frontal horn, and Iranotheriinae, with a terminal nasal horn. Guerin (1980) considered that all elasmotheres belong to one subfamily. Similarly to Matthew (1931), Heissig (1973, 1989, 1999) and Fortelius and Heissig (1989) suggested that elasmotheres are within the tribe Elasmotheriini under the subfamily Rhinocerotinae. Prothero et al. (1986) and Prothero and Schoch (1989), however, reduced elasmotheres to the subtribe Elasmotheriina under the tribe Rhinocerotini. Cerdeño (1995) divided elasmotheres into two subtribes under the tribe Rhinocerotini: the subtribe Iranotheriina, and the subtribe Elasmotheriina, which includes the traditionally non-elasmothere *Coelodonta* and *Stephanorhinus*. McKenna and Bell (1997) further reduced elasmotheres to the infratribe Elasmotheriini under the subtribe Rhinocerotina. The classification of Antoine (2002) for elasmotheres is very peculiar: the traditional elasmotheres are combined with *Diceratherium* and *Menoceras* to constitute the subfamily Elasmotheriinae; they are combined with *Menoceras* to constitute the tribe Elasmotheriini, the sister group of the tribe Diceratheriini; and they belong to the subtribe Elasmotheriina, the sister group of the subtribe Menocerotina. In the present paper, the taxonomy follows Heissig (1999). All elasmotheres are within the tribe Elasmotheriini under the subfamily Rhinocerotinae.

In all cladistic analyses related to elasmotheres, only that of Antoine (2002) discussed the phylogenetic position of the genus *Parelasmotherium*. Unfortunately, he mistakenly used the cranial characters of *Ningxiatherium* as those of *Parelasmotherium*. As the true skull of *Parelasmotherium* and other materials of elasmotheres (Qiu and Xie, 1998; Deng, 2001, 2003, 2005a) were found from the Miocene deposits in the Linxia Basin (Gansu, China), the phylogenetic relationship of *Parelasmotherium* is discussed herein.

Parelasmotherium and *Ningxiatherium* should be considered sister taxa. Many of the apparent differences between *Parelasmotherium* and *Ningxiatherium* are in dental or cranial characters, and reflect the fundamentally diverging trophic adaptations of these genera: *Parelasmotherium* tends towards a grazing direction in its extremely hypsodont teeth, whereas *Ningxiatherium* is partially hypsodont, a browsing adaptation. The highly specialized cranial and dental modifications, particularly those in *Parelasmotherium*, leave a thick morphological overprint that obscures phylogenetic relationship. The following is a list of derived characters shared by *Parelasmotherium* and *Ningxiatherium*. Polarity is determined through comparisons with the following outgroups from the basal members of major clades of perissodactyls or rhinocerotids: basal rhinocerotiform *Hyrachyus*, hyracondontine *Hyracodon*, rhinocerotid *Trigonias*, and acerathere *Chilotherium*.

1. Anterior border of orbit: The anterior border of the orbit in *Parelasmotherium* and *Ningxiatherium* is far behind the level of M3, as opposed to a more anteriorly located border in most rhinocerotids, also including other elasmotheres.
2. Orbit: The orbits with raised rims are nearly identical in *Parelasmotherium* and *Ningxiatherium*. While the orbits essentially retain the primitive condition for most rhinocerotids,

the orbit with raised rims is certainly a derived character (Antoine, 2002:101). The fact that *Ceratotherium* and *Diceros* still have raised orbital rims suggests that those in *Parelasmotherium* and *Ningxiatherium* may be a synapomorphy acquired independently of the extant white and black rhinoceroses.

3. Nasal bones: The nasal bones in most rhinocerotids are usually short, anteriorly narrow, separated, and straight or roundly curved. The long, anteriorly wide, fused, and pointedly bent nasal bones in *Parelasmotherium* and *Ningxiatherium*, especially on the anterior part, are prominent and apparently unique to these two genera among elasmotheres. Although the skull of HMV 1411 is somewhat deformed due to lateral compression, the bending of the nasals is a natural condition.
4. Nasal notch: The posterior border of the nasal notch in *Parelasmotherium* is at the level of the P4/M1 boundary. The posteriorly located border appears homologous to the deep nasal notch in *Ningxiatherium*. Although a deep nasal notch may exist in some rhinocerotids that is at the level above P4-M1, the deep nasal notch in *Parelasmotherium* and *Ningxiatherium* has a very narrow anterior part and is unique to *Parelasmotherium* and *Ningxiatherium*.
5. Parietal crests: Primitively, parietal crests are fused to form a sagittal crest or little separated. In *Ningxiatherium*, the parietal crests are broadly separated. The wide surface between the parietal crests is developed to the extreme in *Parelasmotherium*, and its minimal width reaches 113.6 mm.
6. Tooth row: Both *Parelasmotherium* and *Ningxiatherium* have the derived condition of tooth rows restricted to the anterior half of skull. This differs from elasmotheres such as *Hispanotherium*, which have the primitive condition of tooth rows with the posterior edge located in the posterior half of skull. The extinct *Coelodonta* and the extant *Diceros* still have a derived condition of tooth rows restricted to the anterior half of skull, which suggest that the derived condition may have evolved more than once.
7. Hypocone: The hypocone is small or moderate on the upper molars in most elasmotheres. In *Parelasmotherium* and *Ningxiatherium*, the hypocones of molars are extremely expanded, with a very large end of ectometaloph of M3.
8. Metaloph: Primitively, the metaloph is wide on the upper cheek teeth in rhinocerotids. Within elasmotheres, the metaloph becomes narrow, especially compared with the enlarged hypocone. The metaloph is extremely narrow in *Parelasmotherium* and *Ningxiatherium*, while the hypocone is strongly enlarged in the two genera. *Elasmotherium* also has a very narrow metaloph, but its hypocone is not enlarged.
9. Protoloph of M3: The protoloph of M3 in most rhinocerotids, including many elasmotheres, is transverse. But the protoloph of M3 in *Parelasmotherium* and *Ningxiatherium* is lingually elongated. Such a character is also seen in two other large elasmotheres, *Sinootherium* and *Elasmotherium*.

In the previous list, four cranial and dental characters are unique to *Parelasmotherium* and *Ningxiatherium* (1, 3, 4, 8), two dental characters are shared with other elasmotheres (7, 9), and three cranial characters have more extensive distributions within the rhinocerotids (2, 5, 6). These characters are likely to be morphotypical conditions for a *Parelasmotherium-Ningxiatherium* clade.

On the other hand, the partially ossified nasal septum in *Ningxiatherium* is obviously autapomorphic, and the more primitive dental characters in *Parelasmotherium*, such as the presence of DP1 in the adult and the unconstricted protocone of M3, are closer to the primitive condition in the *Parelasmotherium-Ningxiatherium* clade. In addition, the *Parelasmotherium-Ningxiatherium* clade has

a sister relationship to the *Sinootherium-Elasmotherium* clade (Antoine, 2003).

BIOSTRATIGRAPHY AND PALEOECOLOGY

Fossils of *Parelasmotherium* are rare in general, and all of them are found in China, in only two areas, Kutschwan, near the Yellow River in Shanxi Province (Killgus, 1923), and Dongxiang, within the Linxia Basin in Gansu Province (Qiu and Xie, 1998; Deng, 2001). Because *Parelasmotherium schansiense*, described by Killgus (1923), was collected as “dragon bones” from a traditional Chinese drugstore, its exact collection locality and age were impossible to determine.

The Guonigou fauna in the Linxia Basin comes from the lower part of the Liushu Formation, and its fossils include *Dinocrocota gigantea*, *Machairodus* sp., *Tetralophodon* sp., *Hipparion dongxiangense*, *Parelasmotherium simplum*, *P. linxiaense*, *Ningxiatherium* sp., and *Shaanxispira* sp. (Deng, 2001; Deng et al., 2004a, b). According to paleomagnetic measurements, the Guonigou fauna is within Chron C5r.1r, with an age of 11.1 Ma, corresponding to MN 9 (Deng, 2005b).

The Guonigou fauna is characteristic of early late Miocene age. *Dinocrocota gigantea* is a representative of the early *Hipparion* fauna in Asia, chiefly found in the early late Miocene deposits corresponding to the European Vallesian Age or MN 9–10 (Howell and Petter, 1985). The materials of *Dinocrocota* found in China show the same trend. The fossils of *Dinocrocota* were found in strata corresponding to the Vallesian (Li et al., 1984; Qiu and Qiu, 1995; Qiu et al., 1999; Deng, 2006) from Bahe in Lantian, Shaanxi (Liu et al., 1978; Zhang et al., 2002) and Bulong in Biru, Tibet (Zheng, 1980). *Dinocrocota* was also reported from Songshan in Tianzhu, Gansu (Zheng, 1982), and Laogaochuan in Fugu, Shaanxi (Xue et al., 1995; Zhang and Xue, 1996). Both localities were considered to be equivalent to the European Turolian Age; however, the specimens of the former came from a traditional Chinese drugstore, and the age of the latter needs further study. The size of *Hipparion dongxiangense* is smaller than that of *H. parvum*, the smallest known species of *Hipparion* in China, and its characteristic structures of the hypocone and the hypocone groove frequently occur among the middle Miocene hipparionines from North America, but are infrequent among the late hipparionines. As a result, *H. dongxiangense* indicates an earlier age (Qiu and Xie, 1998). *Parelasmotherium*, the earliest member of the giant elasmotheres developing hypsodont teeth, is more primitive than *Sinootherium*, the representative taxon in the Baode fauna (Qiu and Xie, 1998; Deng, 2001). *Shaanxispira* also appears in the Bahe fauna (Liu et al., 1978; Zhang et al., 2002). Based on mammal correlations, consequently, the age of the Guonigou fauna should be early late Miocene, corresponding to the Vallesian Age of the Europe, which is consistent with the paleomagnetic dating (Deng, 2005b).

At the Guonigou locality in the Linxia Basin, *Parelasmotherium* and *Ningxiatherium* were excavated from the same locality. The cheek teeth of *Parelasmotherium* are very highly crowned, but those of *Ningxiatherium* are obviously lower. The high crown and strong wear of the cheek teeth of *Parelasmotherium* imply that this elasmotherine rhino grazes on tough grasses. The massive cement filling, well-developed secondary folds, and wrinkled enamel provide a means for the cheek teeth of *Parelasmotherium* to resist the abrasion of high-fiber diets. Thus we conclude that *Parelasmotherium* was a grazer because it had a dental morphology unique to certain rhinoceroses and horses, such as *Elasmotherium* and *Hipparion*, which have the grazing adaptations of high-crowned and strongly plicate teeth.

The dominant mammalian taxon accompanying *Parelasmotherium* at Guonigou is *Hipparion dongxiangense*, the earliest species of *Hipparion* in China. *Hipparion* migrated into Asia from North America through the Bering land bridge at the be-

gining of the late Miocene, then rapidly dispersed to Europe and northern Africa. This adaptive radiation was an important event in Eurasia (Woodburne and Swisher, 1995; Bernor et al., 1996), which would in itself have initiated the diversification of other ungulate groups, perhaps through direct impact on the vegetation and feeding successions (Janis, 1982). As a result, the dental morphology of *Parelasmotherium* became specialized for grazing on tough grasses in arid habitats. The coexistence of *Parelasmotherium* and *Ningxiatherium* indicates that the ecological differentiation occurred in the Linxia Basin during the early late Miocene. The two genera occupied different ecological niches with distinct diets, grazing tough grasses for *Parelasmotherium* and browsing tender leaves and soft twigs for *Ningxiatherium*.

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